

**Conservation and Ecological Restoration of Rocky Mountain
Subalpine Meadows: Understanding Vegetation Responses to
Tree Encroachment**

by

Adrienne Kara Shaw

BSc, Simon Fraser University, 2001

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science

in the School of Environmental Studies

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University of Victoria

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Abstract

Over the past century tree encroachment has occurred in North American sub-alpine meadows. Causes of tree establishment have been related to climate influences and exclusion of fire, but very few studies have looked at the consequence of tree encroachment on meadow vegetation. Within the southern Canadian Rocky Mountains, Waterton Lakes National Park and Castle Special Management Area, 14 meadows were randomly selected at wet and dry sites. Nonmetric multidimensional scaling showed that species composition changed during the transition of open meadow to forest for both wet and dry habitats. There were no significant differences in these two management areas in terms of conifer encroachment and the effects on meadow species. Results of this study show that conifer encroachment has increased over the last century with the consequences of loss in meadow species through a decrease in abundance, richness and diversity. Wet sites were significantly more sensitive to conifer encroachment than dry sites. The greatest

inhibitory effects of trees on meadow vegetation within the ecotone occurred when trees were 54-72 years old for wet sites and 77-112 years old for dry sites. Ecological restoration of these meadows is important for ongoing habitat conservation, maintaining species and landscape diversity and ecosystem resilience.

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Chapter 1

Introduction

1.1 Introduction

Over the past century, climatic warming and fire exclusion throughout Western North America have been factors in the advancement of forest cover in to open meadow habitats and in the decline of meadow vegetation (Luckman 1998, Barrett and Arno 1999, Keane et al. 2002, Rhemtulla et al. 2002, Lepofsky et al. 2003). It is well documented that subalpine meadows have decreased in size due to tree seedling establishment (Magee and Antos 1992, Lepofsky et al. 2003, Haugo and Halpern 2007)(Figure 11). The effect of subalpine meadow habitat loss on plant and wildlife species is an ongoing concern. Wildlife presence, activities and movements throughout the landscape, particularly those of bighorn sheep (Wakelyn 1987), grizzly bears (Hamer et al. 1991) and migratory birds (Wilson and Martin 2005), are adversely affected by a reduction in both size and quality of habitat. Subalpine meadows are crucial not only for wildlife species, but also for sustaining plant and landscape diversity. As the impacts of fire exclusion and climatic warming exist we continue to affect the ecological integrity of the landscape (Odion and Hanson 2006, Odion and Sarr 2007). Ecological restoration of subalpine meadow habitat can help set the ecosystem back on a historical trajectory or one more consistent with ecological integrity and resilience. Despite the ensuing habitat

loss and its powerful consequences, comprehensive long-term historical information detailing these changes in the Southern Alberta Rocky Mountains remains sparse. This present research provides a distinctive opportunity to document and correlate environmental variables and land management histories with subalpine meadow vegetation changes.

The objectives of this work are to describe regional historical patterns of conifer encroachment, to examine the effects of conifer encroachment on subalpine meadow species and to explore the implications for ecological restoration and management in Waterton Lakes National Park and the Castle Special Management Area. To meet these objectives, I ask three sets of questions:

1. What are the regional historical patterns of conifer encroachment?
 - (a) Are trees establishing synchronously in the transition from open meadow to forest at each site?
 - (b) Are trees establishing synchronously among wet and dry habitats?
2. What are the effects of conifer encroachment on meadow and forest under-story species for wet and dry habitats and between management area?
 - (a) How does species composition change during the transition from open meadow to forest?
 - i. Which attributes of forest structure and the physical environment show the strongest relationships with species composition?
 - (b) Does abundance of species change during the transition from open meadow to forest?
 - (c) Does species richness and diversity change during the transition from open meadow to forest?
3. What are the implications for ecological restoration and management?

(a) What role could fire play in ecological restoration?

1.2 Study area

Waterton Lakes National Park (WLNP) and the Castle Special Management area (CSMA) are located in the Southern Alberta Rocky Mountains, bordered by the United States to the south, British Columbia to the West, and the Prairies to the East (Figure 1.3 and 1.2). The health of the regional ecosystem is a major concern. Alberta's Natural Resources Conservation Board, during a 1993 review of a proposed resort 23 km north of Waterton in the CSMA, determined that the cumulative effects of development and disturbance have led to a deterioration in the state of the regional ecosystem, both in quantitative and qualitative terms (Parks Canada 2000). They also reached the conclusion that the Crown of the Continent ecosystem is at risk and that the Waterton-Castle area in particular, has deteriorated.

The ecological diversity of the southern Canadian Rocky Mountains results, in part, from the transition from a moist maritime climate to a semiarid continental grassland over a short distance in an area of great topographical diversity. As a result of this transition, habitats in the park and surrounding area support more than 970 species of vascular plants, thousands of kinds of insects, arthropods and other invertebrates, and 300 vertebrate species (Parks Canada 2000). Many plants and animals in Waterton Lakes National Park of Canada are at the edge, or even beyond the edge, of their normal range because they have managed to persist in one or more unique local habitats (Parks Canada 2000). According to the WLNP Park Management Plan (2000) the best way to protect ecological integrity is by maintaining natural biodiversity, which requires special attention to ensure its continuing viability. Subalpine meadows represent biological diversity on the landscape, community, species and genetic levels. This biodiversity is linked to

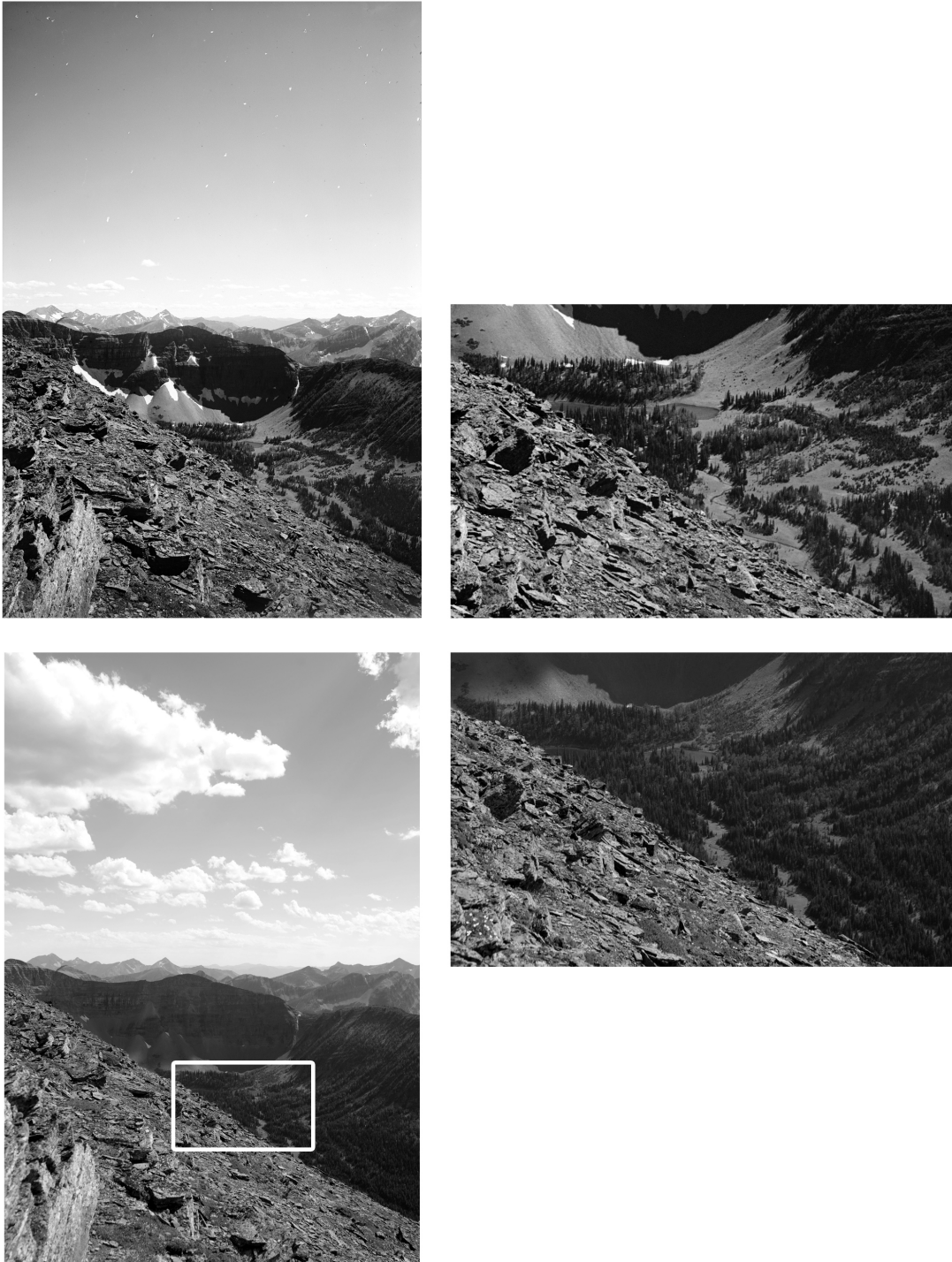


Figure 1.1: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2005. The meadow study site is Ruby, located in the Castle Special Management Area (CSMA), Alberta, Canada. The upper left photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The lower left photograph was taken in 2005 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The photographs on the right show the specific meadow study site in 1914 (upper) and 2005 (lower). The meadow study site is indicated by the white box in the landscape photograph.

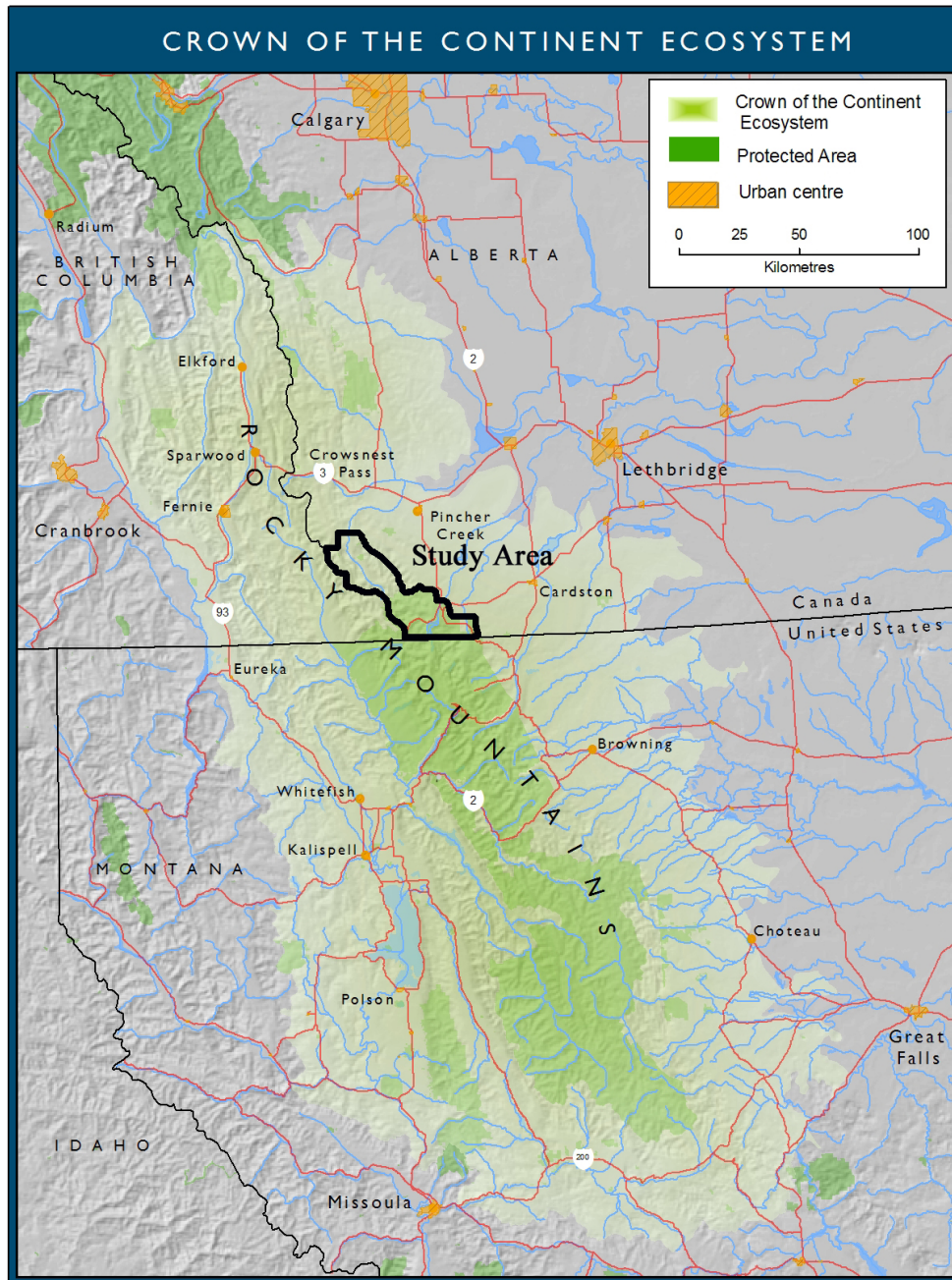


Figure 1.2: Rocky Mountains including the crown of the continent ecosystem, protected areas, and the study area in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA), Alberta, Canada.

ecological processes, such as fire, flood, avalanches, predation, pollination, seed dispersal, grazing and climate change. These natural processes and the physical environment that produces and supports the diversity of life are also a management priority.

The climate of the southern Alberta Rocky Mountains is highly variable. The region is characterized by short, cool, moist summers and long, cold winters with abundant snowfall (Poliquin 1973). The Castle region is one of the wettest in Alberta, with the deepest provincial snowpacks occurring in the upper Southcastle and Westcastle valleys (Perraton 1994). In Alberta, the greatest winter snowpack occurs in the subalpine region; snowpack progressively decreases with decreasing elevations. In winter, unstable weather patterns west of the continental divide and the windy Chinook phenomenon to the east make this area highly varied. West and southwest winds can reach 125-160 km/h in the fall and winter (Poliquin 1973, Achuff 1992). At high elevation sites, temperatures differ with aspect, elevation and slope. Temperatures are often cooler at high elevation sites, averaging 8 °C cooler for every elevation gain of 1000m (Lesica 2002). The closest climate station is Beaver Mines (1257m), 19km east of the study region, where average minimum and maximum temperatures are -11.5 and -1.6 °C in January and 8.3 and 22.6 °C in July. Annual precipitation averages 196.4mm, with 30% falling from June to August; annual snowfall averages 270cm.

The geology of the area is influenced by numerous base materials that were deposited in several sedimentary sequences. Red and green argillites, mudstones and limestones originated in a shallow inland sea between 900 and 1500 million years ago (Flathead Transboundary Network 1999, Lesica 2002). Vegetation grew and decayed, resulting in oil and gas deposits between layers of limestone, dolomite and shale. Between 5 and 140 million years ago, inland waters eroded these mountains to create sandstone, shales, and conglomerate rocks. These sed-

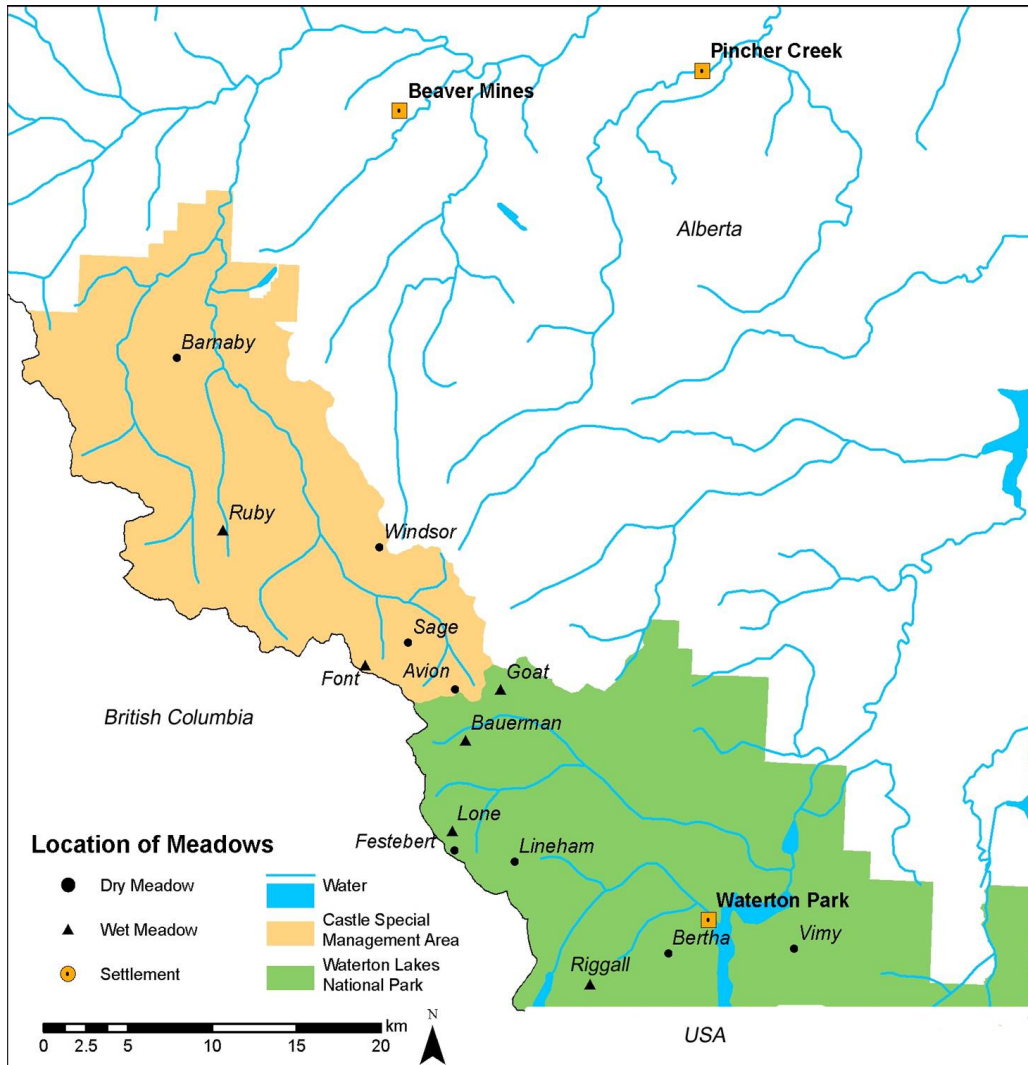


Figure 1.3: Study area in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA), Alberta, Canada.

imentary deposits were folded and uplifted beginning 85 million years ago in an event known as the Lewis Overthrust. The harder basement granite sheared off and slid cleanly over younger material. This action resulted in younger rocks lying underneath older formations. Glaciation events (over 10,000 years ago) produced the resulting glaciers, lakes, hanging valleys, and cirques, including some subalpine meadows, in the region.

Geology can influence vegetation, especially when the poorly developed soils still reflect the chemical composition of the parent rock (Lesica 2002). The limestone-dominated mountains provide a calcium-rich environment with a higher pH than granitic rocks or mudstones. The physical features and climate of the landscape highly influence vegetation communities. The Alberta Rocky Mountains are divided into three general vegetation types - montane, subalpine and alpine subregions (Strong and Leggat 1981, Achuff 1992).

The subalpine ecoregion in the Rocky Mountains is an intermediate zone between the montane and the treeless alpine expanses. The elevation ranges from 1520 to 2250 metres, categorized into low, mid and high elevation. Low elevation forested areas consist primarily of lodgepole pine (*Pinus contorta*). The understory is characterized by pussytoes (*Antennaria racemosa*), arnica (*Arnica cordifolia*), soopolallie (*Shepherdia canadensis*), bearberry (*Arctostaphylos uva-ursi*) and Utah honeysuckle (*Lonicera utahensis*) (Kuijt 1982). Mid elevation sites are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Understory vegetation includes false azalea (*Menziesia ferruginea*), round-leaved violet (*Viola orbiculata*), baneberry (*Actaea rubra*), wintergreen (*Pyrola spp.*), beargrass (*Xerophyllum tenax*) and several ferns. The upper subalpine forests consist of dwarfed Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) as well as alpine larch (*Larix lyallii*), limber pine (*Pinus flexilis*), and whitebark pine (*Pinus albicaulis*). Typical understory plants are woodrush (*Luzula glabrata*),

western spring beauty (*Claytonia lanceolata*), bronze bells (*Stenanthium occidentale*), glacier lily (*Erythronium grandiflorum*), and Indian paintbrush (*Castilleja rhexifolia*).

Trees commonly grow in patches and are interspersed with open meadow. Subalpine meadows are usually dominated by broad-leaved herbaceous plants and sedges (Lesica 2002). Meadows typically are classified into two categories: dry and wet sites. Dry meadows occur on steep, usually warm slopes, with stony, poorly-developed soil. In dry meadows alpine pussytoes (*Antennaria lanata*), mountain heather (*Phyllodoce glanduliflora*), alpine veronica (*Veronica wormskjoldii*), alpine milkvetch (*Astragalus alpinus*), alpine willowherb (*Epilobium alpinum*), fescue (*Festuca brachyphylla*), sedge (*Carex paysonis*), and mountain hair grass (*Deschampsia atropurpurea*) are common (Kuijt 1982, Lesica 2002). Wet meadows are generally found on gentle to level terrain and soils are relatively deep and retain more moisture for most of the growing season, compared with dry meadows. Common species that appear immediately following snow melt are glacier lily (*Erythronium grandiflorum*), spring beauty (*Claytonia lanceolata*) and buttercup (*Ranunculus eschscholtzii*). In the low-lying areas, these flowers are then replaced by Arnica spp., arrow-leaved groundsel (*Senecio triangularis*), globeflower (*Trollius albiflorus*) and sitka valerian (*Valeriana sitchensis*). Steeper sites are dominated by beargrass (*Xerophyllum tenax*). Common grass-like species include common sedge (*Carex nigricans*), drummond's rush (*Juncus drummondii*) and mountain timothy (*Phleum alpinum*).

1.3 Management area policies

The Castle Special Management area (CSMA) is managed under the Castle River Sub-Regional Integrated Resource Plan (Alberta Energy and Natural Resources 1985), which sets policy and provides the guidelines for land use planning, zoning, and management in the region. As a result, grazing, petroleum extraction,

forestry and tourism activities (including motorized vehicles) occur. The Castle River Integrated Resource Plan provides a policy level framework from which land and resource management can proceed on an integrated basis. The plan is considered to be a 'living document' which enables the Government of Alberta to practice adaptive management in order that the area be maintained in a state that reflects current natural resource conditions in the area, resource management policies and scientific principles.

Waterton Lakes National Park (WLNP) is managed under the Park Management Plan (Parks Canada 2000). The protection of the park's ecological integrity and cultural resources is the primary consideration in management of this area. This management plan provides a framework for how these principles of no net negative environmental impact, appropriate use, responsible growth management, and leadership in environmental and heritage conservation will be applied to the preservation, restoration and conservation of ecological and cultural integrity. National parks are, first and foremost, places for nature but they must also continue to be places for people and for heritage tourism, places to visit, to experience and to learn. As a result no grazing, petroleum extraction, forestry and recreational motorized vehicles are allowed. Movement of people through the landscape is restricted to limited biking, hiking, and horse travel.

The interdependence of WLNP and neighbouring ranches and forestry lands was recognized in 1979 with the establishment of the Waterton Biosphere Reserve. A biosphere reserve has a core protected area and a surrounding landscape, used for a variety of purposes, where active consideration is given to sustainability.

1.4 Disturbance history

Historical records of cattle and horse grazing, use by people, and fire are sparse for the subalpine in Waterton Lakes National Park (WLNP) and the Castle Special

Management Area (CSMA). Despite limited information we can get a picture of the disturbance history for subalpine meadows.

Cattle and horse ranching on a large scale were permitted inside the Park boundaries from 1895 until the late 1940s; grazing was phased out entirely in the early 1970s, although small numbers of horses continue to travel in the subalpine (MacDonald 2000). Within the CSMA, cattle grazing continues today throughout the valleys. Horse outfitting is also popular in this area, with groups camping in subalpine meadows on their travel routes. All types of grazing generally reduces the abundance of fine fuels on the landscape, lowering competition with shrubs and seedlings, resulting in successional advances (Gruell 1983). Conversely, the presence of large animal herds of any kind would likely result in some trampling of conifer and shrub seedlings. As compared to elk and bighorn sheep, however, cattle do not browse conifer seedlings as heavily (Burton 2003). Historic livestock grazing records for WLNP and CSMA are scarce, and a review of existing grazing records, from WLNP library and Alberta Sustainable Resource Development, revealed that general licenses were granted for large portions of the study area, and were not specific enough to quantify the amount of grazing in subalpine meadows. In WLNP cattle and horses were present in large numbers, possibly several thousand, until the late 1940s, when their numbers dropped to less than 100 animals.

Oral histories, ethnographic records and archaeological studies indicate that humans have been living in and managing Rocky Mountain landscapes for thousands of years (Reeves 1975, Peacock 1992, Barrett 1996). Archaeologists have recorded evidence of indigenous peoples in the southern Alberta Rocky Mountains since glaciers retreated from the land some 10,000 years ago (Reeves 1975). The Ktunaxa (also known as Kutenai or Kootenay) and the Piikani (Peigan) (one of the tribes of the Blackfoot Confederacy) lived, and in some cases still live, within

this ecosystem. The Southern Rockies were a major transportation corridor, allowing people to travel south to lands in present-day Montana, east to the Prairies, or west to the Kootenay river. Akamina, Kootenay and Sage Passes were used where many subalpine meadows occur (Reeves 1979). Subalpine meadows were used as transitory sites but also had ethnobotanical importance. In fact, ethnographic evidence suggests that the Piikani selected campsites based on proximity to plant resources (Peacock 1992) such as glacier lily (*Erythronium grandiflorum*), spring beauty (*Claytonia lanceolata*), and various berries (*Vaccinium* spp.). Prime berry picking areas were returned to annually, with people using the same seasonal campsites (Wissler 1986). Camps found at higher elevations were also identified as transitory hunting camps used in spring to late summer. Summer camps were identified in cirque basins where many subalpine meadows exist at high elevation (Reeves 1975).

Anthropogenic fires were common on many North American landscapes, before and during the arrival of European settlers, and were a critical influence on the development of vegetation communities (Lewis 1993, Barrett 1996, Barrett and Arno 1999, Boyd 1999, Turner 1999, Kimmerer and Kanawha Lake 2001, Keane et al. 2002). The use of fire by indigenous peoples served as a means to enhance growth and production of plant food resources. One of the first edible roots to be harvested each season in the subalpine, was western spring beauty (*Claytonia lanceolata*), otherwise known as wild potato (Peacock 1992). Open meadow habitat was preferred for harvesting this species, and fires could have been an ideal way to promote future harvest. Such burning techniques required an in-depth knowledge of ecosystems and were carried out frequently throughout various ecosystems (Turner 1999). Knowledge of vegetation dynamics, climate, and geography played a crucial role in site selection, seasonal timing, frequency, and size of fires. Black mountain huckleberry (*Vaccinium membranaceum*) was also frequently

burned to prevent encroachment of trees. Indigenous fires in high elevation sites were also used to maintain open campsites and trails; to corral animals for hunting; communication; spiritual activities; and to improve plant growth for browse by game animals (e.g. increase food availability for hunted species such as deer); (Barrett and Arno 1999).

Historic fires in the subalpine are considered to be low intensity, and infrequent with a fire return interval estimated at 100 years (Weisberg and Swanson 2003). Evidence of fire was found at all the dry high elevation sites in the CSMA. Trees struck by lightning were also located in one of the dry meadows with poor fuel load surrounding the adjacent area.

Chapter 2

Literature Review

2.1 The Importance of Reference Conditions in Ecological Restoration

2.1.1 What is Ecological Restoration?

The Society for Ecological Restoration International defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER International Science and Policy Working Group 2004). Ecological restoration is an intentional activity that initiates or accelerates recovery of an ecosystem with respect to its function (processes), integrity (species composition and community structure), and sustainability (resistance to unnatural disturbance and resilience). It enables abiotic support from the physical environment, suitable flows and exchanges of organisms and materials with the surrounding landscape, and the reestablishment of cultural interactions upon which the integrity of some ecosystems depends (SER International Science and Policy Working Group 2004). These principles and guidelines focus on the restoration of natural heritage, including native biodiversity and ecosystem functions (Parks Canada 2007). At the same time, they recognize the long-standing inextricable interrelationship between humans and the environment and respect the need to

integrate considerations relevant to the protection of cultural heritage.

2.1.2 Reference Conditions

The next step is to address the importance of reference conditions. These are conditions or evidence from the past that provide an idea of a future trajectory. Reference information can emerge from dendrochronology, long-term monitoring studies, paleoecological evidence, baseline studies, historical land uses and numerous other sources. Reference information offers a glimpse into the history of a landscape. Dendrochronological research allows us to see a component of ecological history that aids in the determination of reference conditions. Restorationists need reference conditions because: 1) they help define a preferred condition (composition, structure, processes, function); 2) they assist in the determination of what factors caused the degradation; 3) they contribute to the delineation of what needs to be done to restore the ecosystem; and 4) they provide the criteria for measuring the success of restoration treatments or experiments (Egan and Howell 2001). Using reference conditions is therefore integral to ecological restoration practices.

2.1.3 Complexity of Ecosystems

To determine reference conditions within a landscape, we need to try to understand the myriad variables that allow that landscape to function. Restorationists are working with dynamic systems that are constantly changing over space and time. Deciphering a reference model for restoration goals can never be complete, as the complexity of ecological systems is practically infinite.

“Although sound ecological generalizations and predictions arise from regularities in species characteristics, environmental properties, and the interaction of species with one another and with physical environments, the specific dynamics of any one system will be contingent on its history, the accidents of arrival of species at the site, and the nature

of the system's connections to the surrounding landscape" (Picket and Parker 1994).

Reference conditions are therefore complex and nonlinear, where no specific point in time can provide all the required information. Holling and Goldbert (1981) summarize four basic properties of ecosystems: 1) They have systemic qualities that indicate that the components are interacting in complex ways; 2) they are historical, meaning that their current conditions are shaped by past events; 3) they are open and spatial, meaning that their current conditions are shaped by the surrounding environment; 4) they are nonlinear, meaning that successional pathways and other ecosystem processes are often multidirectional and may be characterized by lags and thresholds. By identifying these properties, ecologists have acknowledged that systems are highly influenced by multiple factors on many scales. This understanding suggests that the history of influences on a landscape can have great effects on the future of that landscape.

Historical events play a major role in ecology, and current ecological practices strongly influence future trajectories. 'Seemingly insignificant changes in abiotic conditions or species composition that happened long ago or far away can have large, irreversible effects on the structure and dynamics of local ecosystems"(Brown 1995). Complex systems can be sensitive to changes in the conditions within a landscape. Even a small initial change within a system can have great ramifications for the system's future.

Human influences on the landscape vary from the nurturing to the destructive. As with other ecological interactions, people interact with the landscape in a dynamic way. A record of the history of people and the landscape provides important information used in determining reference conditions. If human influence directly or indirectly causes degradation of a landscape, then that information helps to discern effective restoration goals. Unless we identify disturbances and

remove possible stressors, we have little chance of restoring the landscape. An understanding of ecological complexities helps restorationists define complexities in their practice.

2.1.4 Historic Range of Variability

No matter how vast our knowledge of historical conditions and present characteristics, there will always be more reference information that cannot be gathered, or has yet to be recorded. Historic range of variability implies multiple trajectories over time and space. Selecting the appropriate temporal and spatial scale for the historic range of variability is critical. No fixed time period has to be used in restoration. We must also determine the scale of the study area, whether it is a single site, or an entire landscape, in order to identify enough heterogeneity to produce valuable information. The dynamics of each system and area will reflect different restoration goals and historic range of variability. This variability will explain the type, frequency and magnitude of potential disturbances required to restore an ecosystem.

Inherent problems arise when we try to represent reference conditions in restoration projects. It is difficult to implement disturbances to restore ecosystems in the proper sequence and magnitude to reflect historical disturbance. An example of a disturbance is fire. Restoring fire in the landscape, where fire was once a natural disturbance, is important in keeping with that landscape's history. One must also realize that fire is but one process of many in an evolving landscape. Knowing the conditions that allow ecosystems to exist, or even a fraction of those conditions, provides an approximate guide to restorationists.

2.1.5 Approximation of Reference Conditions

Approximation of reference conditions is realistic; we cannot possibly obtain all the information necessary to paint the whole picture of historical qualities. We

may not be able to obtain full information on reference conditions, but we can research and interpret the pieces of history to make wise decisions in restoration. White and Walker (1997) provided a series of research questions that fit into five categories: 1) understanding ecological variation at multiple scales; 2) developing models for integrating diverse sources of information; 3) achieving sensitivity of restoration to variation in reference information; 4) determining site specific restoration goals; and 5) increasing the occurrence of self-sustaining ecosystems (ecological variation, diversity and resilience). The last category emphasizes self-sustaining ecosystems, and its inclusion in the list leads to controversy over human influence or participation in restoration goals and management.

The self sustainability of ecosystems suggests a lack of participation of people in the landscape, or at least an indirect role given to human engagement with landscapes. Higgs (2003) suggests that the idea of self sustainable ecosystems “tends to underrate the significance of coevolved cultural and ecological practices in the past, including those by First Nations peoples”. Instead, he argues that we need to examine exactly how people have been involved with ecological processes and how they themselves are ecological agents. A goal of restoration is achieving thriving ecosystems that may depend, to varying degrees, on respectful human practices. This strikes a challenge but an important hurdle in understanding respectful human practices. “One of the largest challenges for those who care about remarkable places is helping people understand when enough is enough, and when it is better to back away from something than trek forward. It is difficult to imagine a practice of abnegation more hostile to the contemporary spirit” (Higgs 2003).

2.1.6 Historicity: Nostalgia, Narrative Continuity, Depth

Why reference conditions are important in restoration, and more generally why does history matter in ecological restoration? To examine why restorationists should be concerned about history, or more properly, historicity, we need to under-

stand the practice of ecological restoration. Higgs (2003) suggests there are three reasons for valuing restoration practice and taking historicity seriously: 1) nostalgia, the knowledge things bring of a better past, and what historicity means to us; 2) narrative continuity, the continuous stories that inform our understanding of place; and 3) depth of time, the temporal depth of our affiliations.

To explain nostalgia, we must first ask ourselves why we are drawn to history in the first place. What is it about history that attracts us? As we look into the past, we often think of a simpler or better model than what we have now. The few landscapes that now remain undamaged by human industry, not necessarily human presence, represent to most people the attachment to the past, a time that was ultimately better. We tend to understand the world on the basis of our experiences, not unlike the way in which we perceive ecosystems. These experiences are a part of the past and provide knowledge of the continuity of history. When we examine, as we all do at certain stages in our life, the definition of self, we see ourselves in the context of our past. Our memories represent a specific time and place. These existential memories give us the foundation of who we are, where we have been and what we will become. Similarly, stories of our ancestors and their relationship with the environment provide a sense of where we have been, or our roots. Naturally, since people are driven to know ultimately who they are, we see the importance of historical perspective.

Memories or moments make up the stories that are told through time across a landscape. Ecosystems also have a past, and in an anthropogenic way, they have many stories. These stories or histories will continue in the present and into the future. The constant evolution and adaptation of ecosystems is represented through what Higgs (2003) describes as narrative continuity. Narrative continuity is represented in the idea that what *was* somehow flows into what *is* and then what *will* be. The narrative continuity of a place forms through both ecological

and cultural histories, allowing for a continuous flow of information on multiple levels through place and time.

Time depth is crucial in understanding the importance of history in restoration. “Depth is the reach of history, the amount of time, and also the engagements that form between people and place over that interval” (Higgs 2003). Depth typically increases when we go further back in time. Old growth forests represent depth in time because there is a long continuity within this landscape. Depth also depends on rarity, as we place value in older ecosystems that are typically unusual or scarce. This perception can be related to individual species. The value of an individual species or an ecosystem increases because that system or species is irreplaceable. Time depth is therefore a part of historicity, as it represents the temporal depth of our affiliations.

2.1.7 Striking a Balance

White and Walker (1997) point out four types of reference models: contemporary sites to be restored (same time, same place); historic models of restoration sites (different time, same place); contemporary remnants (same time, different place); and historic remnants (different time, different place). Using the appropriate combination of these reference models, contemporary information and historic information, we can gain a clearer picture for restoration goals. Most certainly, restorationists will be faced with incomplete reference information. Acquiring historic data and conducting extensive research is often difficult and rarely done. Using a combination of White and Walker’s four reference models can help balance the reference condition deficiencies in any one particular model. Although finding a balance is crucial, piecing together a history of the landscape certainly poses numerous challenges for restorationists.

Restorationists face uncertainty when they work out restoration goals from piecing these fragments of information that are a part of a long and continuous his-

tory. Using reference information helps us define a range of variability or boundaries for restoration goals, but too broad of a range of variability will not be specific enough to truly represent future conditions. Not only do restorationists need to discern the past, but also how the future should be in relation to the past.

Climatic change and other human induced environmental problems pose further challenges for restorationists (Harris et al. 2006). If climatic conditions and environmental problems are outside the long term range of variability, restoration goals become difficult to set. As there are many possibilities and challenges for restoration, there is a risk that people will give up on the past. Uncertainty can possibly lead to people's frustration and the loss of history in restoration practice. The risk is then that restoration may become ahistorical (Higgs 2003). To ignore history is no way to do ecological restoration.

Achieving adequate reference information is difficult, but without this information, we have no context for the future. Without history, restorationists run the risk of being confined by social perceptions rather than the reality of the system being restored. The past, present and future play important roles in understanding the system we choose to restore. Ecological restoration truly can not take place in the absence of historicity. Reference conditions are crucial pieces of history that provide guideposts for ecological restoration, especially when coping with climate change.

2.2 Tree Encroachment in Subalpine Meadows

The decrease of subalpine meadows in North America is an ongoing concern that has been attributed to tree establishment (Haugo and Halpern 2007, Rochefort and Peterson 1996, Moore and Huffmant 2004). The causes of tree establishment in meadows are difficult to discern. Recent research has identified a number of key factors that contribute to tree establishment. These factors include climatic

trends (Taylor 1995, Woodward et al. 1995, Rochefort and Peterson 1996, Miller and Halpern 1998), environmental conditions (Magee and Antos 1992, Moore and Huffmant 2004, Lepofsky et al. 2003), fire suppression (Hadley 1999), livestock grazing (Vale 1981, Dunwiddie 1977, Miller and Halpern 1998) and other land use histories (Lepofsky et al. 2003). These factors are not mutually exclusive, but that they all can contribute, on varying spatial and temporal scales. It is not surprising that multiple factors influence landscape change, but specifically why trees invade meadows remains a complex question. The interplay of mechanisms for tree establishment varies in importance across multiple gradients of environmental characteristics, disturbances, vegetation and land use histories. If predicting change in meadow structure and composition is our goal, we must then understand how these mechanisms interact on varying scales.

Changes in subalpine meadows can be attributed to varying spatial and temporal effects. Coarse-scale processes such as climate variation and trends or fine-scale processes such as variation in site conditions can cause dramatic impacts. The duration, intensity and size of these impacts will, in turn, have varying effects. The prediction of future tree growth becomes even more challenging when we consider the interaction of numerous processes on varying spatial and temporal scales (Daniels and Veblen 2003, 2004). Within such compounding dynamics, causality becomes difficult to identify. The ecological history of a meadow is therefore not explained by a single factor (Norman and Taylor 2005).

2.2.1 Components of Multifactorial Impacts

Climatic Trends

Tree establishment in subalpine meadows is frequently associated with climatic patterns (Taylor 1995, Woodward et al. 1995, Rochefort and Peterson 1996, Miller and Halpern 1998). The concern is that with warmer climate in the next century,

tree development in the subalpine meadows will occur more rapidly than in the past. At high elevation sites, tree establishment is often attributed to warming temperatures and a reduced snowpack (Taylor 1995, Hessel and Baker 1997). This is true for some meadows, but depending on the location and environmental characteristics of these meadows, climatic trends will effect tree establishment differently. Each landscape has a multiplicity of characteristics, including landforms, soil types, moisture regimes, slopes, elevation and many other unique properties. The variability of these characteristics will in turn impact the effects of changing climatic trends.

Precipitation in the form of snow melt or summer rain can have different effects for topographically different meadows. For example, abundant precipitation was found to limit tree establishment on mesic sites and to promote it on xeric sites (Taylor 1995). Woodward et al. (1995) found that in the Olympic Mountains tree establishment occurred in dry areas when weather conditions were wetter than average, and in wet areas under drier conditions than average. They concluded that if climatic trends continued to warm, establishment would increasingly occur in mesic sites.

In Yellowstone National Park, tree establishment in dry meadows was attributed to warmer and wetter growing seasons (Jakubos and Romme 1993). Summer precipitation can support tree seedling development on originally drier sites; conversely, it can create unsuitable microclimatic conditions on already moist sites where increased moisture deters seedling growth (Magee and Antos 1992, Mast et al. 1997, Miller and Halpern 1998). When predicting tree establishment, we must consider that warming temperature trends on a global scale may not translate to the same effects on a regional, landscape or even microsite scale.

In the Pacific Northwest, a drought period from 1920 to 1940 promoted tree establishment in wet meadows (Magee and Antos 1992). During warmer wet pe-

riods, dry sites had an increase in the frequency of tree establishment (Jakubos and Romme 1993). Establishment on north facing slopes coincided with warming trends because snowpacks were reduced and melted earlier (Miller and Halpern 1998). Establishment on south facing slopes (typically dry sites experiencing increased moisture) occurred later, when conditions were wetter. Snow accumulation in the winter can also provide moisture for seedlings and reduce productivity of meadow vegetation (Magee and Antos 1992). As we can see, much variation occurs in relation to warming climatic trends. Once trees have become established, additional factors play a role in the rate of that establishment. Vegetation dynamics certainly play an important role for continued tree expansion in meadows.

Changes in local vegetation

Conifer encroachment has detrimental consequences for plant composition and diversity of meadow vegetation (Haugo and Halpern 2007). Established trees provide conducive physical conditions for seedlings in places where once meadow vegetation inhibited tree establishment. Tree establishment often occurs in the forest meadow ecotone, partially due to the reduction of herbaceous plants, whereas dense grass-dominated vegetation inhibits seedlings (Dunwiddie 1977, Vale 1981).

The process is gradual, but over time a meadow can disappear and be converted to forest. Sapling establishment often occurs within a short distance from the meadow forest boundary (Wearne and Morgan 2001). Once forest is established, meadow vegetation is unlikely to out-compete trees or re-establish in this area.

It is also possible that in large meadows, seed supply is a limiting factor for tree establishment (Brown 1941, Billings and Mark 1957). As tree encroachment increases, the seed supply will most likely increase, and possibly increase the rate of tree establishment. Although vegetation changes play an important role in tree establishment, physical disturbances can alter a meadow system dramatically.

Contributors to disturbance regimes

The many contributors to disturbance regimes include avalanches, wind and fire. Meadows are often exposed to rock and snow avalanches that can cause tree damage or complete removal. Trees are also commonly destroyed by high winds in the subalpine environments. Wind can also create microclimate conditions that are not conducive to new tree establishment. Daniels and Veblen (2003) found that local disturbance occurred more frequently than expected on slopes with cool aspects, steep slope angles and concave slope configuration. Another important factor contributing to tree destruction is fire.

Fire

Throughout North America, successful fire suppression and exclusion policies over the past century have contributed greatly to the advancement of forest cover into open habitats and the decline of meadow vegetation (Barrett 1996, Luckman 1998, Barrett and Arno 1999, Keane et al. 2002, Rhemtulla et al. 2002). The influence of fires in the landscape has a direct relationship to forest composition and structure (Barrett 1996, Barrett and Arno 1999). In the past century the forest composition and structure has been altered due to changes in landscape management, including fire suppression and exclusion.

Jakubos and Romme (1993) suggest that fire suppression is less important in explaining seedling establishment in subalpine meadows, than in lower elevation sites. However, it is also thought that subalpine meadows in the Pacific Northwest Mountains were caused and maintained by fire (Magee and Antos 1992, Woodward et al. 1995, Miller and Halpern 1998, Norman and Taylor 2005). Although fires may be considered less common in higher elevation sites compared to valley bottoms, tree seedlings may be sufficiently suppressed by infrequent and low intensity fires to maintain meadows. Since meadow species occur beneath the open

canopy of advancing forests, fire can remove the overstory trees along the forest edge, allowing meadow expansion (Magee and Antos 1992). The frequency and size of fires can occur at a small enough scale to not be documented in historical records but be crucial for maintenance of meadows.

Meadows exist in subalpine environments for various reasons; one possible explanation is fire. Although fire in subalpine environments has not been well studied or documented, the suppression of fire may be a major factor in current tree establishment. Naturally caused fires, such as lightning fires, are often what we think of when it comes to high elevation sites, but anthropogenic fire also influenced these areas.

Anthropogenic Disturbances

Subalpine meadows have been impacted by people through burning, logging, mining, recreational activities, livestock grazing, plant harvesting, hunting, and other activities. Human induced impacts can have great effects on vegetation dynamics.

Indigenous resource management

Ecosystems have been managed for thousands of years by indigenous people. Indigenous peoples traveled through a variety of mountain elevations throughout the year in order to take advantage of the food resources available at different places and during different seasons (Reeves 1975, Peacock 1992). Berries were harvested in the late summer and fall, in the subalpine, after the harvest at lower elevation (Hart 1972, Peacock 1992, Turner 1999). Mechanical techniques were common for managing plant resources including selective harvesting, replanting of seeds, pruning or coppicing and burning to stimulate plant growth of selected species (Peacock and Turner 2000).

Anthropogenic fire

Anthropogenic fires were common on many North American landscapes before and during the arrival of European settlers, and were a critical influence on the development of vegetation communities (Lewis 1993, Barrett 1996, Barrett and Arno 1999, Boyd 1999, Turner 1999, Kimmerer and Kanawha Lake 2001, Keane et al. 2002). In British Columbia, Turner (1999) found that, for optimal plant resource productivity, the burning of an area generally occurred in rotation after harvesting and on a three-year burning cycle. This timing would be frequent enough to assist in the prevention of tree establishment in subalpine meadows and could have been an important historical influence on subalpine meadows. By the late 1800s, indigenous burnings were extremely rare, due to European dictation and influence. Although Europeans used fire to clear land for farming, livestock grazing became a primary factor in influencing subalpine meadow tree establishment.

Livestock grazing

Livestock grazing by European settlers has obvious impacts such as herbivory and compaction of soils, but the ability of trees to establish in these impacted meadows is variable. Grazing has been reported to both decrease and enhance seedling establishment depending on past or present grazing intensity (Dunwiddie 1977, Miller and Halpern 1998, Norman and Taylor 2005). Norman and Taylor (2005) found that tree establishment was greater after historic sheep grazing, when sheep were restricted in numbers. When sheep grazing was heaviest, tree establishment was lower than when sheep were absent. Although this pattern does not apply to all herbivores, it provides interesting insight into not only the variation in disturbance but also the variation in severity and the ways in which these can cause varying impacts. In areas where herbaceous vegetation has not adapted to herbivory, grazing may also promote higher tree establishment than in areas where

vegetation has high resilience to this type of disturbance. Grazing can therefore affect different areas with varying intensity.

Although historical human disturbances have occurred at high elevation sites, the effects of such disturbances are difficult to recognize within present day ecosystems. Subalpine meadows may not show evidence of past fire or of past grazing. This difficulty in detection raises an obstacle to a full understanding of the potential drivers for tree establishment. Without historical records or oral history, it can become difficult to discern past human use.

Concluding thoughts

To understand the impact of tree establishment in subalpine meadows, we must consider many factors that are layered within the complexities of their interrelationships. There is little doubt that continued tree establishment will diminish the presence of meadows. Tree establishment is likely the outcome of varying scales of processes, from fine-scale processes, such as microsite conditions to coarse-scale processes, such as climate and grazing. The challenge is to anticipate the rate of tree establishment in meadows across the landscape, and then react with resource management practices. Knowledge of the causes and impacts of tree establishment is crucial to the conservation and restoration of subalpine meadows.

Chapter 3

Methods

3.1 Sampling methods

The first step in site selection was completed by identifying the population of subalpine meadows that had conifer encroachment by comparing historical (1913, 1914) and recent (2004, 2005, 2007) oblique photographs and aerial photographs. A complete helicopter inventory of meadows was then conducted across the study area to ensure accuracy of photo interpretation. A total of 42 subalpine meadows were located, with 38 exhibiting conifer encroachment. Meadows were stratified by management area (WLNP and CSMA), and by meadow type (wet and dry). Subalpine meadows were selected based on the following criteria; 1) located in the upper subalpine (greater than 1900m) and 2) not influenced by avalanche activity. Based on this criteria Waterton Lakes National Park (WLNP) had 7 dry meadows and 5 wet meadows and the Castle Special Management Area (CSMA) had 13 dry meadows and 2 wet meadows. Fourteen meadows were randomly selected from the population of subalpine meadows that met the selection criteria (n=27). Meadow types were defined by existing classification (Moss and Packer 1983, Lesica 2002). Of the 14 meadows, 8 are located at dry meadow sites dominated by larch (*Larix lyallii*) and subalpine fir (*Abies lasiocarpa*) (4 in WLNP and 4 in CSMA). Six meadows are located at wet sites dominated by subalpine fir (*Abies*

lasiocarpa) and/or Engelmann's spruce (*Picea engelmannii*) (4 in WLNP and 2 in CSMA); (Table 12).

Table 3.1: Site descriptions for wet and dry meadows in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA).

Site	Management area	Elevation (m)	Aspect	Transect length (m)
<i>Wet Meadows</i>				
Font	CSMA	2070	NE	35
Ruby	CSMA	1980	N	25
Bauerman	WLNP	1970	N	60
Goat	WLNP	2010	SE	30
Lone	WLNP	1970	NE	40
Riggall	WLNP	1990	S	55
<i>Dry Meadows</i>				
Avion	CSMA	2280	NW	40
Barnaby	CSMA	2210	N	35
Sage	CSMA	2260	SW	45
Windsor	CSMA	2240	SW	35
Bertha	WLNP	2200	NE	30
Festebert	WLNP	2150	NE	35
Lineham	WLNP	2190	E	45
Vimy	WLNP	2010	NE	50

At each subalpine meadow selected, one belt transect was used to sample conifer ages and herbaceous understory. Belt transects were randomly located in areas exhibiting conifer encroachment, with at least 10m of meadow and 10m of forest, in order to encompass the range in variation of forest-meadow ecotones and conifer encroachment patterns. The vegetation boundaries were fairly distinct and therefore delineated into three areas: 1) open meadow, with little or no conifer encroachment; 2) ecotone (the transition between the forest and the meadow), with conifer encroachment; and 3) forest, with mature trees. Belt transects varied from 25m to 60m long because of variation in width of the ecotone. Belt transects were

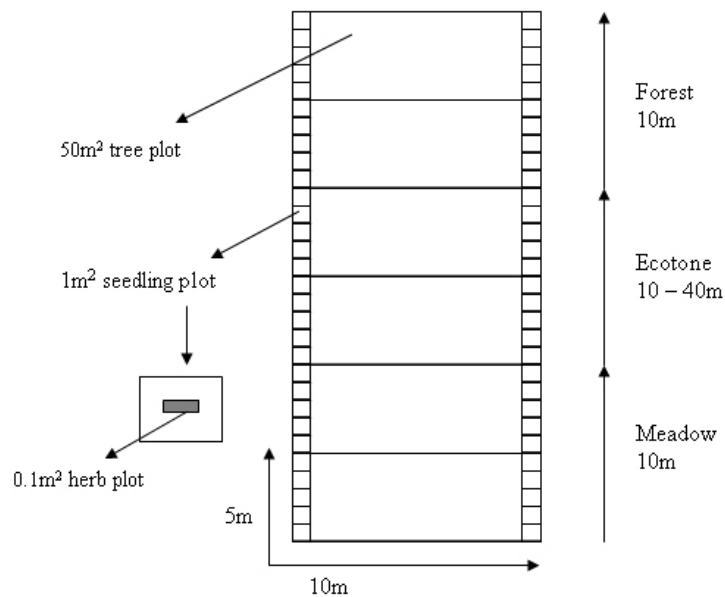


Figure 3.1: Diagram of a belt transect with 50m² tree plots, 1m² seedling plots and 0.1m² herb plots. Forest plots were a minimum of 10m, Ecotone plots ranged from 10 to 40m and meadow plots were a minimum of 10m.

10m wide and were perpendicular to the forest margin and extended 10m into the forest, 5 to 40m through the ecotone and 10m in the meadow. Each belt transect was divided into contiguous 50m² (5x10m) tree plots, with 10 1m² seedling plots (5 plots on each side) and 0.1m² (0.2x0.5m) herb plots placed in the centre of each seedling plot. All trees less than 10cm dbh, and taller than 5cm were sampled in the seedling plots. All trees greater than 10cm dbh were sampled in the tree plots.

Cover was estimated for each vascular plant species in each herb plot (1060 plots). Conifers less than 5cm dbh were felled below the root collar by removing soil to expose the roots (n=1216). Basal sections were cut at the root collar and sanded using standard dendrochronological methods (Stokes1968). At four sites,

where trees exceeded the removal allowance (ca. 50 seedlings per site) in Waterton Lakes National Park, branch whorls and/or bud scale scars were also counted, and age was determined from age-branch whorl regressions from basal sections (Appendix 1). Trees less than 5cm dbh were not crossdated, as tree ring widths were inconsistent. Conifers greater than 5cm dbh were cored as close to the root collar as possible, and core height was recorded (n=202). Tree cores were mounted and sanded using standard dendrochronological methods. Age-height regressions of the basal sections were used to estimate age to coring height (Appendix 2). Ring counts were made with 10-80x magnification for both cores and basal sections. If the pith was missed, the missing rings were estimated from ring pattern templates. For trees with rotten or incomplete cores, age was not estimated.

Environmental variables were sampled at each tree plot and included elevation, aspect, landform, slope, and soil depth (average and maximum). Soil depth was measured at the 4 corners of each tree plot using a steel rod pounded into the ground until bedrock was hit.

A fire scar inventory was completed at all 14 subalpine meadows to aid in the development of ecological restoration strategies. Fire scarred trees were located through systematic searches of the forest surrounding each meadow. Searches consisted of walking traverses observing every living tree, log, and snag for fire scars. Trees were sampled by taking cores or cut disc samples where maximum numbers of well-preserved fire scars could be obtained. Each of the four dry sites in the Castle had evidence of fire.

3.2 Classification of species

Species were grouped by habitat affinity and growth form based on regional floras (Moss and Packer 1983, Lesica 2002)(Table 3.2). Habitat groups included meadow (n = 63 species), ecotone understory (n = 23 species) and forest understory (n =

12 species). Understory trees and unknown species were not classified. Growth forms were categorized by shrub (n = 6), herb (n = 60), grass (n = 16) and sedge/rush/horsetail (n = 17). Species presence in wet or dry meadow types are based on observed occurrence.

Table 3.2: Meadow, forest and ecotone species at wet and dry subalpine meadow sites in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA). Meadow type shows the occurrence of these species at wet and dry study sites. Species that could not be assigned are not listed.

Growth form / Species	Family	Meadow type
Meadow species		
Herbs		
<i>Achillea millefolium</i>	Asteraceae	wet/dry
<i>Agoseris glauca</i>	Asteraceae	dry
<i>Allium schoenoprasum</i>	Liliaceae	wet
<i>Antennaria alpina</i>	Asteraceae	wet/dry
<i>Antennaria lanata</i>	Asteraceae	dry
<i>Arabis drummondii</i>	Brassicaceae	dry
<i>Arenaria capillaris</i>	Caryophyllaceae	wet/dry
<i>Arnica diversifolia</i>	Asteraceae	wet/dry
<i>Astragalus alpinus</i>	Fabaceae	dry
<i>Botrychium multifidum</i>	Ophioglossaceae	wet
<i>Castilleja occidentalis</i>	Scrophulariaceae	wet
<i>Castilleja rhexifolia</i>	Scrophulariaceae	wet/dry
<i>Chamerion angustifolium</i>	Onagraceae	wet/dry
<i>Dodecatheon pulchellum</i>	Primulaceae	wet
<i>Epilobium anagallidifolium</i>	Onagraceae	wet/dry
<i>Erigeron peregrinus</i>	Asteraceae	wet/dry
<i>Erigeron divergens</i>	Asteraceae	dry
<i>Erythronium grandiflorum</i>	Liliaceae	wet/dry
<i>Galium trifidum</i>	Rubiaceae	wet
<i>Geum macrophyllum</i>	Rosaceae	wet
<i>Hedysarum sulphurescens</i>	Fabaceae	dry
<i>Hieracium triste</i>	Asteraceae	wet/dry
<i>Hypericum formosum</i>	Hypericaceae	wet
<i>Parnassia fimbriata</i>	Saxifragaceae	wet
<i>Pedicularis bracteosa</i>	Scrophulariaceae	wet/dry
<i>Penstemon confertus</i>	Scrophulariaceae	dry
<i>Phyllodoce empetriformis</i>	Ericaceae	wet
<i>Phyllodoce glanduliflora</i>	Ericaceae	dry
<i>Platanthera dilatata</i>	Orchidaceae	wet
<i>Potentilla diversifolia</i>	Rosaceae	wet/dry

Continued on next page

Table 3.2 – continued from previous page

Growth form / Species	Family	Meadow type
<i>Ranunculus eschscholtzii</i>	Rununculaceae	wet/dry
<i>Sedum lanceolatum</i>	Crassulaceae	wet/dry
<i>Senecio cymbalarioides</i>	Asteraceae	wet/dry
<i>Sibbaldia procumbens</i>	Rosaceae	wet/dry
<i>Silene parryi</i>	Caryophyllaceae	wet/dry
<i>Taraxacum officinale</i>	Asteraceae	wet
<i>Trollius albiflorus</i>	Rununculaceae	wet/dry
<i>Veronica wormskjoldii</i>	Scrophulariaceae	wet/dry
Sedges/rushes/horsetails		
<i>Carex albonigra</i>	Cyperaceae	dry
<i>Carex atosquama</i>	Cyperaceae	wet
<i>Carex aurea</i>	Cyperaceae	wet
<i>Carex nigricans</i>	Cyperaceae	wet/dry
<i>Carex pachystachya</i>	Cyperaceae	wet/dry
<i>Carex paysonis</i>	Cyperaceae	dry
<i>Carex phaeocephala</i>	Cyperaceae	wet/dry
<i>Carex podocarpa</i>	Cyperaceae	wet
<i>Carex saxatilis</i>	Cyperaceae	wet
<i>Carex scirpoidea</i>	Cyperaceae	wet/dry
<i>Carex spectabilis</i>	Cyperaceae	dry
<i>Equisetum pratense</i>	Equisetaceae	wet
<i>Juncus drummondii</i>	Juncaceae	wet/dry
<i>Juncus mertensianus</i>	Juncaceae	wet/dry
<i>Juncus parryi</i>	Juncaceae	wet/dry
Grasses		
<i>Agrostis scabra</i>	Poaceae	wet
<i>Agrostis thurberiana</i>	Poaceae	wet/dry
<i>Calamagrostis canadensis</i>	Poaceae	wet
<i>Danthonia intermedia</i>	Poaceae	dry
<i>Festuca brachyphylla</i>	Poaceae	dry
<i>Koeleria macrantha</i>	Poaceae	wet/dry
<i>Phleum alpinum</i>	Poaceae	wet/dry
<i>Poa alpina</i>	Poaceae	wet/dry
<i>Poa arctica</i>	Poaceae	wet/dry
<i>Poa cusickii</i>	Poaceae	wet
<i>Trisetum spicatum</i>	Poaceae	wet/dry
Ecotone species		
Shrubs		
<i>Potentilla fruticosa</i>	Rosaceae	wet
Herbs		

Continued on next page

Table 3.2 – continued from previous page

Growth form / Species	Family	Meadow type
<i>Anemone multifida</i>	Ranunculaceae	wet/dry
<i>Angelica dawsonii</i>	Apiaceae	wet/dry
<i>Arnica latifolia</i>	Asteraceae	wet
<i>Aster foliaceus</i>	Asteraceae	dry
<i>Campanula rotundifolia</i>	Campanulaceae	wet
<i>Claytonia lanceolata</i>	Portulacaceae	wet/dry
<i>Fragaria virginiana</i>	Rosaceae	wet/dry
<i>Hackelia micrantha</i>	Boraginaceae	wet
<i>Heracleum spondylium</i>	Apiaceae	wet
<i>Senecio triangularis</i>	Asteraceae	wet/dry
<i>Stellaria crispa</i>	Caryophyllaceae	dry
<i>Thalictrum occidentale</i>	Ranunculaceae	wet/dry
<i>Valeriana sitchensis</i>	Valerianaceae	wet/dry
<i>Veratrum viride</i>	Liliaceae	wet/dry
<i>Xerophyllum tenax</i>	Liliaceae	wet/dry
<i>Zigadenus elegans</i>	Liliaceae	wet
Grasses		
<i>Danthonia spicata</i>	Poaceae	wet
<i>Deschampsia atropurpurea</i>	Poaceae	wet/dry
<i>Elymus spicatus</i>	Poaceae	wet
<i>Elymus glaucus</i>	Poaceae	wet
<i>Elymus trachycaulus</i>	Poaceae	dry
Sedges/rushes/horsetails		
<i>Equisetum arvense</i>	Equisetaceae	wet/dry
Forest species		
Shrubs		
<i>Menziesia ferruginea</i>	Ericaceae	wet
<i>Salix</i> sp.	Salicaceae	wet/dry
<i>Vaccinium membranaceum</i>	Ericaceae	wet/dry
<i>Vaccinium myrtillus</i>	Ericaceae	wet/dry
<i>Vaccinium scoparium</i>	Ericaceae	wet/dry
Herbs		
<i>Arnica cordifolia</i>	Asteraceae	wet/dry
<i>Mitella breweri</i>	Saxifragaceae	wet/dry
<i>Orthilia secunda</i>	Ericaceae	wet
<i>Stenanthium occidentale</i>	Liliaceae	wet
<i>Viola orbiculata</i>	Violaceae	wet
Sedges/rushes/horsetails		
<i>Luzula hitchcockii</i>	Juncaceae	wet/dry

Continued on next page

Table 3.2 – continued from previous page

Growth form / Species	Family	Meadow type
<i>Luzula parviflora</i>	Juncaceae	wet/dry
Unclassified species		
Trees		
<i>Abies lasiocarpa</i>	Pinaceae	wet/dry
<i>Larix lyallii</i>	Pinaceae	dry
<i>Picea engelmannii</i>	Pinaceae	wet/dry

3.3 Encroachment classification

Encroachment classes were created for the 14 meadow sites for both wet and dry meadows. Six encroachment classes were created to accommodate the varying lengths of the ecotone plots across multiple sites. All 14 sites had 2 forest plots and 2 meadow plots with varying ecotone lengths. Forest plots were confirmed to include trees that were older than those in the ecotone, and meadows plots were confirmed to have little or no tree establishment at all 14 sites. The forest plots were then classified as encroachment classes 1 and 2 and the meadow plots were classified as encroachment classes 5 and 6. The ecotone was classified into encroachment classes 3 and 4 by dividing the ecotone into 2 groups, taking the average of the plots located adjacent to the forest for encroachment class 3 and to plots located adjacent to the meadow for encroachment class 4.

3.4 Changes in species composition

Nonmetric multidimensional scaling (NMDS)(Kruskal 1964^{b,a}, Mather 1976) was used to assess changes in species composition for wet and dry meadows separately. NMDS was used for wet meadows on a matrix of 49 plots and 124 species using Sorensen's distance measure and the thorough autopilot in PC-ORD v5.1

(McCune and Mefford 1999). The autopilot conducted 250 runs producing 1 to 6 dimensional solutions, with 500 iterations. Three major gradients captured most of the variance in the plant communities, with the first 3 dimensions containing 35.1%, 20.7%, 14.3% respectively, of the information in the data (cumulative = 70.1%). I selected a final 3 dimensional solution with a stress of 14.3004; the final instability was 0.00000 with 95 iterations. I assessed the stability of the solution by plotting stress versus iteration number. To test whether the final solution provided significantly more reductions in stress than expected by chance, stress from the final solution was compared to 250 runs of randomized data using a Monte Carlo test, where $p=0.004$ (McCune et al. 2002).

For dry meadows NMDS was used on a matrix of 63 plots and 96 species using Sorensen's distance measure and the thorough autopilot in PC-ORD v5.1 (McCune and Mefford 1999) as done for wet meadows. Three major gradients captured most of the variance in the plant communities, the first 3 dimensions containing 36.1%, 20.3%, 13.8% respectively, of the information in the data (cumulative = 70.2%). I selected a final 3 dimensional solution with a stress of 13.77089 with a final instability of 0.00000 and 80 iterations. I assessed the stability of the solution by plotting stress versus iteration number. To test whether the final solution provided significantly more reductions in stress than expected by chance, stress from the final solution was compared to 250 runs of randomized data using a Monte Carlo test, where $p=0.004$ (McCune et al. 2002).

Backwards stepwise multiple regression was used to explore the relationships between species composition and forest structure and environmental variables. Potential predictors in these models were mean and maximum tree ages, tree density, distance along transect, aspect, elevation, slope, mean soil depth, management area (WLNP or CSMA) and presence versus absence of fire in the dry meadows. Backward stepwise regression was used with a probability of 0.05 to add and

0.10 to remove variables. Regression analysis was conducted using SPSS (2005). Correlations between forest structures, environmental, management variables and ordination axes were conducted using SPSS 15.0 (2005).

3.5 Changes in cover and richness of meadow and forest species

Abundance (total summed cover), richness and Shannon's diversity index (Shannon and Weaver 1949) were calculated for meadow, ecotone and forest species and for growth forms within these groups. Wet and dry meadows were assessed separately. Averages were calculated for each encroachment class for all wet sites and all dry sites. Changes in abundance and richness were displayed in graphs showing the transition from open meadow to forest. The top 5 most frequent meadow and forest species for wet and dry sites were graphed, displaying individual species changes across the meadow-forest transition.

Chapter 4

Results

4.1 Conifer encroachment

Conifer encroachment in subalpine meadows in Wateron Lakes National Park (WLNP) and the Castle Special Management Area (CSMA) were composed of three dominant species: subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and subalpine larch (*Larix lyallii*)(Figure 4.1). All three conifers were found at dry sites and only *A. lasiocarpa* and *P. engelmannii* were found at wet sites. The most common tree species establishing within the ecotone between the meadow and the forest was *A. lasiocarpa*. Combined, the wet sites had an increase in conifer establishment and subsequent survival from the early 1940s to the mid 1950s (Figure 4.2), which was observed at three of the six individual sites (Font, Goat and Lone)(Figure 4.3). Bauerman had two *A. lasiocarpa* establish during this time period. The Ruby and Riggall sites had fairly consistent conifer establishment over the past century. *P. engelmannii* showed an overall increase in establishment from the mid 1970s to the mid 1980s and then a decline to the mid 1990s. However, 90% of *P. engelmannii* establishing in the ecotone occurred at Bauerman meadow and *P. engelmannii* only occurred at three of the six sites. *A. lasiocarpa* at dry sites showed an overall increase in establishment from the early 1940s to the mid 1950s (Figure 4.4) and an increase in establishment occurred at each individual site ex-

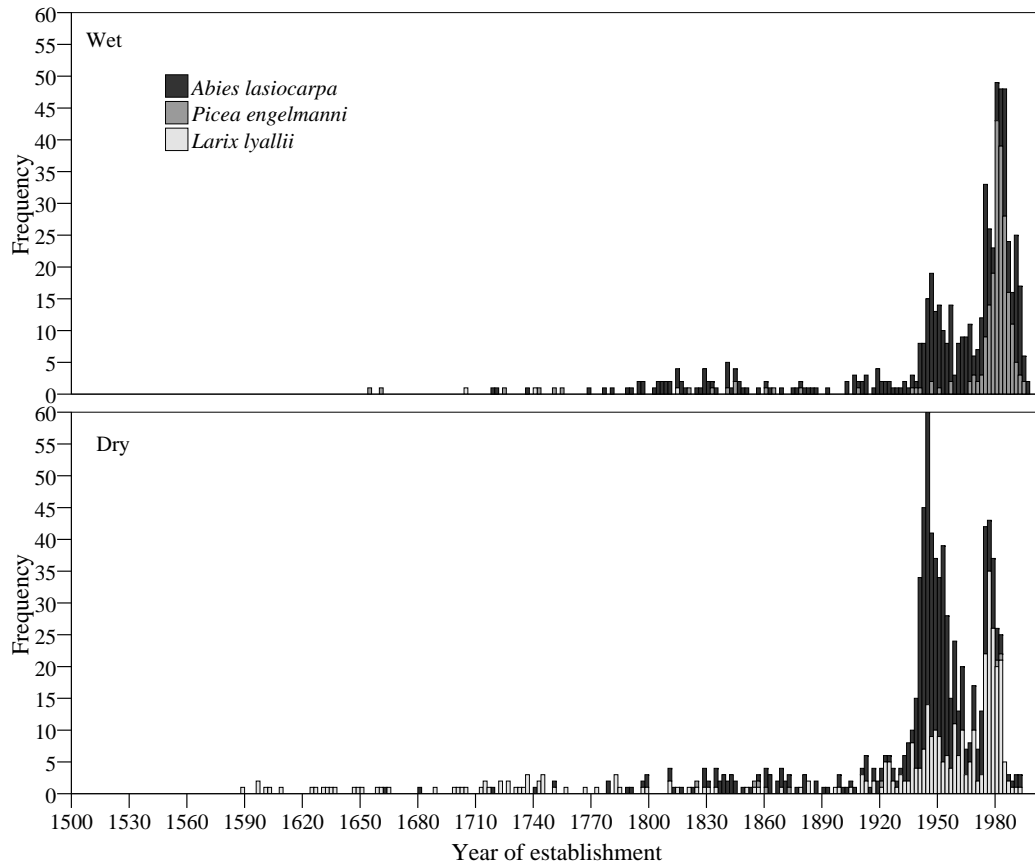


Figure 4.1: Frequency of age (2 year age class) for all conifers >5cm tall for each meadow type within the 112 50 m² plots.

cept for Vimy (Figure 4.5). *L. lyallii* had an overall increase in establishment in the early 1970s to the mid 1980s (Figure 4.4) which is attributable to three of the eight sites (Avion, Sage and Festebert. Prior to the 1970s *L. lyallii* established intermittently.

4.1.1 Fire

Evidence of fire was found within the surrounding forest at four of the 14 meadow sites. The four sites with fire scars are located in high elevation dry sites in the CMSA (Barnaby, Sage, Avion and Windsor). No fire scars were recorded at any of the wet meadow sites in the CSMA, or any sites within WLNP. Two of the four

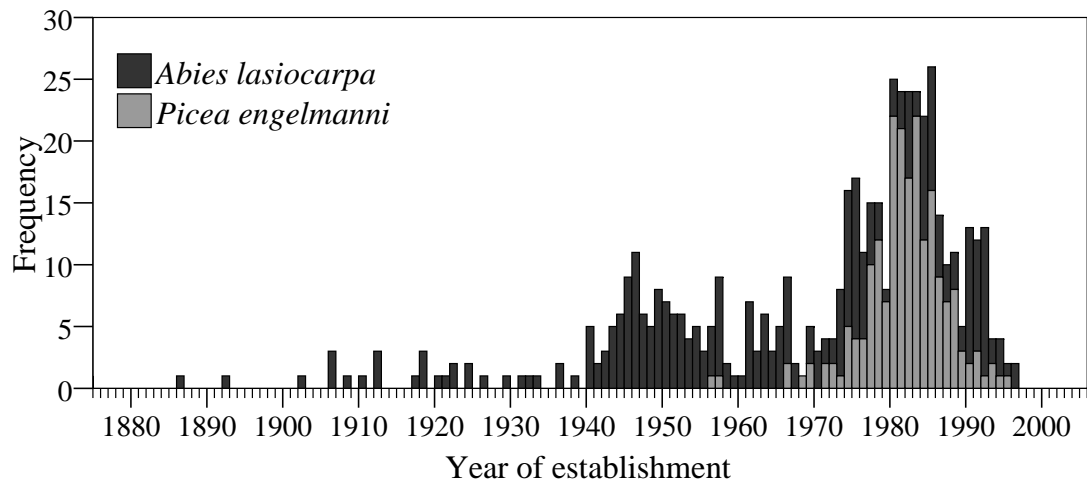


Figure 4.2: Frequency of age (1 year age class) for conifers <5cm dbh for all wet sites combined within 1120 1 m² plots.

sites with evidence of fire had adequate fire scars to sample (Avion and Windsor). Results did not show consistent historical fire dates because of the small number of fire scarred trees and difficulty in determining the exact year of the fire from increment cores. Scars were small indicating a presence of low intensity historical fires that occurred within these sites.

4.2 Changes in species composition

In total, 185 species across the 14 meadow sites were identified from the 1120 subplots; these represented 30 families (Table 3.2). Families with the greatest diversity of species included Poaceae (16), Asteraceae (13), and Cyperaceae (11). Based on nonmetric multidimensional scaling (NMS) ordination for species of wet sites, meadow species typically had lower scores for NMS1 and NMS3 (Figure 4.6). The meadow species, *Arnica diversifolia* and *Juncus parryi*, had the lowest scores on NMS 1. *Carex podocarpa* and *Carex phaeocephala* had the lowest scores for NMS 3. *Dodecatheon pulchellum*, *Juncus mertensianus*, and *Carex atosquama* had the lowest

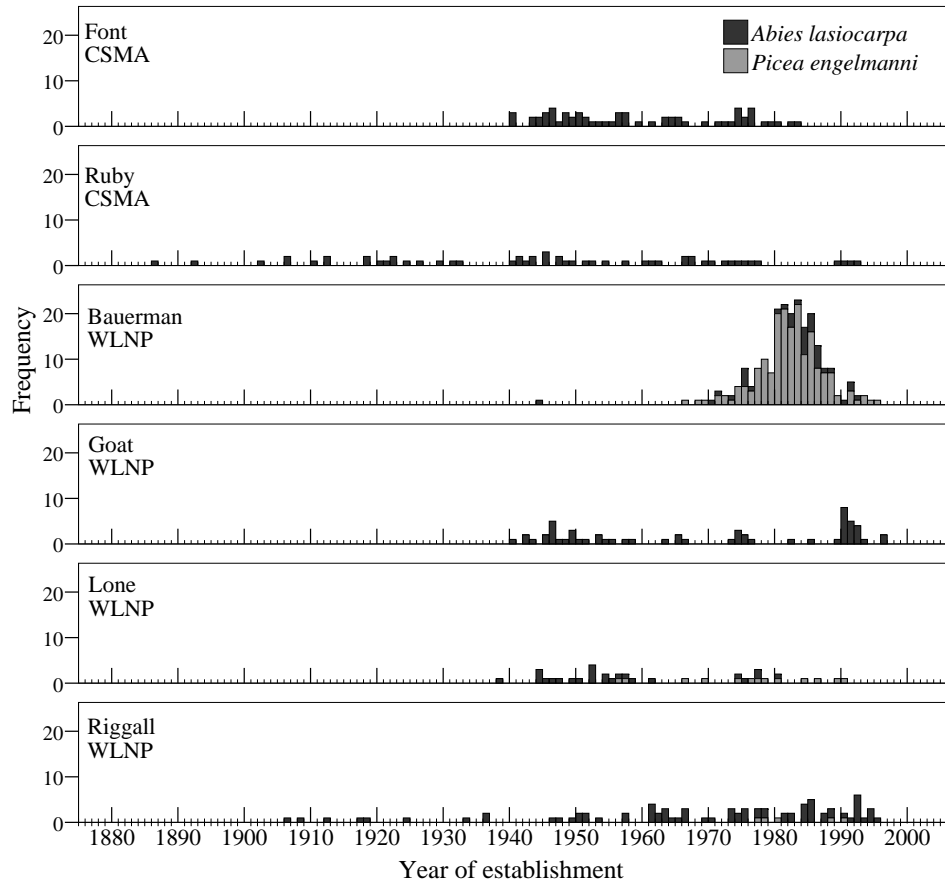


Figure 4.3: Frequency of age (1 year age class) for conifers <5cm dbh for all 6 wet sites within 1120 1 m² plots.

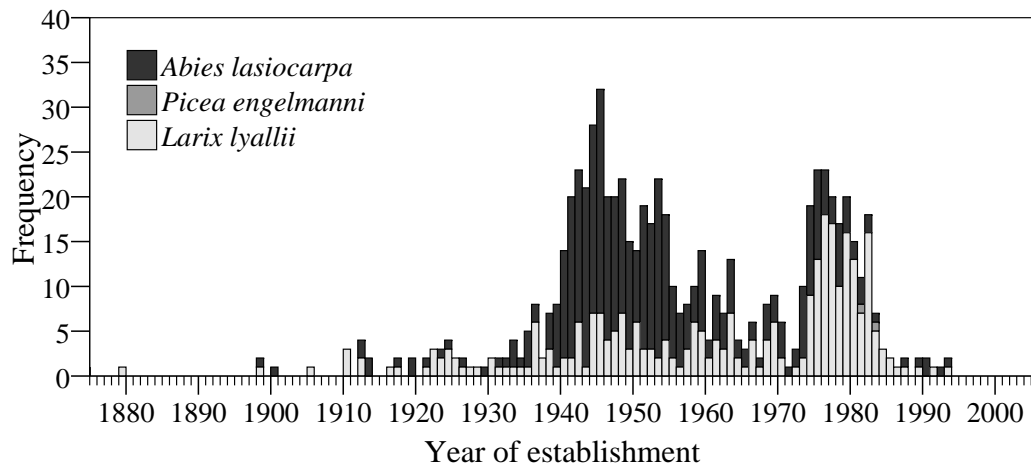


Figure 4.4: Frequency of age (1 year age class) for conifers <5cm dbh for all dry sites combined within 1120 1 m² plots.

combined scores for NMS1 and NMS3. Forest shrubs, *Vaccinium membranaceum* and *Vaccinium scoparium* scored the highest for NMS 3 and *Menziesia ferruginea* scored the highest for NMS1. *Arnica cordifolia* and *Orthilia secunda*, had the highest NMS1 scores for forest herbs. NMS ordination axes for plots show a gradual change for species composition from mature forest (Class 1; high scores on NMS 1) to open meadow (Class 6; low scores on NMS 1) for wet sites (Figure 4.7). NMS 2 ordination axes for plots did not correlate to forest structure. Age distribution across encroachment classes revealed a decline in age from forest to meadow (Figure 4.8).

NMS ordination axes for species of dry sites did not show a clear distinction between meadow and forest species (Figure 4.9). Forest species have a smaller sample size but meadow species appear to not have a distinct gradient. NMS 2 ordination axes for plots of dry sites revealed variation among sites but had a slight shift for species composition from mature forest (class 1; low scores for NMS1) to open meadow (class 6; high scores on NMS 1) (Figure 4.10). For NMS

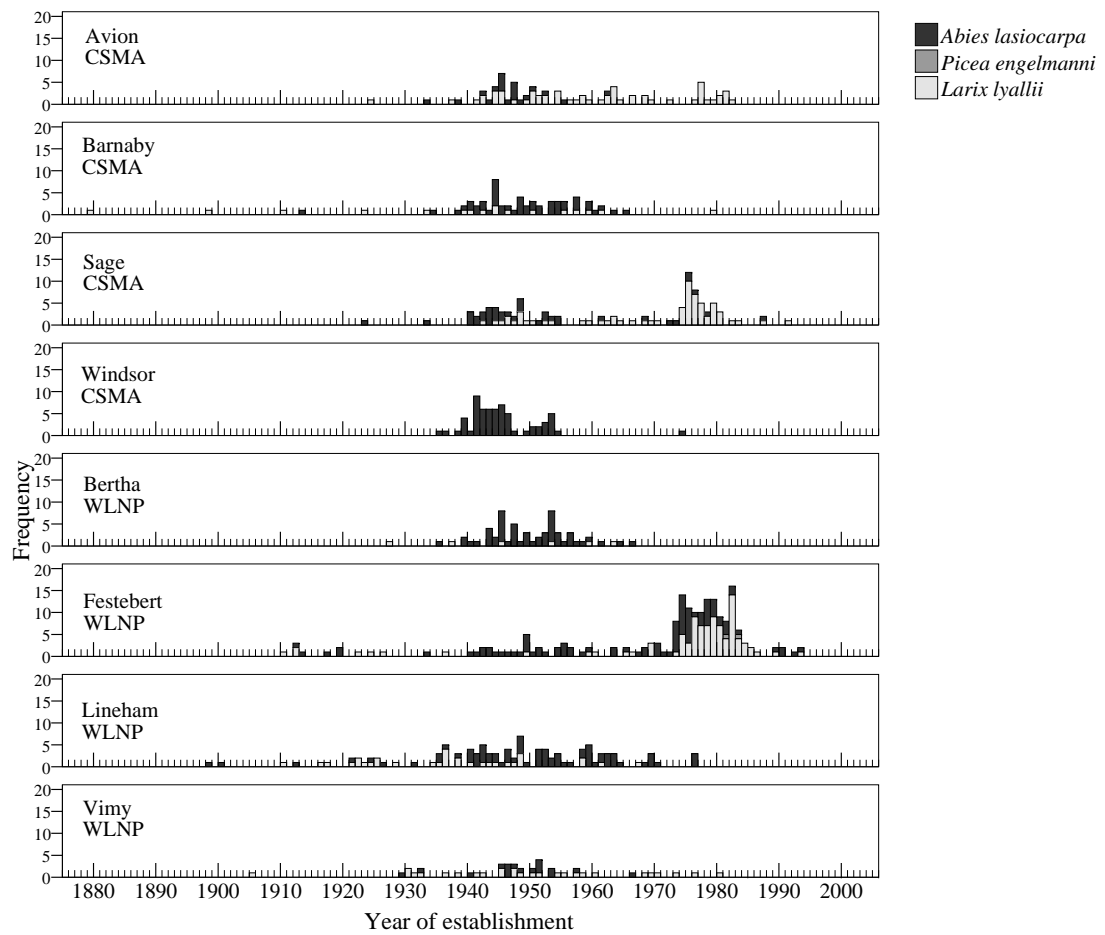


Figure 4.5: Frequency of age (1 year age class) for conifers <5cm dbh for all 8 dry sites within 1120 1 m² plots.

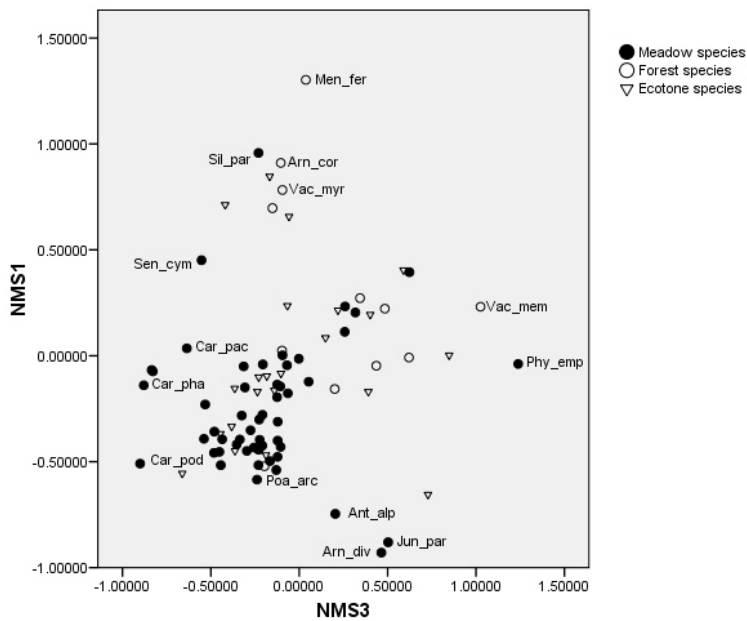


Figure 4.6: NMS 1 and 2 ordination axes of species for wet sites coded by functional type. Codes first three letters of genus and species) are shown for a subset of common species: *Antennaria alpina*, *Arnica cordifolia*, *Arnica diversifolia*, *Carex pachystachya*, *Carex phaeocephala*, *Carex podocarpa*, *Juncus parryi*, *Menziesia ferruginea*, *Poa arctica*, *Senecio cymbalarioides*, *Silene parryi*, *Vaccinium membranaceum*, and *Vaccinium myrtillus*.

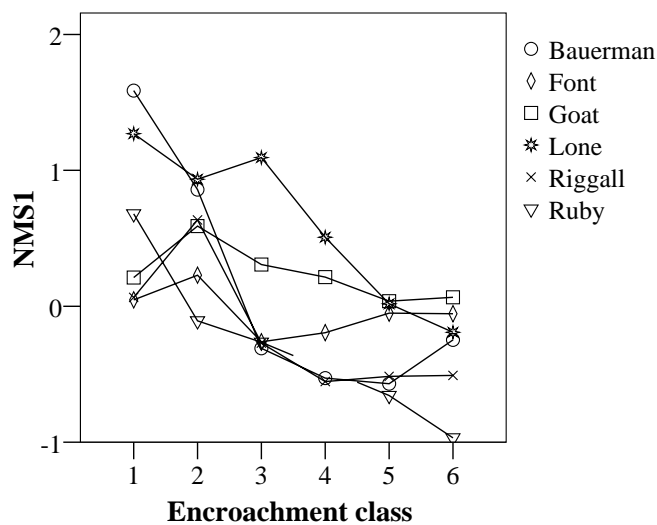


Figure 4.7: NMS 1 ordination axes of plots for wet sites across encroachment classes for each site (Bauerman, Font, Goat, Lone, Riggall and Ruby).

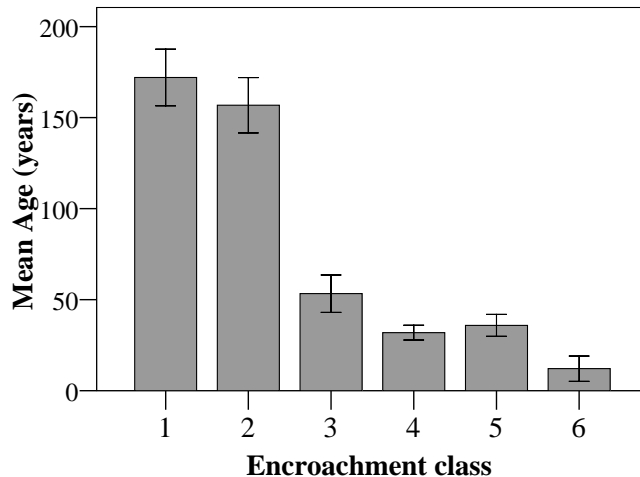


Figure 4.8: Mean tree age (+/- 1 SE) for wet sites across encroachment classes.

1 and 3 ordination axes for plots, which did not correlate to forest structure, the shift is opposite to NMS 2 where species composition from mature forest (class 1) has high NMS scores and open meadow (class 6) has low NMS scores. Age distribution across encroachment classes revealed a decline in age from forest to meadow (Figure 4.11).

4.2.1 Relationships between ground-layer vegetation, environmental variables, and forest structure

Stepwise regression models show a stronger influence of tree age on wet site than on dry site understory plants (Table 4.1). Tree age was significant in the models for NMS1 and NMS2 at wet sites ($R^2 = 0.77$ and 0.61 ; $p < 0.05$). Tree age in dry sites was only significant in the model for NMS 2 ($R^2 = 0.58$; $p < 0.05$).

NMS 1 axes for plots of wet sites was highly correlated to the maximum age of conifers ($r = 0.69$) and the mean age of conifers ($r = 0.69$) ($p < 0.01$) (Appendix 3). NMS 2 for wet sites was correlated with the maximum age of conifers ($r = -0.38$) and mean age of conifers ($r = -0.37$) ($p < 0.01$). NMS 3 was highly correlated with the maximum age of conifers ($r = 0.56$) and mean age of conifers ($r = 0.523$) ($p < 0.01$). Management

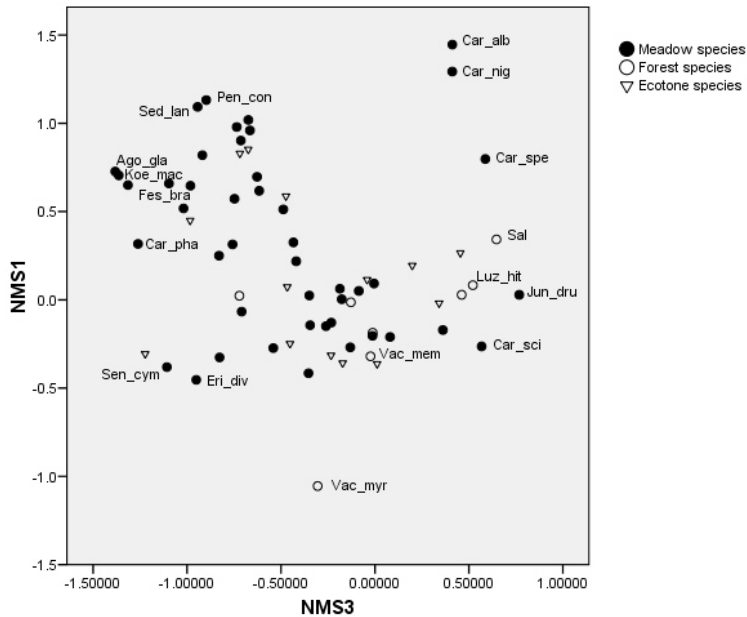


Figure 4.9: NMS 1 and 3 ordination axes of species for dry sites coded by functional type. Codes first three letters of genus and species) are shown for a subset of common species: *Agoseris glauca*, *Carex pachystachya*, *Carex albonigra*, *Carex nigricans*, *Carex scirpoidea*, *Carex spectabilis*, *Erigeron divergens*, *Festuca brachyphylla*, *Juncus drummondii*, *Koeleria macrantha*, *Luzula hitchcockii*, *Penstemon confertus*, *Salix* sp., *Sedum lanceolatum*, *Senecio cymbalarioides*, *Vaccinium membranaceum*, and *Vaccinium myrtillus*.

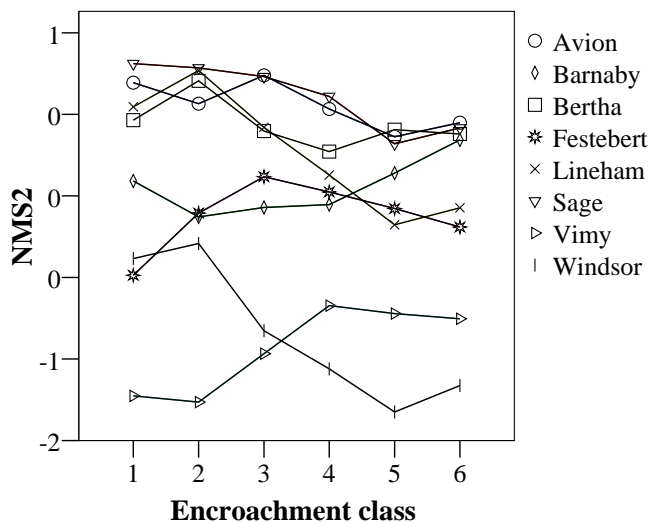


Figure 4.10: NMS 2 ordination axes of plots for dry sites across encroachment classes for each site (Avion, Barnaby, Bertha, Festebert, Lineham, Sage, Viny and Windsor).

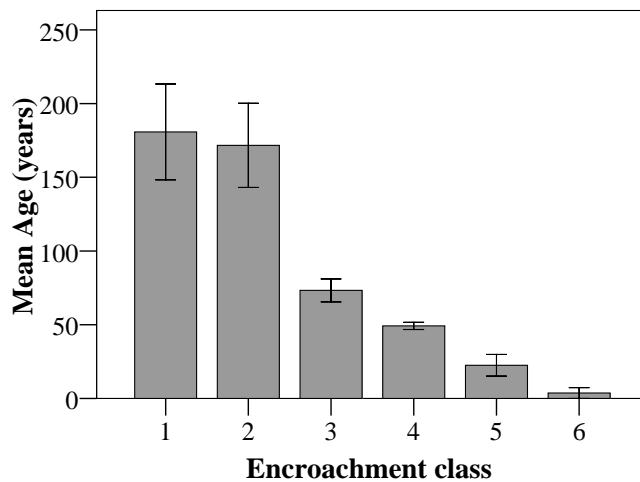


Figure 4.11: Mean tree age (+/- 1 SE) for dry sites across encroachment classes.

area was correlated to NMS 2 ($r=-0.377$) and NMS 3 ($r=0.551$) ($p<0.01$). Management area was also significantly correlated to aspect ($r=-0.43$), elevation ($r=0.55$) and slope ($r=0.56$) ($p<0.01$). All wet site NMS ordination axes showed no correlation to density of conifers. NMS 1 for dry sites was correlated with the maximum age of conifers ($r=-0.39$) and the mean age of conifers ($r=0.373$) ($p<0.01$). NMS 2 and NMS 3 did not show significant correlation to conifer age nor density. All dry site NMS ordination did not show significant correlation to fire or management area.

4.3 Changes in cover and richness of meadow and forest species

Meadow and forest species displayed contrasting trends in cover and richness (Figure 4.12, 4.13, 4.14 and 4.15) for both wet and dry meadows. Cover of meadow species changed gradually in response to increasing establishment of trees, and all growth forms of meadow plants decreased in abundance with the exception of sedges in wet meadows from class 5 to 6. Cover declined to percentages less than 10% for classes 1 and 2 for the forest plots. Richness of meadow species declined

Table 4.1: Stepwise multiple regression was used to explore the relationships between NMS ordination axes of species composition and forest structure and environmental variables. 50m² plots were used with a sample size of 63 for dry meadows and 49 for wet meadows. Potential predictors in these models were maximum and mean tree ages, density, distance along transect, soil depth (mean), slope, aspect, and elevation. Backward stepwise regression was used with a probability of 0.05 to add and 0.10 to remove variables. Regression analysis was conducted using SPSS 15.0 (2005).

Model (meadow type)	Adj R ²	Max age (years)	Mean age (years)	Density (stems/ha)	Distance (m)	Soil depth (cm)	Slope (degrees)	Aspect (degrees)	Elevation (m)
<i>Wet n=49</i>									
NMS1	0.769	0.005	-0.005	-0.094	-0.013			-1.111	0.003
<i>p</i>		(<0.001)	(0.03)	(0.036)	(0.011)			(<0.001)	(0.002)
NMS2	0.432				0.019	-0.026			-0.003
<i>p</i>					(<0.001)	(0.004)			(0.017)
NMS3	0.611		0.003		-0.013			0.57	-0.003
<i>p</i>			(0.027)		(0.016)			(0.009)	(0.013)
<i>Dry n=63</i>									
NMS1	0.47				0.022	-0.14		0.41	
<i>p</i>					(<0.001)	(<0.001)		(0.029)	
NMS2	0.577	0.001			0.013	0.01	0.017		0.01
<i>p</i>		(0.049)			(0.079)	(0.036)	(0.002)		(<0.001)
NMS3	0.633			-0.252		-0.016	0.007	-0.901	
<i>p</i>				(0.001)		(<0.001)	(0.032)	(<0.001)	

more slowly than did cover for both meadow types. A sharp decline in richness occurred in class 1 and 2 (forest plots) relative to other classes for wet and dry meadows. Cover of forest species decreased slowly across the encroachment classes, surpassing cover of meadow species in class 1 and 2 for both meadow types and also class 3 and 4 for dry meadows. In contrast, richness of forest species did not surpass that of meadow species in any of the classes. Increases along the gradient for cover and richness of forest species were primarily attributable to herbaceous taxa.

4.3.1 Individual species response across encroachment classes

Allium schoenoprasum, *Erigeron peregrinus*, *Phleum alpinum*, *Trollius albiflorus* and *Veronica wormskjoldii* decreased in cover and richness in class 1 and 2 for wet sites (Figure 4.16). For dry sites common meadow species did not show a consistent decline in cover and frequency (Figure 4.18). At dry sites *Carex pachystachya* and *Erigeron peregrinus* declined in cover and frequency from meadow to forest decreasing in class 3. Although, *C. pachystachya* increased in frequency in class 1 and *E. pere-*

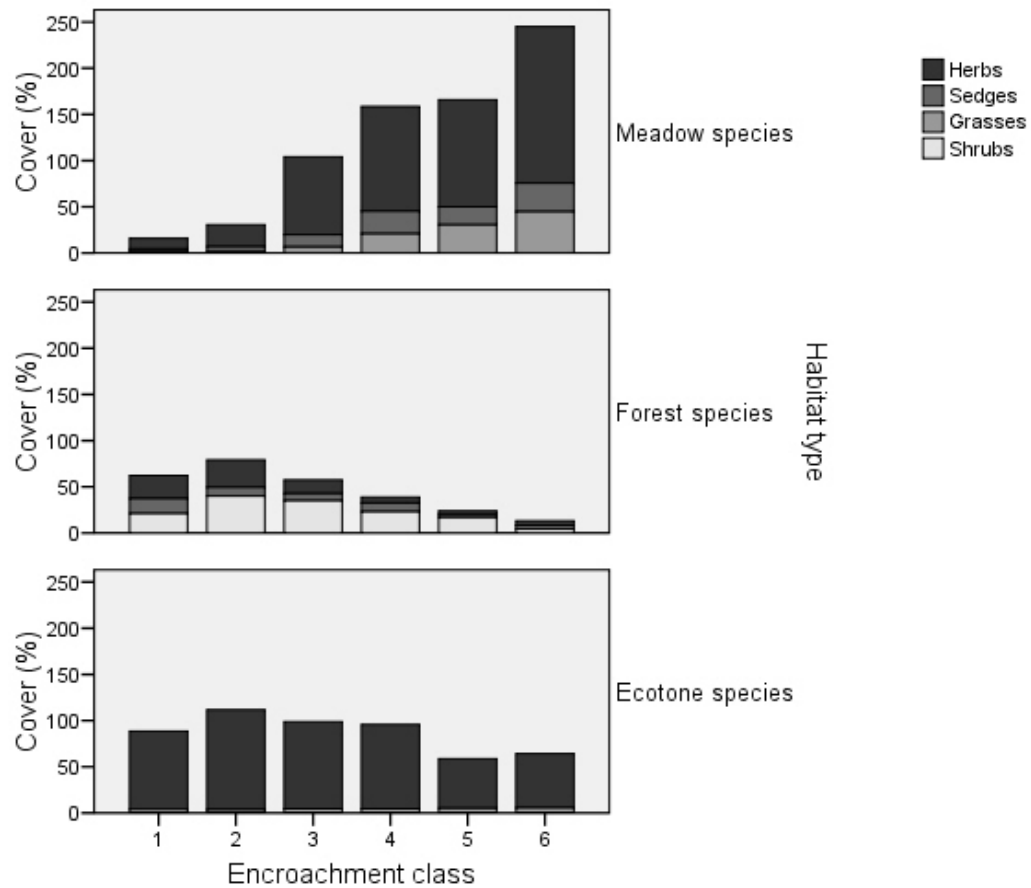


Figure 4.12: Changes in mean cover of wet meadow, forest and ecotone species by growth form among encroachment classes (1 = Forest, 6 = Meadow). From 0.1m²plots (n=490).

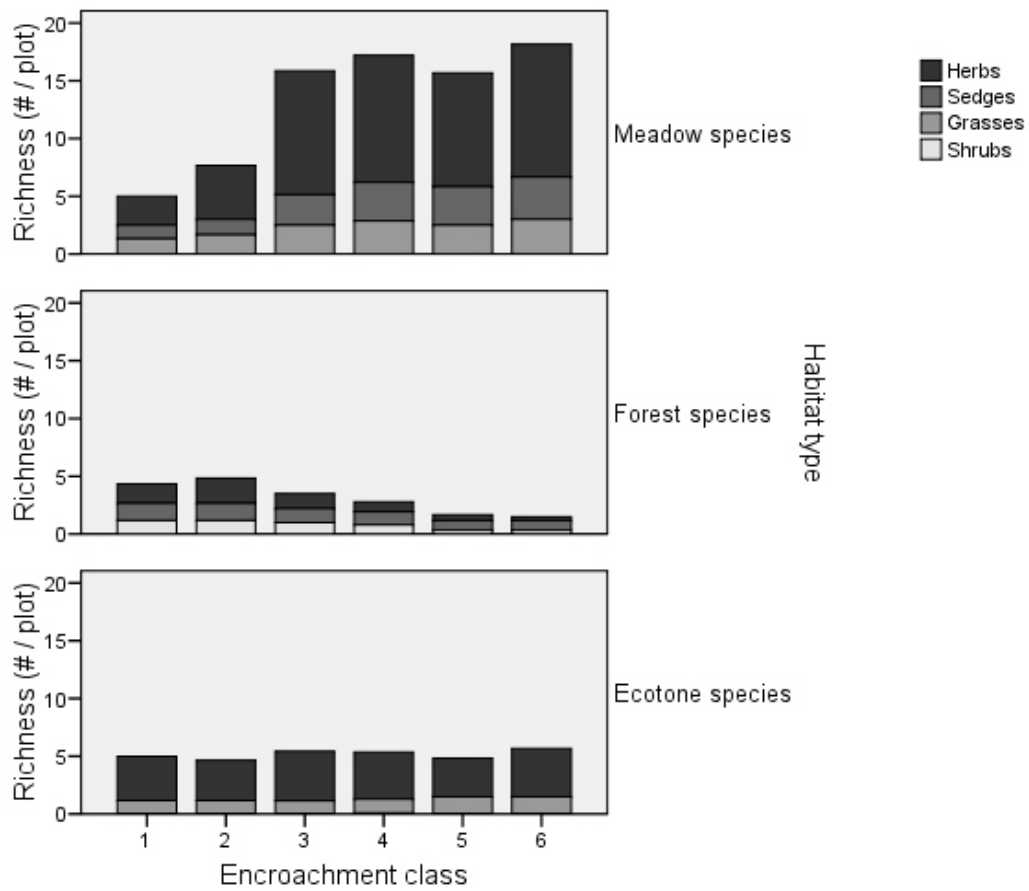


Figure 4.13: Changes in mean richness of wet meadow, forest and ecotone species by growth form among encroachment classes (1 = forest, 6 = meadow). From 0.1m²plots (n=490).

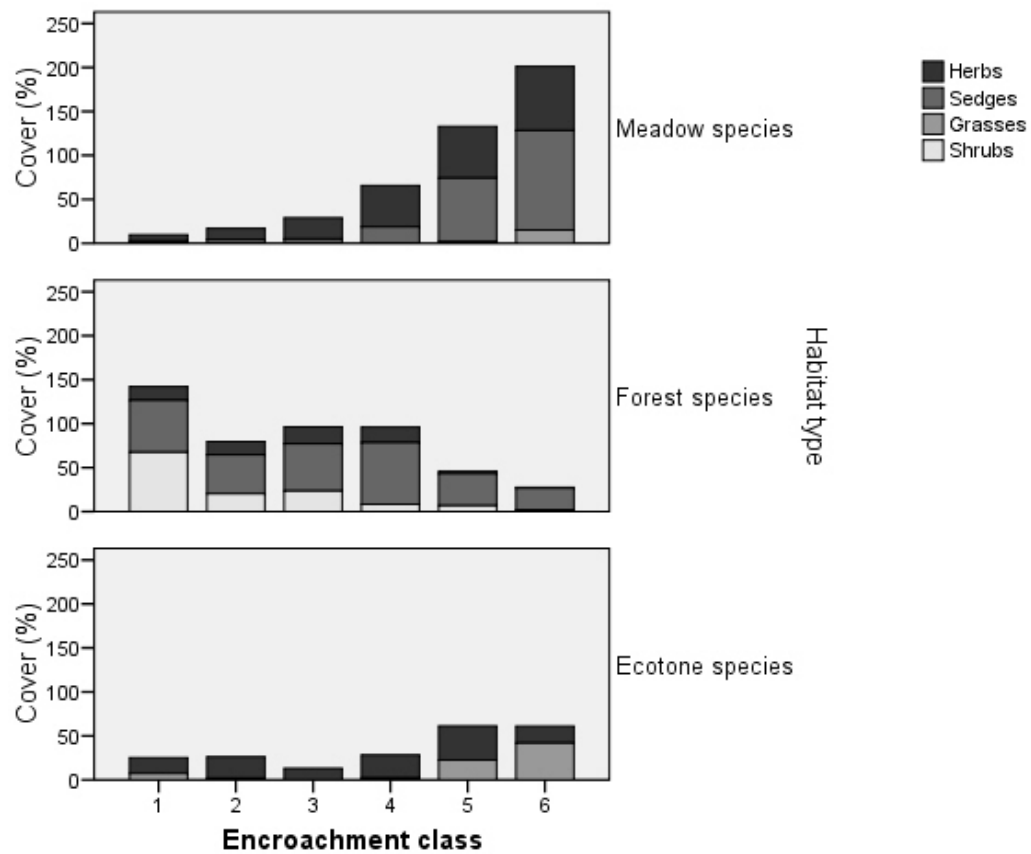


Figure 4.14: Changes in mean cover of dry meadow, forest and ecotone species by growth form among encroachment classes (1 = forest, 6 = meadow). From 0.1m²plots (n=630).

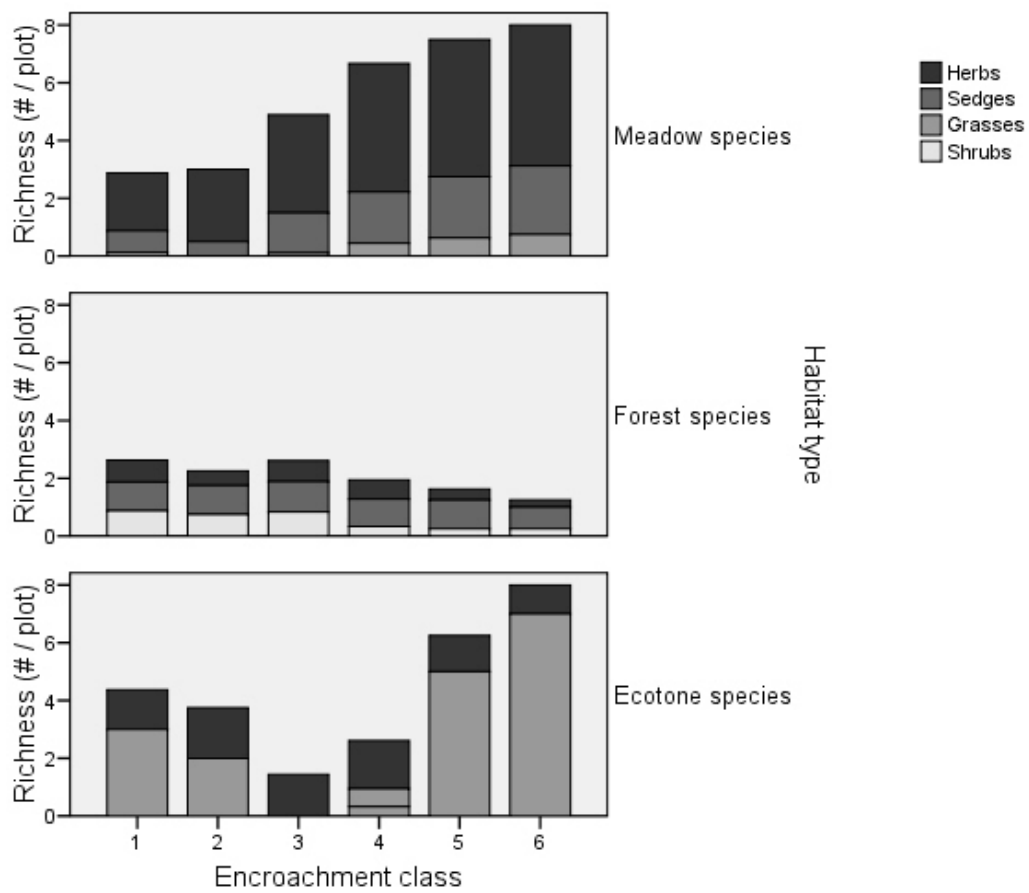


Figure 4.15: Changes in mean richness of dry meadow, forest and ecotone species by growth form among encroachment classes (1=forest, 6=meadow). From 0.1m²plots (n=630).

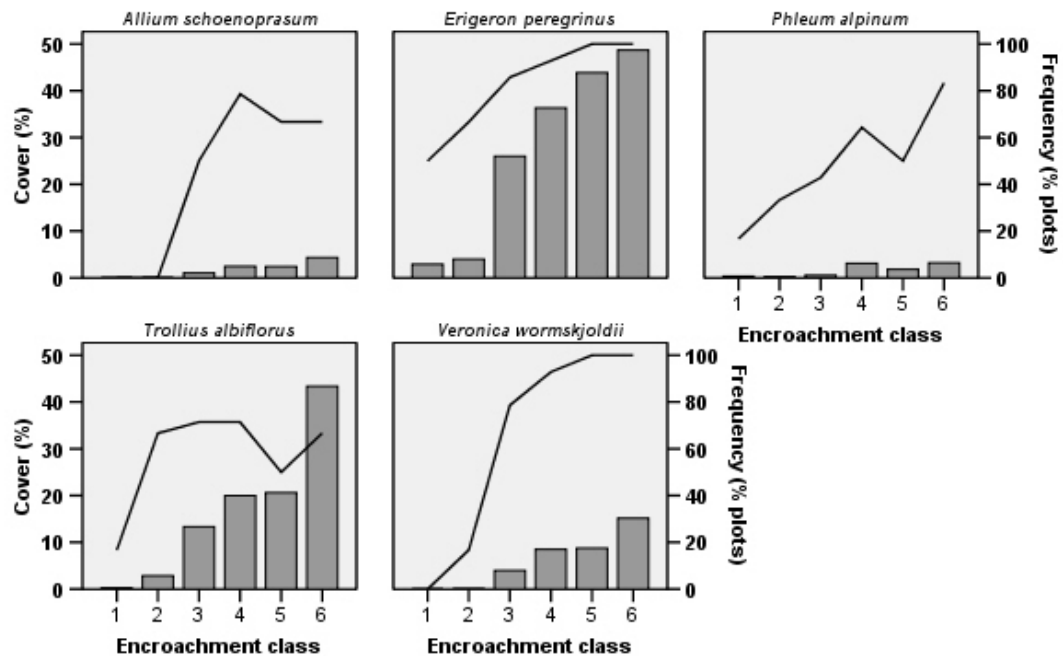


Figure 4.16: Changes in mean cover (bar) and frequency (line) for common wet meadow species (top 5 species present across plots) among encroachment classes (1 = Forest, 6 = Meadow).

grinus decreased in cover in class 6 and the frequency decreased from class 4 to 5. *Epilobium anagallidifolium* and *Veronica wormskjoldii* were highly variable in richness and cover, however, there was an overall decrease from open meadow to mature forest.

Common forest species of wet sites, *Arnica cordifolia*, *Mitella breweri*, *Vaccinium scoparium* decreased in richness steeply where as *Luzula hitchcockii* remained consistent after class 1 and *Viola orbiculata* fluctuated (Figure 4.17). At dry sites *Mitella breweri* and *Vaccinium membranaceum* decreased in both cover and richness from class 1 to class 4 and did not occur in classes 5 and 6 (Figure 4.19). *Arnica cordifolia*,

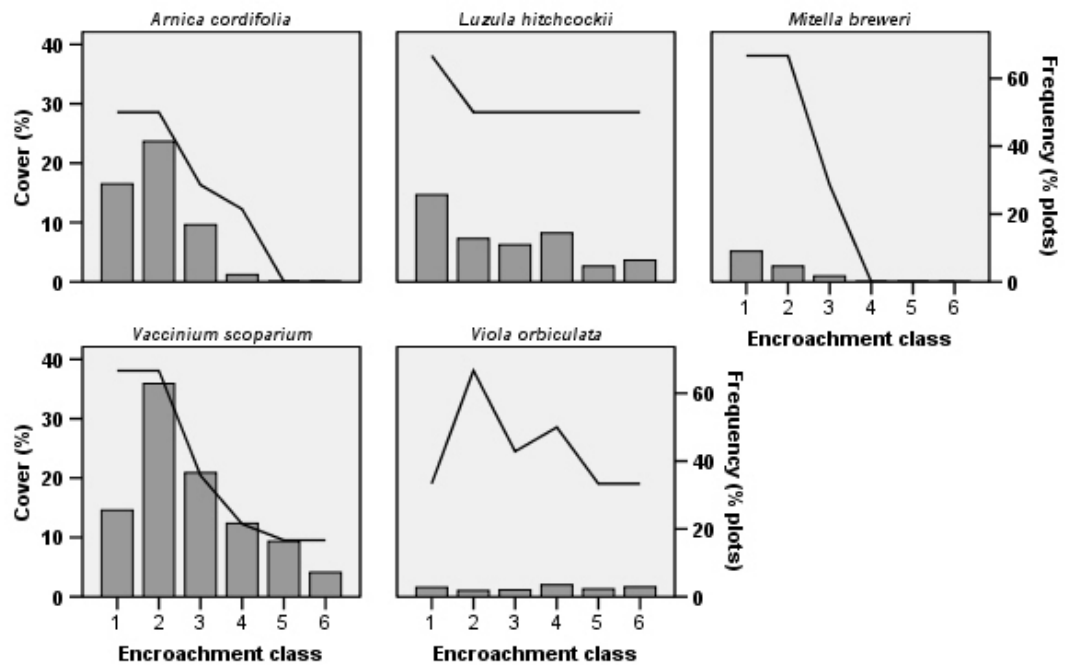


Figure 4.17: Changes in mean cover (bar) and frequency (line) for common wet forest species (top 5 species present across plots) among encroachment classes (1 = Forest, 6 = Meadow).

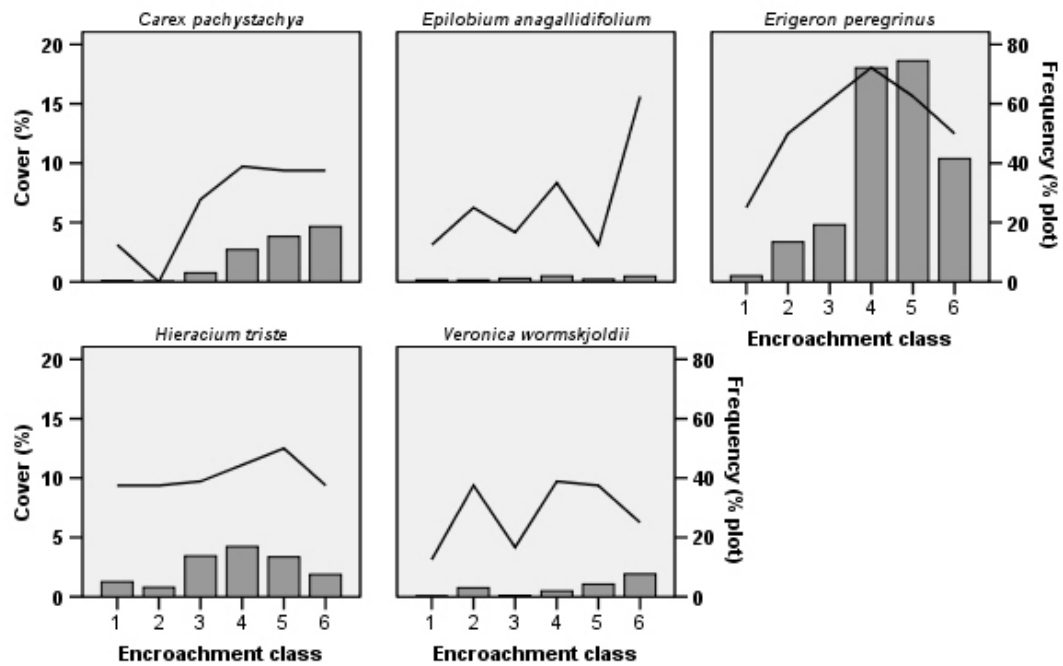


Figure 4.18: Changes in mean cover (bar) and frequency (line) for common dry meadow species (top 5 species present across plots) among encroachment classes (1 = Forest, 6 = Meadow)

Luzula hitchcocki and *Vaccinium scoparium* were variable in richness and cover from class 1 to 4 but declined in classes 5 and 6.

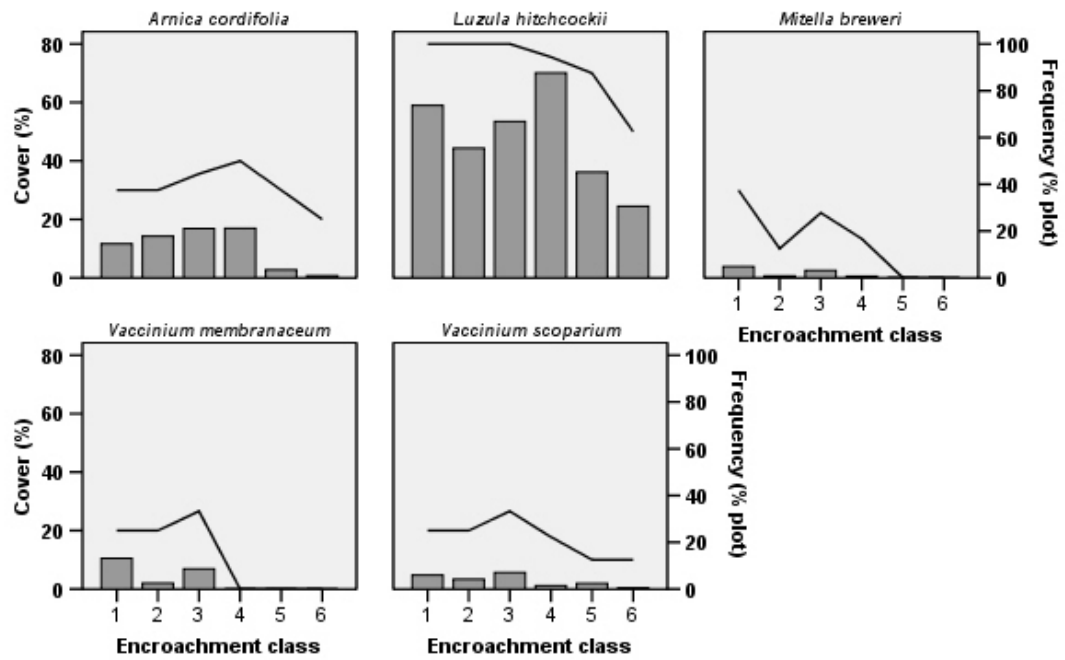


Figure 4.19: Changes in mean cover (bar) and frequency (line) for common dry forest species (top 5 species present across plots) among encroachment classes (1 = Forest, 6 = Meadow)

Chapter 5

Discussion

5.1 Effects of temperature and precipitation on tree establishment

Mean annual temperature has risen approximately 0.6 °C over the last century, with two periods of accelerated warming, from 1920 to 1945 and from 1976 to the present, and two temperature peaks in 1941 and 1987 (IPCC 2001). Tree-ring reconstructions suggest that summer and spring temperatures during these periods, particularly throughout the 1990s, were higher than in any equivalent period over the past (Luckman 1990, 1998, Watson and Luckman 2001). This long-term trend represents a significant departure from past conditions (Mann and Hughes 1999, Esper and Schweingruber 2002) and poses considerable challenges to assessing ecosystem changes in the 21st century (Millar et al. 2004). The temperature peak in 1941 coincides with a pulse in conifer establishment for *A. lasiocarpa* in both wet and dry sites. Accelerated warming after 1976 coincided with establishment of *L. Lyallii* and *P. engelmannii* and, to a lesser extent, *A. lasiocarpa*.

Wet intervals derived from tree ring analysis occurred approximately in the periods of 1585-1610, 1660-1680, 1870-1885, and 1895-1910, with higher precipitation levels occurring in the latter half of the twentieth century (Watson and Luckman

2001). Tree ring analysis east of the continental divide showed peak precipitation in the late 1940s and through the 1950s (Luckman 1998). This may explain why *A. lasiocarpa* had the highest frequency of establishment at dry sites in the early 1940s during a warming climatic event and a peak in precipitation. High precipitation during the growing season often promotes tree establishment on xeric sites (Taylor 1995, Woodward et al. 1995, Jakubos and Romme 1993); on the other hand, high precipitation has been found to limit tree establishment on mesic sites (Taylor 1995, Woodward et al. 1995).

Positive phase Pacific decadal oscillation (PDO) brings generally warmer and wetter conditions, while negative phase PDO bring drier and cooler weather. Positive departures of PDO indices in the last century occurred in the periods from 1920 to 1945 and from 1976 to 1998 (Wolter 2000), which generally coincides with all three conifer species establishment histories. An exception is *P. Engelmannii*, in that its establishment history does not coincide with the 1920 to 1945 time period. It is possible that *P. engelmannii* is responding to site-specific influences, as 90% of establishment occurred at one site (Bauerman). A strong negative phase occurred from 1946 to 1975, and a weak negative phase occurred prior to 1920; those periods coincided with a decrease in establishment for all conifer species. Statistical analysis was not conducted to show significant relationships between conifer establishment and temperature, precipitation or PDO indices. However, qualitative inference can help explain episodic ecological responses of conifer encroachment.

It is difficult to predict tree establishment based on climatic trends. Warming temperature trends on a global scale may not translate to the same effects on a regional, landscape or even microsite scale. The variation in establishment among site suggests that there are multiple drivers contributing to successful seedling growth besides climate.

5.2 Decline of meadow species

Conifer encroachment in meadows has led to a loss of landscape diversity, plant diversity and a decline in ecological integrity. Wet sites clearly respond to conifer encroachment with decreases in meadow species abundance, richness and diversity. Dry meadows also respond to conifer encroachment in all those ways, but not as strongly. In both meadow types, meadow species are sensitive to conifer encroachment. The species composition changes and the richness, abundance and diversity of meadow vegetation declines as the forest encroaches into open meadows.

Species composition showed significant changes from meadow to forest. NMS ordinations for wet sites showed three major gradients capturing most of the variance in the plant communities. NMS ordinations showed that the first three dimensions explained 70% of the variation in the species composition data and multiple regression models showed that forest structure (maximum tree age, mean tree age and tree density) significantly influenced 49% of the variation for two gradients. At dry sites, three major gradients captured most of the variance (70%) in the plant communities; two gradients were significantly influenced by forest structure (maximum tree age and tree density). Understory plants are influenced not only by forest structure, but also by environmental variables (distance, soil depth, slope, aspect, elevation). Environmental variables showed significance in all six multiple regressions. Gradients are therefore defined by more than one predictor. Residual variation may also be explained by environmental variables that were not measured, such as light availability and soil resources.

Although management area had significance in the multiple regression model for wet meadows, it was also highly correlated with four of the five environmental variables. This suggests high collinearity, which could produce a false response in

the multiple regression model and was therefore removed from the model. The collinearity could be the result of the coincidence that the Castle Special Management Area (CSMA) sites tended to be at higher elevations and of a different aspect than Waterton Lakes National Park (WLNP) sites. Forest structure information was not correlated to management area; the lack of correlation suggests that tree encroachment is occurring across the landscape, despite the protected and unprotected area designations.

Meadow species at wet sites declined in encroachment class 3 where trees were on average 54-72 years of age. In class 1 and 2, where meadow species declined even more, 95% of trees were greater than 120 years of age. Most meadow species showed greatest abundance in classes 5 and 6. As Classes 5 and 6 were both open meadow classes (no conifers), variation between these classes could reflect variation in site-specific conditions. Even with variation, a decline in abundance and richness occurred across the meadow to forest transition. Extirpation of meadow taxa in the mature forest (Class 1 and 2) occurred in 43 out of 55 species for wet sites, and 27 out of 45 species for dry sites. Species that were not extirpated showed declines in cover and richness even though they persisted in the forest understory. Dry sites showed greater fluctuation in the decline of meadow species across the meadow forest transition. Despite variability among individual species, overall richness and cover declined from open meadow to mature forest and was initiated in class 3 where trees were on average 77-113 years of age. The persistence of these open-habitat species may reflect the patchy nature of forest development at dry sites, leaving small patches of meadow within larger blocks of forests (Huago2007). Some meadow taxa (e.g. *Hieracium triste*) that had relatively stable presence across the transition could more accurately be categorized as ecotonal species.

5.3 Colonization by forest species

Forest species richness and cover for both wet and dry sites declined gradually from forest to open meadow encroachment classes, and occurred synchronously with loss of meadow vegetation. Within 70-90 years, forest species dominated the understory vegetation. Common forest species at wet site, *Arnica cordifolia*, *Mitella breweri*, *Vaccinium scoparium* decreased in richness steeply from forest into meadow where as *Luzula hitchcockii* remained consistent after class 1 and *Viola orbiculata* fluctuated from class 1 to 6. Common dry site forest species did not show a consistent decrease in richness or in cover from class 1 to 4 but did show a decline in classes 5 and 6. As dry sites contain open mature forest, there is greater light availability. Light availability is strongly reduced in the presence of woody plants (Scholes and Archer 1997, Lett and Knapp 2003, Siemann and Rogers 2003). Haugo and Halpern (2007) found that light was a significant predictor in the decline of meadow species. This may explain why dry sites do not respond as strongly to conifer encroachment as do wet sites, which contain closed canopy forest. The strong relationship between subalpine meadow species and forest structure may be indicative of changes in below ground resources and environment. Griffiths et al. (2005) found that litter depth, soil moisture, nitrogen availability, microbial activity, and the presence of ectomycorrhizal mats associated with tree roots had strong gradients from open meadow to old forest in a dry montane meadow in the Pacific Northwest.

Autogenic factors of trees can reduce inhibitory effects of ground-layer communities in subalpine meadows (Magee and Antos 1992). Established trees provide conducive physical conditions for seedlings where once the physical conditions of the meadow had inhibited their establishment (Bekker 2005). This positive feedback can lead to increased tree establishment and dominance of forest under-

story vegetation. Tree establishment often occurs in the forest-meadow ecotone, partially because of the forest influence reduces dense, grass dominated vegetation that inhibits seedling establishment and growth (Billings and Mark 1957, Dunwidie 1977, Vale 1981, Magee and Antos 1992). Declines in meadow species may be driven by these changes in litter or soil properties (Belsky et al. 1989, Facelli and Pickett 1991) or by competition for resources with the newly established trees and forest understory plants (Callaway et al. 1991).

5.4 Implications for conservation and ecological restoration

If we value diversity, landscape connectivity, resilience of the landscape and our connection with special places, or if we believe that these are integral parts to ecosystem health and survival of species, then we need to consider intervention in subalpine meadows. I began this research to assess the need for intervention such as ecological restoration in subalpine meadows. Conducting the research I came to appreciate the complexity of ecosystem dynamics in wet and dry meadows and the variation that occurs across the landscape. Based on my research and despite complications for traditional ideas of restoration arising from rapid climate change, I believe that ecological restoration is an appropriate intervention to ensure the survival of subalpine meadows.

Subalpine meadows are currently degraded and without intervention will become damaged or even destroyed. Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER International Science and Policy Working Group 2004) and therefore is a solution to ensure the long-term survival of meadows. It is necessary to restore the function (processes), integrity (species composition and community structure) and sustainability (resistance to unnatural disturbance, and resilience) (Parks Canada 2007) which are all important components for the ecological restoration of subalpine

meadows.

Changing grazing regimes for cattle, changes in human use, lack of fire, and climate change have all played a role in trees establishing and subsequently surviving in meadows more frequently this past century than the three centuries before. The tree establishment and survival before the 1900s is likely indicative of conditions for several centuries earlier, where meadows were maintained. The impacts on the landscape are linked to our past management decisions and values. The consequences from our past decisions coupled with rapid environmental change makes it appropriate to consider historical references in future management decisions. We need to take our hand that has altered the landscape and guide the subalpine meadows gently on an historic trajectory that will aid in the sustainability of these communities. Even under conditions of rapid climate change the search for historical understanding of these meadows remains important knowledge for management.

The present climate model projections suggest that hotter springs and summers will occur in the Rocky Mountains over the next few decades (IPCC 2001). With increased temperatures, snow is melting earlier and the dry season is lasting longer (National Assessment Synthesis Team 2000, Houghton et al. 2001), allowing for conditions conducive to tree establishment and survival. The Intergovernmental Panel on Climate Change's consensus range of 1.5°C to 5.8°C projected global surface temperature warming by the end of the 21st century is considerably larger than the warming over the last century of approximately 0.6°C (IPCC 2001). It is likely that encroachment will continue or accelerate under likely future climate regimes. Compounding the need for restoration of the landscape and subalpine meadow communities is the transformation of soil properties; as seedlings become established within subalpine meadows, and remain over a certain period of time, they can transform soil properties and thereby inhibiting meadow recovery

(Griffiths et al. 2005, Griffiths 2009). The timing of restoration is crucial, too: as trees aged 54-72 years for wet sites and trees aged 77-112 years for dry show inhibitory effects on meadow vegetation. Haugo and Halpern (2007) suggest that an effective strategy for the conservation and restoration of these systems is to remove or kill trees early before positive feedbacks lead to a potentially irreversible change in community state. Long term investment in ecological restoration of subalpine meadows is needed; with fire exclusion and suppression, climate change, and shifts in human use, positive feedbacks created by trees can favour persistence and further expansion of forest. These complexities, however, do not lessen the value of history; rather they emphasize the need for evaluating both cultural and natural causes of variability as well as characterizing the overall dynamical properties of ecosystems (Swetnam et al. 1999).

5.4.1 Ecological restoration of subalpine meadows

A component of ecological restoration planning is the collection of preliminary information to assess ecosystem condition and define the restoration problem (Parks Canada 2007). In the present research I have assessed the conditions and defined the restoration problem. Beyond this research is the development of a detailed restoration plan that includes further comprehensive research, defines the objectives, targets and scope of the restoration, selects specific restoration prescriptions, implements detailed restoration plans, and monitors for effectiveness (Parks Canada 2007).

Comprehensive research that will aid in restoration planning will need to meet the objectives that are defined through collaboration with regional stakeholders, managers, communities and First Nations. Now that we know that tree encroachment is occurring across the landscape, a detailed landscape inventory of subalpine meadows will aid in prioritizing meadows for restoration. Once an inventory is complete and meadows are prioritized a meadow species inventory at each

site will provide a baseline for potential restoration prescriptions. Further research can also include discerning the specific causes of tree establishment, for example a dendroclimatology study.

Once objectives, targets and the scope of the restoration plan are addressed specific restoration prescriptions need to be considered. A detailed restoration prescription needs to take into account that ecological restoration of wet and dry sites will likely differ and that each meadow restoration could vary because of site characteristics. Through my research fire has been identified as a potential restoration tool. Fire is a process that can maintain meadows through removal of trees and is a natural disturbance in dry subalpine meadows.

The maximum tree age ranged from 218 - 384 years old, suggesting that high intensity stand replacing fires have not occurred for at least two centuries within high elevation meadow sites. However, in the case of two dry sites (Vimy and Windsor), high intensity fires reached very close to these meadows but the adjacent trees surrounding the meadow did not burn, as observed in repeat photographs (Appendix 4). This suggests that meadows can act as fire breaks against high intensity stand replacing fires.

Historically, low intensity fires in subalpine meadows were ignited by lightning strikes, and could have been isolated to small areas because of poor fuel load. It is also thought that some subalpine meadows in the Pacific Northwest Mountains were caused and maintained by fire (Magee and Antos 1992, Woodward et al. 1995, Miller and Halpern 1998, Norman and Taylor 2005). Fires may be less common in higher elevation sites when compared to valley bottoms, but tree seedlings may be suppressed by infrequent and low intensity fires that are sufficient to maintain meadows. Since meadow species occur beneath the open canopy of advancing forests, fire can remove the overstory trees along the forest edge, thereby allowing meadow expansion (Magee and Antos 1992). The small

size and remote locations of lightning ignited fires near subalpine meadows may occur on such a small scale that they are not documented in historical records, and yet they are crucial for maintenance of meadows.

Caution should be taken when attempting to restore meadows with prescribed burning: there can be many consequences. Most meadow species do not maintain viable seeds in the soil, precluding the potential for restoration from a seed bank (Lang and Halpern 2007). Seed banks in both meadow and forest soils are likely to be dominated by early successional species that could outcompete meadow vegetation. Therefore, prescribed burning in dry subalpine meadows would need to occur in a small proportion of the total area of the meadow to ensure that adjacent meadow vegetation can repopulate the burned area from seed sources. Restoring meadows with fire may also expose and heat mineral soil, providing ideal sites for conifer establishment, and thus limiting the reestablishment of meadow species. During restoration it is important to reduce disturbance of mineral soils as this may facilitate development of invasive species. Some attempts to restore meadows have had little success using fire (Laycock 1991, Heisler et al. 2004).

Ecological restoration with fire may not be appropriate for wet subalpine meadows: fire was an unlikely disturbance. It is more probably the case that wet meadows have been maintained by high moisture levels through snowmelt and the retention of precipitation throughout the growing season. Fire does occur in wet meadows, but with less frequency than is found in dry meadows. With many consequences to using fire to restore subalpine meadows and fire being an unlikely prescription for wet sites, it may be necessary to remove trees manually to ensure the survival of this habitat. Manual removal of smaller trees along the ecotone can help to restore the integrity (species composition and structure) of these communities. Manually removing trees using large vegetation shears or similar devices will be less costly than site specific fire prescriptions and can reduce soil distur-

bance. However, manually removing trees does not restore processes such as fire and moisture regimes.

Wet meadows are a priority for restoration as vegetation in these ecosystems shows greater inhibitory effects from tree establishment than dry meadows. Smaller meadows have priority for restoration as they are more likely to be fully encroached. Experimental plots with controls and treatments will help to discern the most effective restoration strategies, minimizing consequences of chosen restoration prescriptions and discerning if meadow species are able to recolonize the restored area. Removing trees less than 54 years of age in wet meadows and 77 years in dry will help ensure that meadow vegetation can reestablish.

Meadows that are not an immediate priority for restoration can be monitored for encroachment of trees through using repeat photography (see Appendix 4 for repeat photographic pairs of the 14 subalpine meadows studied) and assessing tree ages using branch whorl counts (see Appendix 1 for age/branch whorl regression models for *Abies lasiocarpa* and *Picea engelmannii*). Repeating photographs can provide a landscape interpretation for tree encroachment and identify sites for further investigation. A relatively quick assessment of age, using branch whorl counts, will provide the rate of tree encroachment and is an effective and efficient monitoring method for *Abies lasiocarpa* and *Picea engelmannii*.

In the WLNP Park Management Plan (2000) park wide objectives included: 1) to maintain biological diversity at broad landscape and community scales, including ecological processes; 2) to maintain and restore viable populations of native species, including the genetic diversity within species; 3) to protect, maintain or restore rare, vulnerable, threatened or endangered genetic resources, species and biotic communities; and 4) to ensure that natural disturbances (e.g., wind, flood, avalanches, grazing) and their effects function unhindered. All of these objectives and values support ecological restoration of subalpine meadows, and follow

the principles of effective, efficient, and engaging restoration (Parks 2007). The challenges faced by managers in the Castle Special Management Area are understandably shaped by different land use patterns and priorities, but the core commitment to ecological integrity is held in common. A clear focus on restoration of subalpine meadows on a landscape level will aid in conserving ecosystem connectivity by providing migration corridors, conserving sources of propagules and colonists, conserving refugia for sedentary species, and increasing opportunities for adaptation of ecosystems to large-scale disturbances such as climate change.

References Cited

- Achuff, P. 1992. Natural regions and sub regions of Alberta. A revised classification for protected areas management. Technical report, Waterton Park, AB.
- Alberta Energy and Natural Resources. 1985. Castle River sub-regional integrated resource plan. Technical report, Alberta Government, Edmonton, AB.
- Barrett, S. 1996. The historic role of fire in Waterton Lakes National Park, Alberta. Final Report Contract No. KWL 30004, Parks Canada, Waterton Park, AB.
- Barrett, S. and S. Arno. 1999. Indian fires in the northern Rockies: ethnohistory and ecology. In R. Boyd, editor, *Indians, Fire and the Land in the Pacific Northwest*, pages 50–64. Oregon State University Press, Corvallis, OR.
- Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, **37**:97–107.
- Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwangi. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid Savanna in Kenya. *The Journal of Applied Ecology*, **26**:1005–1024.
- Billings, W. and A. Mark. 1957. Factors involved in the persistence of montane tree-less balds. *Ecology*, **38**:140–142.

- Boyd, R. 1999. Indians, fire and the Pacific Northwest. Oregon State University Press, Corvallis, OR.
- Brown, D. 1941. Vegetation of Roan Mountain: A phytosociological and succession study. *Ecological Monographs*, **11**:62–97.
- Brown, J. 1995. *Macroecology*. University of Chicago Press, Chicago, IL.
- Burton, D. 2003. Reintroduction of plains Bison to Waterton Lakes National Park: considerations for a feasibility analysis. Technical report, Waterton Park, AB.
- Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus Douglasii* on understory productivity in central California. *Ecology*, **72**:1484–1499.
- Daniels, L. D. and T. T. Veblen. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science*, **14**:733–742.
- Daniels, L. D. and T. T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, **85**:1284–1296.
- Dunwiddie, P. W. 1977. Recent tree invasion of subalpine meadows in Wind River Mountains, Wyoming. *Arctic and Alpine Research*, **9**:393–399.
- Egan, D. and E. Howell, editors. 2001. *The historical ecology handbook: a restoration guide to reference ecosystems*. Island Press, Washington, D.C.
- Esper, C. E. R., J. and F. H. Schweingruber. 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science*, **295**:2250–2253.
- Facelli, J. M. and S. T. A. Pickett. 1991. Indirect effects of litter on woody seedlings subject to herb competition. *Oikos*, **62**:129–138.

- Flathead Transboundary Network. 1999. State of the crown of the continent ecosystem: Flathead/Castle Transboundary Bioregion. Technical report, Miistakis Institute for the Rockies, Calgary, AB.
- Griffiths, R., M. Madritch, and A. Swanson. 2005. Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management*, **208**:347–358.
- Griffiths, R. P. 2009. The effects of topography on forest soil characteristics in the Oregon Cascade Mountains (USA): implications for the effects of climate change on soil properties. *Forest ecology and management*, **257**:1.
- Gruell, G. 1983. Indian fires in the interior west: a widespread influence. In *Wilderness Fire Symposium*, Nov. 15-18, pages 68–74. Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Missoula, MT.
- Hadley, K. S. 1999. Forest history and meadow invasion at the Rigdon Meadows Archaeological site, western Cascades, Oregon. *Physical Geography*, **20**:116–133.
- Hamer, D., S. Herrero, and K. Brady. 1991. Food and habitat used by Grizzly Bears, *Ursus arctos*, along the Continental Divide in Waterton-Lakes-National-Park, Alberta. *Canadian Field-Naturalist*, **105**:325–329.
- Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. *Restoration Ecology*, **14**:170–176.
- Hart, J. 1972. Native plants and early peoples. Montana Historical Society, Helena, MT.

- Haugo, R. D. and C. B. Halpern. 2007. Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Canadian Journal of Botany*, **85**:285–298.
- Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology*, **85**:2245–2257.
- Hessl, A. E. and W. L. Baker. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado USA. *Arctic and Alpine Research*, **29**:173–183.
- Higgs, E. 2003. *Nature by design: people, natural processes and ecological restoration*. MIT Press, Cambridge, MA.
- Holling, C. and M. Goldbert. 1981. *Contemporary anthropology: An anthology, ecology and planning*. Alfred A Knopf, New York, NY.
- Houghton et al. 2001. *IPCC climate change 2001: The scientific basis*. Cambridge University Press, Cambridge, UK.
- IPCC. 2001. *Climate change 2001. Technical report*, Cambridge University Press, Cambridge, UK.
- Jakubos, B. and W. H. Romme. 1993. Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, **25**:382–390.
- Keane, R., K. Ryan, T. T. Veblen, C. Allen, J. Logan, and B. Hawkes. 2002. The cascading effects of fire exclusion in Rocky Mountain ecosystems. In J. Baron, editor, *Rocky mountain futures: An ecological perspective*, pages 133–152. Island Press, Washington, D.C.

- Kimmerer, R. and F. Kanawha Lake. 2001. The role of indigenous burning in land management. *Journal of Forestry*, **99**:36–41.
- Kruskal, J. 1964*a*. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, **29**:1–27.
- Kruskal, J. 1964*b*. Nonmetric multidimensional scaling: a numeric method. *Psychometrika*, **29**:115–129.
- Kuijt, J. 1982. A flora of Waterton Lakes National Park. University of Alberta Press, Edmonton, AB.
- Lang, N. L. and C. B. Halpern. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. *Canadian Journal of Botany*, **85**:557–569.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management*, **44**:427–433.
- Lepofsky, D., E. Heyerdahl, K. Lertzman, D. Schaepe, and B. Mierendorf. 2003. Historical meadow dynamics in southwestern British Columbia: a multidisciplinary analysis. *Conservation Ecology*, **7**:1–18.
- Lesica, P. 2002. Flora of Glacier National Park. Oregon State University Press, Corvallis, OR.
- Lett, M. S. and A. K. Knapp. 2003. Consequences of shrub expansion in mesic grassland: Resource alterations and graminoid responses. *Journal of Vegetation Science*, **14**:487–496.
- Lewis, H. 1993. Patterns of indian burning in California: Ecology and ethnohistory. In T. Blackburn and K. Anderson, editors, *Before the wilderness: native*

- Californians as environmental managers, pages 55–116. Ballena Press, Menlo Park, CA.
- Luckman, B. 1990. Mountain areas and global change: a view from the Canadian Rockies. *Mountain Research and Development*, **10**:183–195.
- Luckman, B. 1998. Landscape and climate change in the central Canadian Rockies during the 20th century. *The Canadian Geographer*, **42**:319–336.
- MacDonald, G. 2000. *Where the mountains meet the prairies: a history of Waterton Country*. University of Calgary Press, Parks and Heritage Series, No. 1, Calgary, AB.
- Magee, T. K. and J. A. Antos. 1992. Tree Invasion into a Mountain-Top Meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science*, **3**:485–494.
- Mann, B. R. S., M. E. and M. K. Hughes. 1999. Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters*, **26**.
- Mast, J., T. Veblen, and M. Hodgson. 1997. Tree invasion within a pine/grassland ecotone: An approach with historic aerial photography and gis modeling. *Forest Ecology and Management*, **93**:181194.
- Mather, P. 1976. *Computational methods of multivariate analysis in physical geography*. Wiley and Sons, London, UK.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR.
- McCune, B. and M. Mefford. 1999. *PC-ORD version 5.0, Multivariate analysis of ecological data*. MjM Software Design, Gleneden Beach, OR.

- Millar, C. I., R. D. Westfall, D. L. Delany, J. C. King, and L. J. Graumlich. 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. *Arctic Antarctic and Alpine Research*, **36**:181–200.
- Miller, E. A. and C. B. Halpern. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science*, **9**:265–282.
- Moore, M. M. and D. W. Huffmant. 2004. Tree encroachment on meadows of the North Rim, Grand Canyon National Park, Arizona, USA. *Arctic Antarctic and Alpine Research*, **36**:474–483.
- Moss, E. H. and J. G. Packer. 1983. *Flora of Alberta : a manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada*. University of Toronto Press, Toronto, ON.
- National Assessment Synthesis Team. 2000. *Climate change impacts on the United States: the potential consequences of climate variability and change*. U.S. Global Change Research Program, Washington, DC.
- Norman, S. P. and A. H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. *Forest Ecology and Management*, **215**:51–68.
- Odion, D. C. and C. T. Hanson. 2006. Fire severity in conifer forests of the Sierra Nevada, California. *Ecosystems*, **9**:1177–1189.
- Odion, D. C. and D. A. Sarr. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. *Forest Ecology and Management*, **246**:57–65.

- Parks Canada. 2000. Waterton Lakes National Park - Park Management Plan. Technical report, Parks Canada.
- Parks Canada. 2007. Principles and guidelines for ecological restoration in Canada's protected natural areas. Technical report, Parks Canada Agency on behalf of the Canadian Parks Council.
- Peacock, S. 1992. Piikani ethnobotany: traditional plant knowledge of the Piikani peoples of the northwest Plains. Phd, University of Calgary.
- Peacock, S. and N. Turner. 2000. Just like a garden: Traditional resource management and biodiversity conservation on the interior plateau of British Columbia. In P. Minnis and W. Elisens, editors, *Biodiversity and Native America*, pages 133–179. University of Oklahoma Press, Norman, OK.
- Perraton, D. 1994. Submission to the Castle River Consultant Group. Technical report, AB.
- Picket, S. and V. Parker. 1994. Avoiding the old pitfalls: Opportunities in a new discipline. *Restoration Ecology*, 5:75–79.
- Poliquin, W. 1973. The climate and hydrology of Waterton Lakes National Park. Technical report, National and Historic Parks Branch, Waterton Park, AB.
- Reeves, B. 1975. Early Holocene (ca. 8000-5500 B.C.) prehistoric land/resource utilization patterns in Waterton Lakes National Park, Alberta. *Arctic and Alpine Research*, 7:237–248.
- Reeves, B. 1979. Prehistoric peoples of the Crowsnest Pass in Crowsnest and Its People. Technical report, Crowsnest Pass Historical Society, Crowsnest Pass, AB.

- Rhemtulla, J. M., R. Hall, E. Higgs, and S. MacDonald. 2002. Eighty years of change: vegetation in the montane ecoregion of Jasper National Park, AB, Canada. *Canadian Journal of Forest Research*, **32**:2010–2021.
- Rocheftort, R. M. and D. L. Peterson. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, USA. *Arctic and Alpine Research*, **28**:52–59.
- Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in Savannas. *Annual Review of Ecology and Systematics*, **28**:517–544.
- SER International Science and Policy Working Group. 2004. The SER International Primer on Ecological Restoration, Version 2. Technical report, Downloaded from: <http://www.ser.org/content/ecologicalrestorationprimer.asp>.
- Shannon, C. E. and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana, IL.
- Siemann, E. and W. E. Rogers. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology*, **91**:923–931.
- SPSS. 2005. SPSS 15.0. SPSS Inc., Chicago, IL.
- Strong, W. and K. Leggat. 1981. *Ecoregions of Alberta*. Technical report, Alberta Energy and Natural Resources, Resource Evaluation and Planning Division, Edmonton, AB.
- Swetnam, T., C. Allen, and J. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications*, **9**:1189–1206.
- Taylor, A. H. 1995. Forest expansion and climate change in the mountain hemlock

- (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California, USA. *Arctic and Alpine Research*, **27**:207–216.
- Turner, N. J. 1999. Time to burn traditional use of fire to enhance resource production by Aboriginal Peoples in British Columbia. In R. Boyd, editor, *Indians, Fire and The Land in the Pacific Northwest*, pages 185–218. Oregon State University Press, Corvallis, OR.
- Vale, T. R. 1981. Tree invasion of montane meadows in Oregon. *American Midland Naturalist*, **105**:61–69.
- Wakelyn, L. A. 1987. Changing Habitat Conditions on Bighorn Sheep Ranges in Colorado. *Journal of Wildlife Management*, **51**:904–912.
- Watson, E. and B. Luckman. 2001. Dendroclimatic reconstruction of precipitation for sites in the southern Canadian Rockies. *The Holocene*, **11**:203–213.
- Wearne, L. J. and J. W. Morgan. 2001. Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arctic Antarctic and Alpine Research*, **33**:369–377.
- Weisberg, N. and F. Swanson. 2003. Regional schroneity in fire regimes of western Oregon and Washington, USA. *Forest Ecology and Management*, **172**:17–28.
- White, P. and J. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology*, **5**:338–349.
- Wilson, S. and K. Martin. 2005. Songbird use of high-elevation habitat during the fall post-breeding and migratory periods. *Ecoscience*, **12**:561–568.
- Wissler, C. 1986. Material Culture of the Blackfoot. In D. H. Thomas, editor, *A*

Blackfoot Source Book: Papers by Clark Wissler. Garland Publishing, New York, NY.

Wolter, K. 2000. Multivariate ENSO Index (MEI). Technical report, Climate Diagnostics Center Report, Boulder, CO.

Woodward, A., E. G. Schreiner, and D. G. Silsbee. 1995. Climate, geography, and tree establishment in sub-alpine meadows of the Olympic Mountains, Washington, USA. *Arctic and Alpine Research*, **27**:217–225.

Appendices

Appendix 1

Trees that exceeded the removal allowance (ca. 50 seedlings per site) in Watterton Lakes National Park, branch whorls and/or bud scale scars were counted, and age was determined from age-branch whorl regressions from basal sections for *Abies lasiocarpa* and *Picea engelmannii*.

Table 1: Statistical output (SPSS 15.0 2005) for linear regression of *Abies lasiocarpa* age and branch whorl counts.

Descriptive Statistics

	Mean	Std. Deviation	N
log transformed age	1.6438	.21619	447
log transformation of whorl counts	1.5926	.20419	447

Correlations

		log transformed age	log transformation of whorl counts
Pearson Correlation	log transformed age	1.000	.908
	log transformation of whorl counts	.908	1.000
Sig. (1-tailed)	log transformed age	.	.000
	log transformation of whorl counts	.000	.
N	log transformed age	447	447
	log transformation of whorl counts	447	447

Variables Entered/Removed^b

Model	Variables Entered	Variables Removed	Method
1	log transformation of whorl counts	.	Enter

a. All requested variables entered.

b. Dependent Variable: log transformed age

Model Summary^b

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.908 ^a	.824	.823	.09084

a. Predictors: (Constant), log transformation of whorl counts

b. Dependent Variable: log transformed age

ANOVA^b

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	17.173	1	17.173	2081.210	.000 ^a
	Residual	3.672	445	.008		
	Total	20.844	446			

a. Predictors: (Constant), log transformation of whorl counts

b. Dependent Variable: log transformed age

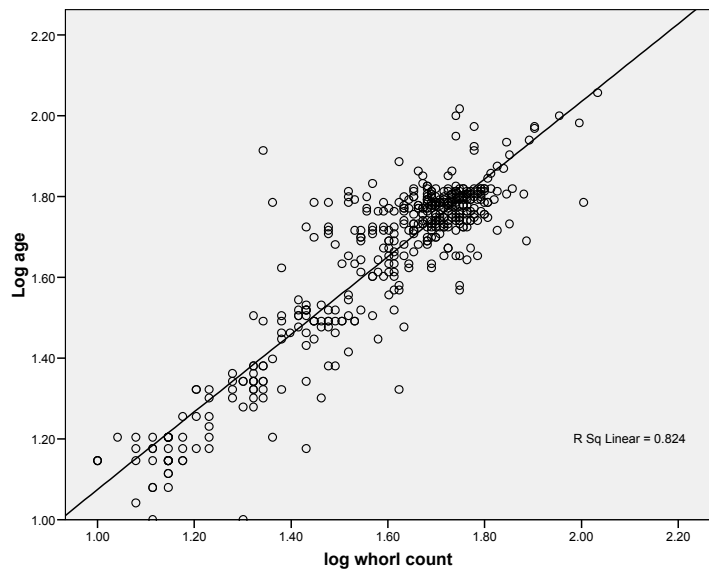


Figure 1: *Abies lasiocarpa* age vs branch whorl counts.

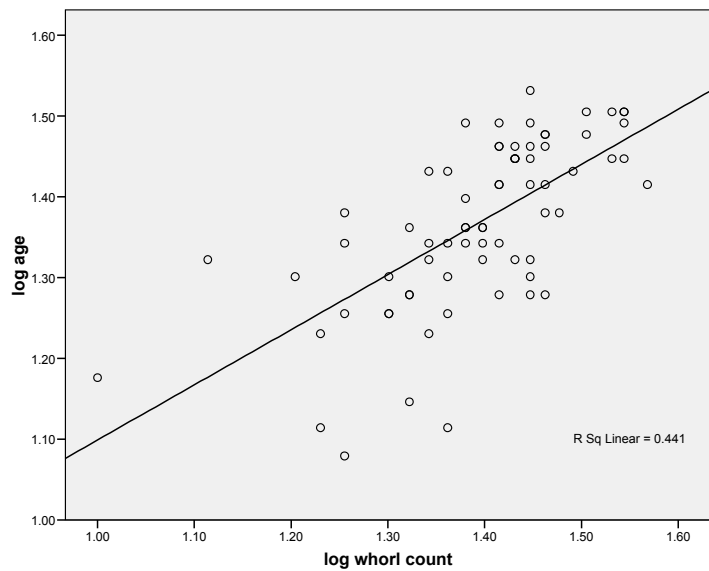


Figure 2: *Picea engelmannii* age vs branch whorl counts.

Table 2: Statistical output (SPSS 15.0 2005) for linear regression of *Picea engelmannii* age and branch whorl counts.

Descriptive Statistics

	Mean	Std. Deviation	N
log transformed age	1.3667	.10451	71
log transformation of whorl counts	1.3924	.10166	71

Correlations

		log transformed age	log transformation of whorl counts
Pearson Correlation	log transformed age	1.000	.664
	log transformation of whorl counts	.664	1.000
Sig. (1-tailed)	log transformed age	.	.000
	log transformation of whorl counts	.000	.
N	log transformed age	71	71
	log transformation of whorl counts	71	71

Variables Entered/Removed^a

Model	Variables Entered	Variables Removed	Method
1	log transformation of whorl counts	.	Enter

a. All requested variables entered.

b. Dependent Variable: log transformed age

Model Summary^b

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.664 ^a	.441	.433	.07873

a. Predictors: (Constant), log transformation of whorl counts

b. Dependent Variable: log transformed age

ANOVA^b

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	.337	1	.337	54.367	.000 ^a
	Residual	.428	69	.006		
	Total	.765	70			

a. Predictors: (Constant), log transformation of whorl counts

b. Dependent Variable: log transformed age

Appendix 2

Age-height regressions of the basal sections were used to estimate age to coring height for *Abies lasiocarpa*, *Picea engelmannii* and *Larix lyallii*.

Table 3: Statistical output (SPSS 15.0 2005) for nonlinear regression analysis of *Abies lasiocarpa* log age and log height using the Michaelis Menton model.

Iteration History^b

Iteration Number ^a	Residual Sum of Squares	Parameter	
		b1	b2
1.0	1297.441	.100	.100
1.1	942.789	2.358	11.145
2.0	942.789	2.358	11.145
2.1	1437.551	-.356	-56.478
2.2	2031.536	2.918	-19.437
2.3	312.127	2.504	3.171
3.0	312.127	2.504	3.171
3.1	29123990	2.109	-1.834
3.2	231.412	2.538	2.694
4.0	231.412	2.538	2.694
4.1	97.182	2.613	1.935
5.0	97.182	2.613	1.935
5.1	20.328	2.782	.945
6.0	20.328	2.782	.945
6.1	8.042	2.872	1.259
7.0	8.042	2.872	1.259
7.1	7.894	2.917	1.336
8.0	7.894	2.917	1.336
8.1	7.894	2.917	1.337
9.0	7.894	2.917	1.337
9.1	7.894	2.917	1.337

Derivatives are calculated numerically.

- a. Major iteration number is displayed to the left of the decimal, and minor iteration number is to the right of the decimal.
 b. Run stopped after 21 model evaluations and 9 derivative evaluations because the relative reduction between successive residual sums of squares is at most SSCON = 1.00E-008.

Parameter Estimates

Parameter	Estimate	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
b1	2.917	.077	2.767	3.068
b2	1.337	.082	1.177	1.498

Correlations of Parameter Estimates

	b1	b2
b1	1.000	.993
b2	.993	1.000

Source	Sum of Squares	df	Mean Squares
Regression	1450.200	2	725.100
Residual	7.894	532	.015
Uncorrected Total	1458.094	534	
Corrected Total	23.977	533	

Dependent variable: logage

a. R squared = 1 - (Residual Sum of Squares) / (Corrected Sum of Squares) = .671.

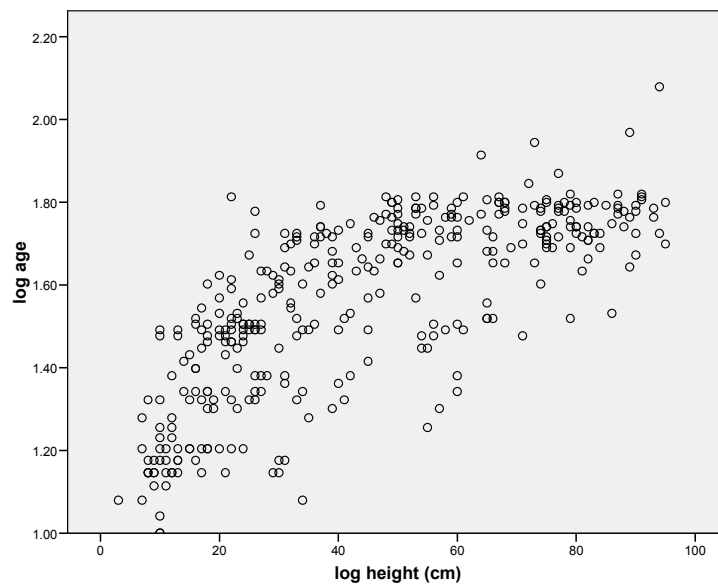


Figure 3: *Abies lasiocarpa* log age vs log height.

Table 4: Statistical output (SPSS 15.0 2005) for linear regression analysis of *Picea engelmannii* log age and log height.

Descriptive Statistics

	Mean	Std. Deviation	N
logage	1.3649	.10487	73
loghght	1.8169	.28619	73

Correlations

		logage	loghght
Pearson Correlation	logage	1.000	.519
	loghght	.519	1.000
Sig. (1-tailed)	logage	.	.000
	loghght	.000	.
N	logage	73	73
	loghght	73	73

Variables Entered/Removed^a

Model	Variables Entered	Variables Removed	Method
1	loghght ^a	.	Enter

a. All requested variables entered.

b. Dependent Variable: logage

Model Summary^b

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.519 ^a	.270	.259	.09025

a. Predictors: (Constant), loghght

b. Dependent Variable: logage

ANOVA^b

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	.213	1	.213	26.202	.000 ^a
	Residual	.578	71	.008		
	Total	.792	72			

a. Predictors: (Constant), loghght

b. Dependent Variable: logage

Coefficients^a

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	1.019	.068		14.912	.000
	loghght	.190	.037	.519	5.119	.000

a. Dependent Variable: logage

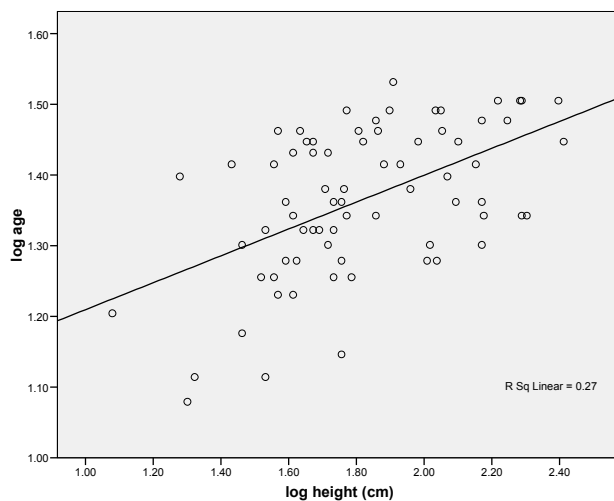


Figure 4: *Picea engelmannii* log age vs log height.

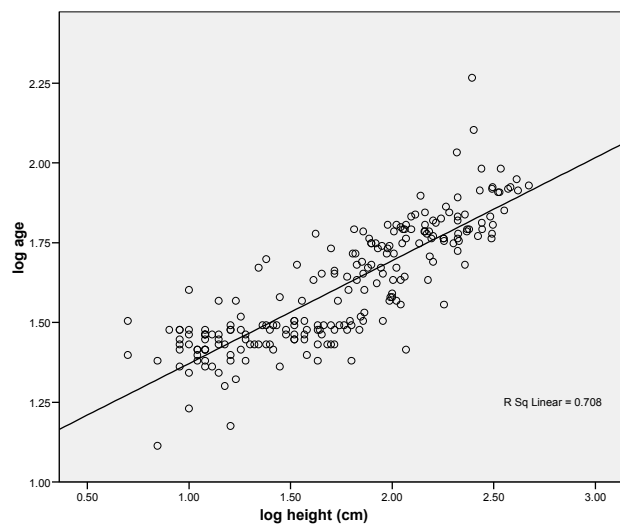


Figure 5: *Larix lyallii* log age vs log height.

Table 5: Statistical output (SPSS 15.0 2005) for linear regression analysis of *Larix lyallii* log age and log height.

Descriptive Statistics

	Mean	Std. Deviation	N
logage	1.6123	.18787	221
loghght	1.7471	.48994	221

Correlations

		logage	loghght
Pearson Correlation	logage	1.000	.842
	loghght	.842	1.000
Sig. (1-tailed)	logage	.	.000
	loghght	.000	.
N	logage	221	221
	loghght	221	221

Variables Entered/Removed^a

Model	Variables Entered	Variables Removed	Method
1	loghght ^a	.	Enter

a. All requested variables entered.

b. Dependent Variable: logage

Model Summary^b

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.842 ^a	.708	.707	.10170

a. Predictors: (Constant), loghght

b. Dependent Variable: logage

ANOVA^b

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	5.500	1	5.500	531.669	.000 ^a
	Residual	2.265	219	.010		
	Total	7.765	220			

a. Predictors: (Constant), loghght

b. Dependent Variable: logage

Coefficients^a

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	1.049	.025		41.299	.000
	loghght	.323	.014	.842	23.058	.000

a. Dependent Variable: logage

Appendix 3

Correlation matrices for 3 dimensional NMS solution (NMS1, NMS2, and NMS3) of species composition with forest structure and physical environmental variables for wet and dry sites.

Table 6: Correlation matrices (SPSS 15.0 2005) for NMS1 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for wet sites.

Correlations											
		NMS1	Aspect	Distance (m)	Max age	Mean age	Density (stems/m ²)	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area
NMS1	Pearson Correlation	1									
	Sig. (2-tailed)										
	N	49									
Aspect	Pearson Correlation	-.293*	1								
	Sig. (2-tailed)	.041									
	N	49	49								
Distance (m)	Pearson Correlation	-.610**	.149	1							
	Sig. (2-tailed)	.000	.307								
	N	49	49	49							
Max age	Pearson Correlation	.685**	-.145	-.750**	1						
	Sig. (2-tailed)	.000	.321	.000							
	N	49	49	49	49						
Mean age	Pearson Correlation	.685**	-.171	-.720**	.912**	1					
	Sig. (2-tailed)	.000	.239	.000	.000						
	N	49	49	49	49	49					
Density (stems/m ²)	Pearson Correlation	-.243	-.020	-.019	-.187	-.355*	1				
	Sig. (2-tailed)	.092	.890	.897	.199	.012					
	N	49	49	49	49	49	49				
Mean soil depth (cm)	Pearson Correlation	-.218	.124	.203	.056	.005	-.312*	1			
	Sig. (2-tailed)	.132	.395	.162	.705	.972	.029				
	N	49	49	49	49	49	49	49			
Slope (degree)	Pearson Correlation	.086	-.282	-.378**	.272	.316*	-.088	.148	1		
	Sig. (2-tailed)	.559	.050	.007	.059	.027	.547	.312	.499**		
	N	49	49	49	49	49	49	49	49	49	
Elevation (m)	Pearson Correlation	.054	-.006	-.292*	.073	.219	-.296*	.124	.499**	1	
	Sig. (2-tailed)	.712	.965	.042	.620	.130	.039	.395	.000	.000	
	N	49	49	49	49	49	49	49	49	49	49
Management area	Pearson Correlation	-.152	-.431**	-.268	.171	.127	-.033	.329*	.555**	.549**	1
	Sig. (2-tailed)	.298	.002	.063	.240	.386	.820	.021	.000	.000	.000
	N	49	49	49	49	49	49	49	49	49	49

*. Correlation is significant at the 0.05 level (2-tailed).

** . Correlation is significant at the 0.01 level (2-tailed).

Table 7: Correlation matrices (SPSS 15.0 2005) for NMS2 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for wet sites.

Correlations

		NMS2	Aspect	Distance (m)	Max age	Mean age	Density (stems/m ²)	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area
NMS2	Pearson Correlation	1	-.029	.492**	-.384**	-.368**	.232	-.283*	-.263	-.469**	-.377**
	Sig. (2-tailed)		.842	.000	.006	.009	.109	.049	.068	.001	.008
	N	49	49	49	49	49	49	49	49	49	49
Aspect	Pearson Correlation	-.029	1	.149	-.145	-.171	-.020	.124	-.282	-.006	-.431**
	Sig. (2-tailed)	.842		.307	.321	.239	.890	.395	.050	.965	.002
	N	49	49	49	49	49	49	49	49	49	49
Distance (m)	Pearson Correlation	.492**	.149	1	-.750**	-.720**	-.019	.203	-.378**	-.292*	-.268
	Sig. (2-tailed)	.000	.307		.000	.000	.897	.162	.007	.042	.063
	N	49	49	49	49	49	49	49	49	49	49
Max age	Pearson Correlation	-.384**	-.145	-.750**	1	.912**	-.187	.056	.272	.073	.171
	Sig. (2-tailed)	.006	.321	.000		.000	.199	.705	.059	.620	.240
	N	49	49	49	49	49	49	49	49	49	49
Mean age	Pearson Correlation	-.368**	-.171	-.720**	.912**	1	-.355*	.005	.316*	.219	.127
	Sig. (2-tailed)	.009	.239	.000	.000		.012	.972	.027	.130	.386
	N	49	49	49	49	49	49	49	49	49	49
Density (stems/m ²)	Pearson Correlation	.232	-.020	-.019	-.187	-.355*	1	-.312*	-.088	-.296*	-.033
	Sig. (2-tailed)	.109	.890	.897	.199	.012		.029	.547	.039	.820
	N	49	49	49	49	49	49	49	49	49	49
Mean soil depth (cm)	Pearson Correlation	-.283*	.124	.203	.056	.005	-.312*	1	.148	.124	.329*
	Sig. (2-tailed)	.049	.395	.162	.705	.972	.029		.312	.395	.021
	N	49	49	49	49	49	49	49	49	49	49
Slope (degree)	Pearson Correlation	-.263	-.282	-.378**	.272	.316*	-.088	.148	1	.499**	.555**
	Sig. (2-tailed)	.068	.050	.007	.059	.027	.547	.312		.000	.000
	N	49	49	49	49	49	49	49	49	49	49
Elevation (m)	Pearson Correlation	-.469**	-.006	-.292*	.073	.219	-.296*	.124	.499**	1	.549**
	Sig. (2-tailed)	.001	.965	.042	.620	.130	.039	.395	.000		.000
	N	49	49	49	49	49	49	49	49	49	49
Management area	Pearson Correlation	-.377**	-.431**	-.268	.171	.127	-.033	.329*	.555**	.549**	1
	Sig. (2-tailed)	.008	.002	.063	.240	.386	.820	.021	.000	.000	
	N	49	49	49	49	49	49	49	49	49	49

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 8: Correlation matrices (SPSS 15.0 2005) for NMS3 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for wet sites.

Correlations

		NMS3	Aspect	Distance (m)	Max age	Mean age	Density (stems/m ²)	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area
NMS3	Pearson Correlation	1									
	Sig. (2-tailed)		-.117	-.619**	.563**	.523**	-.014	.063	.315*	.254	.551**
	N	49	49	49	49	49	49	49	49	49	49
Aspect	Pearson Correlation	-.117	1	.149	-.145	-.171	-.020	.124	-.282	-.006	-.431**
	Sig. (2-tailed)	.425		.307	.321	.239	.890	.395	.050	.965	.002
	N	49	49	49	49	49	49	49	49	49	49
Distance (m)	Pearson Correlation	-.619**	.149	1	-.750**	-.720**	-.019	.203	-.378**	-.292*	-.268
	Sig. (2-tailed)	.000	.307		.000	.000	.897	.162	.007	.042	.063
	N	49	49	49	49	49	49	49	49	49	49
Max age	Pearson Correlation	.563**	-.145	-.750**	1	.912**	-.187	.056	.272	.073	.171
	Sig. (2-tailed)	.000	.321	.000		.000	.199	.705	.059	.620	.240
	N	49	49	49	49	49	49	49	49	49	49
Mean age	Pearson Correlation	.523**	-.171	-.720**	.912**	1	-.355*	.005	.316*	.219	.127
	Sig. (2-tailed)	.000	.239	.000	.000		.012	.972	.027	.130	.386
	N	49	49	49	49	49	49	49	49	49	49
Density (stems/m ²)	Pearson Correlation	-.014	-.020	-.019	-.187	-.355*	1	-.312*	-.088	-.296*	-.033
	Sig. (2-tailed)	.923	.890	.897	.199	.012		.029	.547	.039	.820
	N	49	49	49	49	49	49	49	49	49	49
Mean soil depth (cm)	Pearson Correlation	.063	.124	.203	.056	.005	-.312*	1	.148	.124	.329*
	Sig. (2-tailed)	.669	.395	.162	.705	.972	.029		.312	.395	.021
	N	49	49	49	49	49	49	49	49	49	49
Slope (degree)	Pearson Correlation	.315*	-.282	-.378**	.272	.316*	-.088	.148	1	.499**	.555**
	Sig. (2-tailed)	.027	.050	.007	.059	.027	.547	.312		.000	.000
	N	49	49	49	49	49	49	49	49	49	49
Elevation (m)	Pearson Correlation	.254	-.006	-.292*	.073	.219	-.296*	.124	.499**	1	.549**
	Sig. (2-tailed)	.078	.965	.042	.620	.130	.039	.395	.000		.000
	N	49	49	49	49	49	49	49	49	49	49
Management area	Pearson Correlation	.551**	-.431**	-.268	.171	.127	-.033	.329*	.555**	.549**	1
	Sig. (2-tailed)	.000	.002	.063	.240	.386	.820	.021	.000	.000	
	N	49	49	49	49	49	49	49	49	49	49

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 9: Correlation matrices (SPSS 15.0 2005) for NMS1 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for dry sites.

Correlations

		NMS1	Aspect	Distance (m)	Max age	Mean age	Density (stems/m ²)	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area	Fire	Sum age
NMS1	Pearson Correlation	1	.330*	.470**	-.359**	-.373**	-.151	-.420**	-.140	.257*	.215	.215	-.164
	Sig. (2-tailed)		.008	.000	.001	.003	.236	.001	.275	.042	.091	.091	.199
	N	63	63	63	63	63	63	63	63	63	63	63	63
Aspect	Pearson Correlation	.330**	1	.093	-.128	-.111	-.177	-.301*	-.337**	.287*	.660**	.660**	-.189
	Sig. (2-tailed)	.008		.470	.319	.385	.165	.017	.007	.023	.000	.000	.138
	N	63	63	63	63	63	63	63	63	63	63	63	63
Distance (m)	Pearson Correlation	.470**	.093	1	-.760**	-.724**	-.066	.136	-.186	-.125	-.049	-.049	-.254*
	Sig. (2-tailed)	.000	.470	.000	.000	.008	.608	.288	.145	.329	.704	.704	.044
	N	63	63	63	63	63	63	63	63	63	63	63	63
Max age	Pearson Correlation	-.359**	-.128	-.760**	1	.871**	.004	.019	.055	.057	-.056	-.056	.233
	Sig. (2-tailed)	.001	.319	.000		.000	.977	.886	.668	.655	.663	.663	.067
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean age	Pearson Correlation	-.373**	-.111	-.724**	.871**	1	-.155	-.022	-.044	-.005	-.044	-.044	.032
	Sig. (2-tailed)	.003	.385	.000	.000		.226	.863	.272	.970	.733	.733	.801
	N	63	63	63	63	63	63	63	63	63	63	63	63
Density (stems/m ²)	Pearson Correlation	-.151	-.177	-.066	.004	-.155	1	.162	-.002	.072	-.095	-.095	.911**
	Sig. (2-tailed)	.236	.165	.608	.977	.226		.204	.985	.577	.461	.461	.000
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean soil depth (cm)	Pearson Correlation	-.420**	-.301*	.136	.019	-.022	.162	1	.030	-.725**	-.550**	-.550**	.086
	Sig. (2-tailed)	.001	.017	.288	.886	.863	.204		.816	.000	.000	.000	.504
	N	63	63	63	63	63	63	63	63	63	63	63	63
Slope (degree)	Pearson Correlation	-.140	-.337**	-.186	.055	.141	-.002	.030	1	-.499**	-.420**	-.420**	.566
	Sig. (2-tailed)	.275	.007	.145	.668	.272	.985	.816		.000	.001	.001	.607
	N	63	63	63	63	63	63	63	63	63	63	63	63
Elevation (m)	Pearson Correlation	.257*	.287*	-.125	.057	-.005	.072	-.725**	-.499**	1	.713**	.713**	.095
	Sig. (2-tailed)	.042	.023	.329	.655	.970	.577	.000	.000		.000	.000	.457
	N	63	63	63	63	63	63	63	63	63	63	63	63
Management area	Pearson Correlation	.215	.660**	-.049	-.056	-.044	-.095	-.550**	-.420**	.713**	1	1.000**	-.094
	Sig. (2-tailed)	.091	.000	.704	.663	.733	.461	.000	.001	.000	.000	.000	.462
	N	63	63	63	63	63	63	63	63	63	63	63	63
Fire	Pearson Correlation	.215	.660**	-.049	-.056	-.044	-.095	-.550**	-.420**	.713**	1.000**	1	-.094
	Sig. (2-tailed)	.091	.000	.704	.663	.733	.461	.000	.001	.000	.000	.000	.462
	N	63	63	63	63	63	63	63	63	63	63	63	63
Sum age	Pearson Correlation	-.164	-.189	-.254*	.233	.032	.911**	.086	.066	.095	-.094	-.094	1
	Sig. (2-tailed)	.199	.138	.044	.067	.801	.000	.504	.607	.457	.462	.462	
	N	63	63	63	63	63	63	63	63	63	63	63	63

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Table 10: Correlation matrices (SPSS 15.0 2005) for NMS2 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for dry sites.

Correlations

		NMS2	Aspect	Distance (m)	Max age	Mean age	Density stems/m2	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area	Fire	Sum age
NMS2	Pearson Correlation	1											
	Sig. (2-tailed)		.136	.144	.206	.129	.113	.407**	.140	.640**	.223	.223	.129
	N	63	63	63	63	63	63	63	63	63	63	63	63
Aspect	Pearson Correlation		1										
	Sig. (2-tailed)	.136		.093	.128	.111	.177	.301*	.337**	.287*	.660**	.660**	.189
	N	63	63	63	63	63	63	63	63	63	63	63	63
Distancem	Pearson Correlation			1									
	Sig. (2-tailed)	.144	.093		.780**	.724**	.066	.136	.186	.125	.049	.049	.254**
	N	63	63	63	63	63	63	63	63	63	63	63	63
Max age	Pearson Correlation				1								
	Sig. (2-tailed)	.206	.128	.780**		.871**	.004	.019	.055	.057	.056	.056	.233
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean age	Pearson Correlation					1							
	Sig. (2-tailed)	.129	.111	.724**	.871**		.155	.022	.141	.005	.044	.044	.032
	N	63	63	63	63	63	63	63	63	63	63	63	63
Density (stems/m2)	Pearson Correlation						1						
	Sig. (2-tailed)	.113	.177	.066	.004	.155		.162	.002	.072	.095	.095	.911**
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean soil depth (cm)	Pearson Correlation							1					
	Sig. (2-tailed)	.407**	.301*	.136	.019	.022	.162		.030	.725**	.550**	.550**	.086
	N	63	63	63	63	63	63	63	63	63	63	63	63
Slope (degree)	Pearson Correlation								1				
	Sig. (2-tailed)	.140	.337**	.186	.056	.141	.002	.030		.499**	.420**	.420**	.066
	N	63	63	63	63	63	63	63	63	63	63	63	63
Elevation (m)	Pearson Correlation									1			
	Sig. (2-tailed)	.640**	.287*	.125	.057	.005	.072	.725**	.499**		.713**	.713**	.095
	N	63	63	63	63	63	63	63	63	63	63	63	63
Management area	Pearson Correlation										1		
	Sig. (2-tailed)	.223	.660**	.049	.056	.044	.095	.550**	.420**	.713**		1.000**	.094
	N	63	63	63	63	63	63	63	63	63	63	63	63
Fire	Pearson Correlation											1	
	Sig. (2-tailed)	.223	.660**	.049	.056	.044	.095	.550**	.420**	.713**	1.000**		.094
	N	63	63	63	63	63	63	63	63	63	63	63	63
Sum age	Pearson Correlation												1
	Sig. (2-tailed)	.129	.189	.254**	.233	.032	.911**	.086	.066	.095	.094	.094	
	N	63	63	63	63	63	63	63	63	63	63	63	63

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Table 11: Correlation matrices (SPSS 15.0 2005) for NMS3 solution (PC-ORD v5.1; McCune and Mefford 1999) for species composition with forest structure and physical environmental variables for dry sites.

Correlations

		NMS3	Aspect	Distance (m)	Max age	Mean age	Density stems/m2	Mean soil depth (cm)	Slope (degree)	Elevation (m)	Management area	Fire	Sum age
NMS3	Pearson Correlation	1	-.459**	-.269*	.186	.199	-.082	-.419**	.396**	.146	-.098	-.098	.090
	Sig. (2-tailed)		.000	.033	.145	.119	.524	.001	.001	.253	.444	.444	.484
	N	63	63	63	63	63	63	63	63	63	63	63	63
Aspect	Pearson Correlation	-.459**	1	.093	-.128	-.111	-.177	-.301**	-.337**	.287*	.660**	.660**	-.189
	Sig. (2-tailed)	.000		.470	.319	.385	.165	.017	.007	.023	.000	.000	.138
	N	63	63	63	63	63	63	63	63	63	63	63	63
Distance (m)	Pearson Correlation	-.269*	.093	1	-.780**	-.724**	-.066	.136	-.186	-.125	-.049	-.049	-.254*
	Sig. (2-tailed)	.033	.470	.000		.000	.608	.288	.145	.329	.704	.704	.044
	N	63	63	63	63	63	63	63	63	63	63	63	63
Max age	Pearson Correlation	.186	-.128	-.780**	1	.871**	.004	.019	.055	.057	-.056	-.056	.233
	Sig. (2-tailed)	.145	.319	.000		.000	.977	.886	.668	.655	.663	.663	.067
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean age	Pearson Correlation	.199	-.111	-.724**	.871**	1	-.155	-.022	.141	-.005	-.044	-.044	.032
	Sig. (2-tailed)	.119	.385	.000	.000		.226	.863	.272	.970	.733	.733	.801
	N	63	63	63	63	63	63	63	63	63	63	63	63
Density (stems/m2)	Pearson Correlation	-.082	-.177	-.066	.004	-.155	1	.162	-.002	.072	-.095	-.095	.911**
	Sig. (2-tailed)	.524	.165	.808	.977	.226		.204	.985	.577	.461	.461	.000
	N	63	63	63	63	63	63	63	63	63	63	63	63
Mean soil depth (cm)	Pearson Correlation	-.419**	-.301**	.136	.019	-.022	.162	1	.030	-.725**	-.550**	-.550**	.086
	Sig. (2-tailed)	.001	.017	.288	.886	.863	.204		.816	.000	.000	.000	.504
	N	63	63	63	63	63	63	63	63	63	63	63	63
Slope (degree)	Pearson Correlation	.396**	-.337**	-.186	.055	.141	-.002	.030	1	-.499**	-.420**	-.420**	.066
	Sig. (2-tailed)	.001	.007	.145	.668	.272	.985	.816		.000	.001	.001	.607
	N	63	63	63	63	63	63	63	63	63	63	63	63
Elevation (m)	Pearson Correlation	.146	.287*	-.125	.057	-.005	.072	-.725**	-.499**	1	.713**	.713**	.095
	Sig. (2-tailed)	.253	.023	.329	.655	.970	.577	.000	.000		.000	.000	.457
	N	63	63	63	63	63	63	63	63	63	63	63	63
Management area	Pearson Correlation	-.098	.660**	-.049	-.056	-.044	-.095	-.550**	-.420**	.713**	1	1.000**	-.094
	Sig. (2-tailed)	.444	.000	.704	.863	.733	.461	.000	.001	.000	.000		.462
	N	63	63	63	63	63	63	63	63	63	63	63	63
Fire	Pearson Correlation	-.098	.660**	-.049	-.056	-.044	-.095	-.550**	-.420**	.713**	1.000**	1	-.094
	Sig. (2-tailed)	.444	.000	.704	.863	.733	.461	.000	.001	.000	.000		.462
	N	63	63	63	63	63	63	63	63	63	63	63	63
Sum age	Pearson Correlation	.090	-.189	-.254*	.233	.032	.911**	.086	.066	.095	-.094	-.094	1
	Sig. (2-tailed)	.484	.138	.044	.067	.801	.000	.504	.607	.457	.462	.462	
	N	63	63	63	63	63	63	63	63	63	63	63	63

** . Correlation is significant at the 0.01 level (2-tailed).

* . Correlation is significant at the 0.05 level (2-tailed).

Appendix 4

Repeat photographic pairs showing conifer encroachment in subalpine meadows ranging from 1910 to 2007 in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA), Alberta.

Table 12: Site descriptions for wet and dry meadows in Waterton Lakes National Park (WLNP) and the Castle Special Management Area (CSMA).

Site	Management area	Elevation (m)	Aspect	Transect length (m)
<i>Wet Meadows</i>				
Font	CSMA	2070	NE	35
Ruby	CSMA	1980	N	25
Bauerman	WLNP	1970	N	60
Goat	WLNP	2010	SE	30
Lone	WLNP	1970	NE	40
Riggall	WLNP	1990	S	55
<i>Dry Meadows</i>				
Avion	CSMA	2280	NW	40
Barnaby	CSMA	2210	N	35
Sage	CSMA	2260	SW	45
Windsor	CSMA	2240	SW	35
Bertha	WLNP	2200	NE	30
Festebert	WLNP	2150	NE	35
Lineham	WLNP	2190	E	45
Vimy	WLNP	2010	NE	50

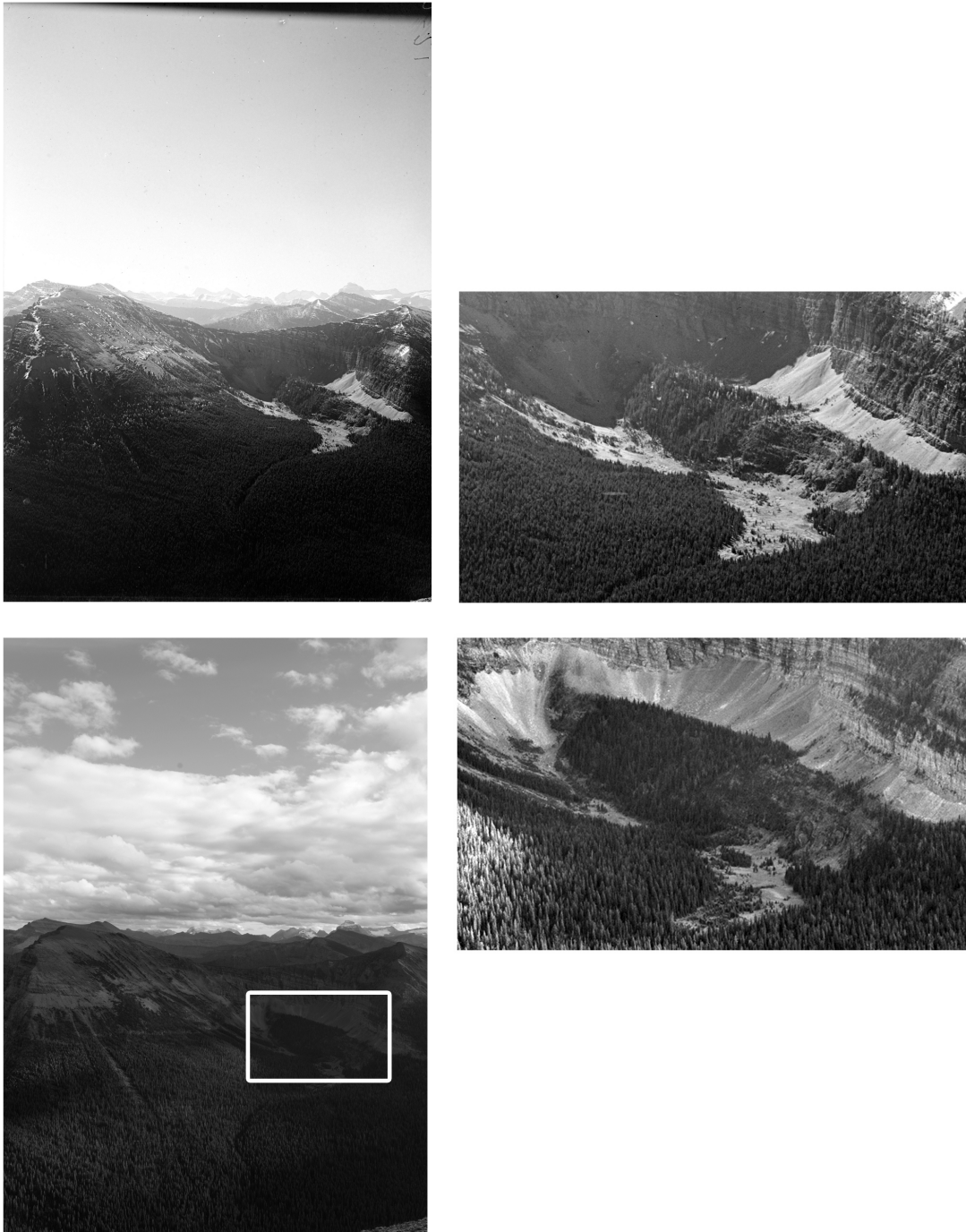


Figure 6: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Bauerman, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The upper left photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The lower left photograph was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The photographs on the right show Bauerman meadow in 1914 (upper) and 2004 (lower). Bauerman meadow is indicated by the white box in the landscape photograph.

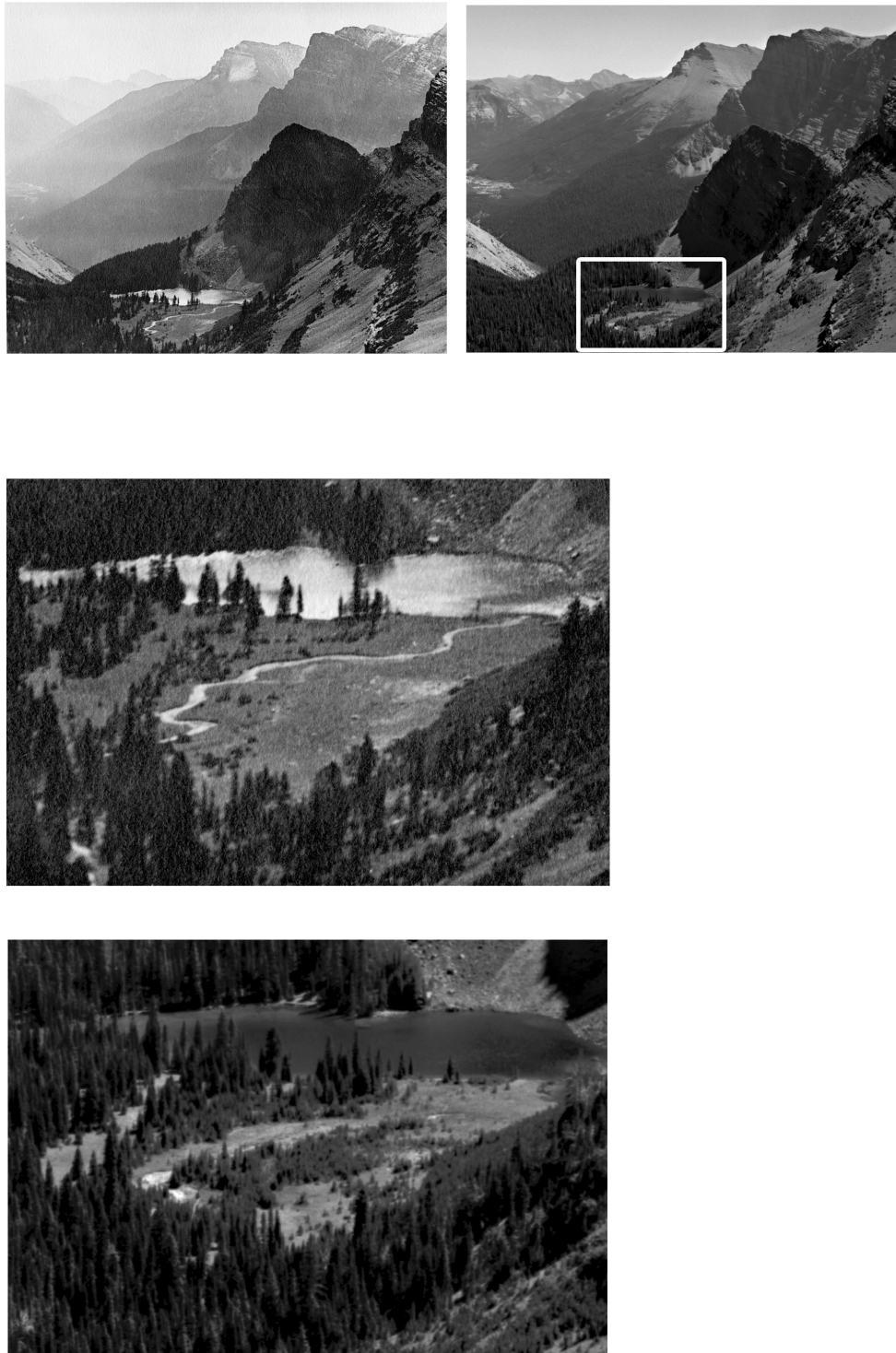


Figure 7: Repeat photograph showing conifer encroachment in subalpine meadows from 1932 to 2007. The meadow study site is Goat, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The upper left photograph was taken in 1932 by A. Riggall, a horse outfitter (courtesy of the Whyte Museum). The upper right photograph was taken in 2007 by Trudi Smith. The photographs below show Goat meadow in 1932 (centre) and 2007 (lower). Goat meadow is indicated by the white box in the landscape photograph.

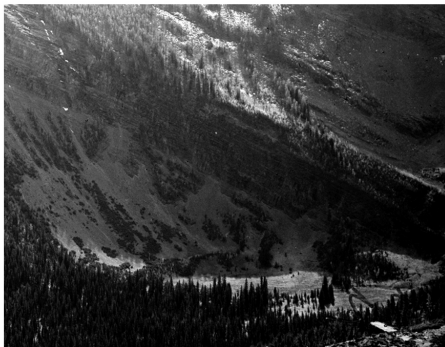


Figure 8: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Lone, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The upper left photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The centre photograph was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The photographs on the bottom show Lone meadow in 1914 (left) and 2004 (right). Lone meadow is indicated by the white box in the landscape photograph.



Figure 9: Repeat photograph showing conifer encroachment in subalpine meadows from 1934 to 2004. The meadow study site is Riggall, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The top photograph was taken in 1934 by A. Riggall, a horse outfitter (courtesy of the Whyte Museum). The second photograph from the top was taken in 2004 by Trudi Smith. The photographs on the bottom show Riggall meadow in 1934 (upper) and 2004 (lower). Riggall meadow is indicated by the white box in the landscape photograph.

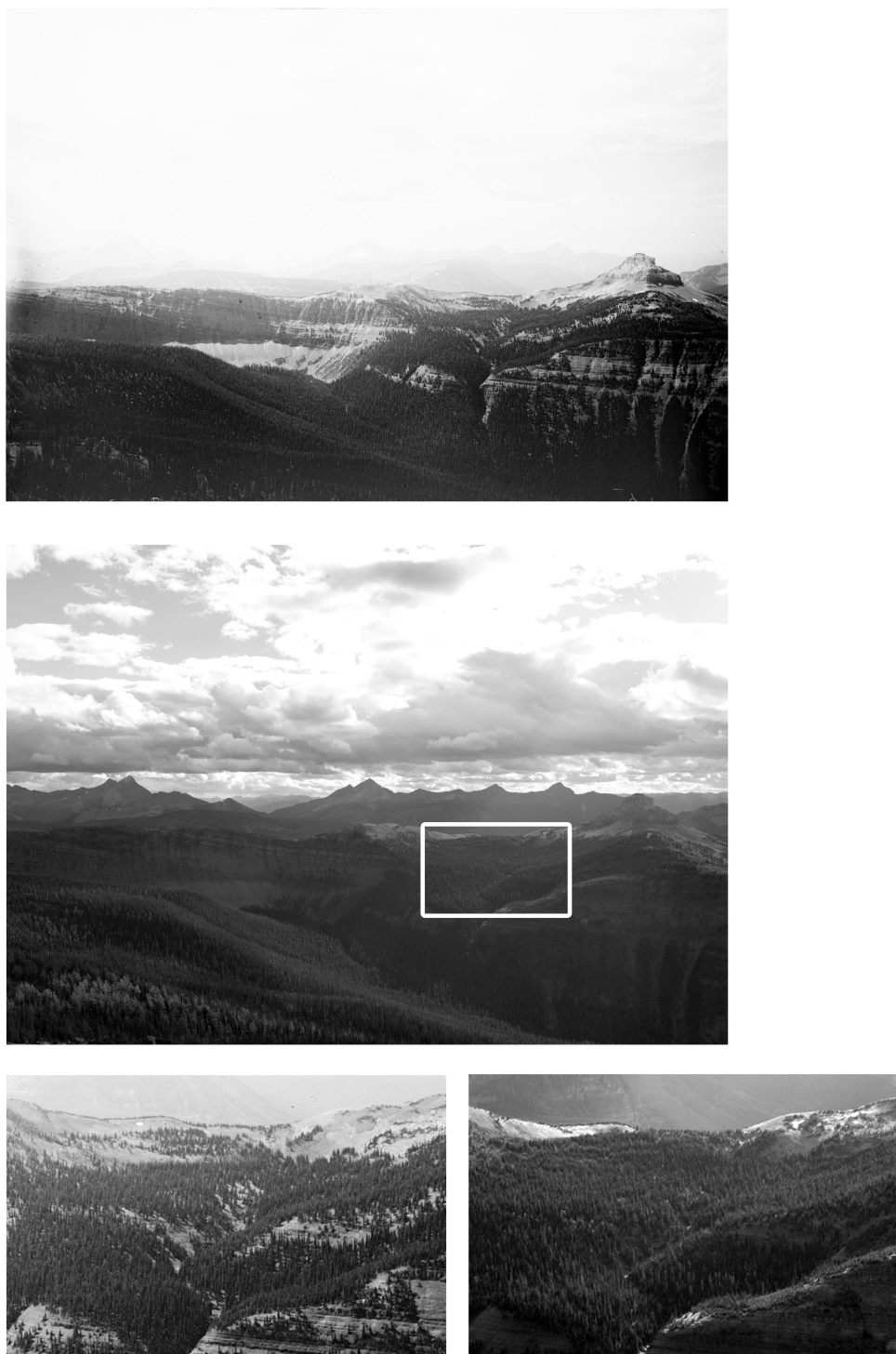


Figure 10: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Font, located in the Castle Special Management Area (CSMA), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The centre photograph was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Font meadow in 1914 (left) and 2004 (right). Font meadow is indicated by the white box in the landscape photograph.

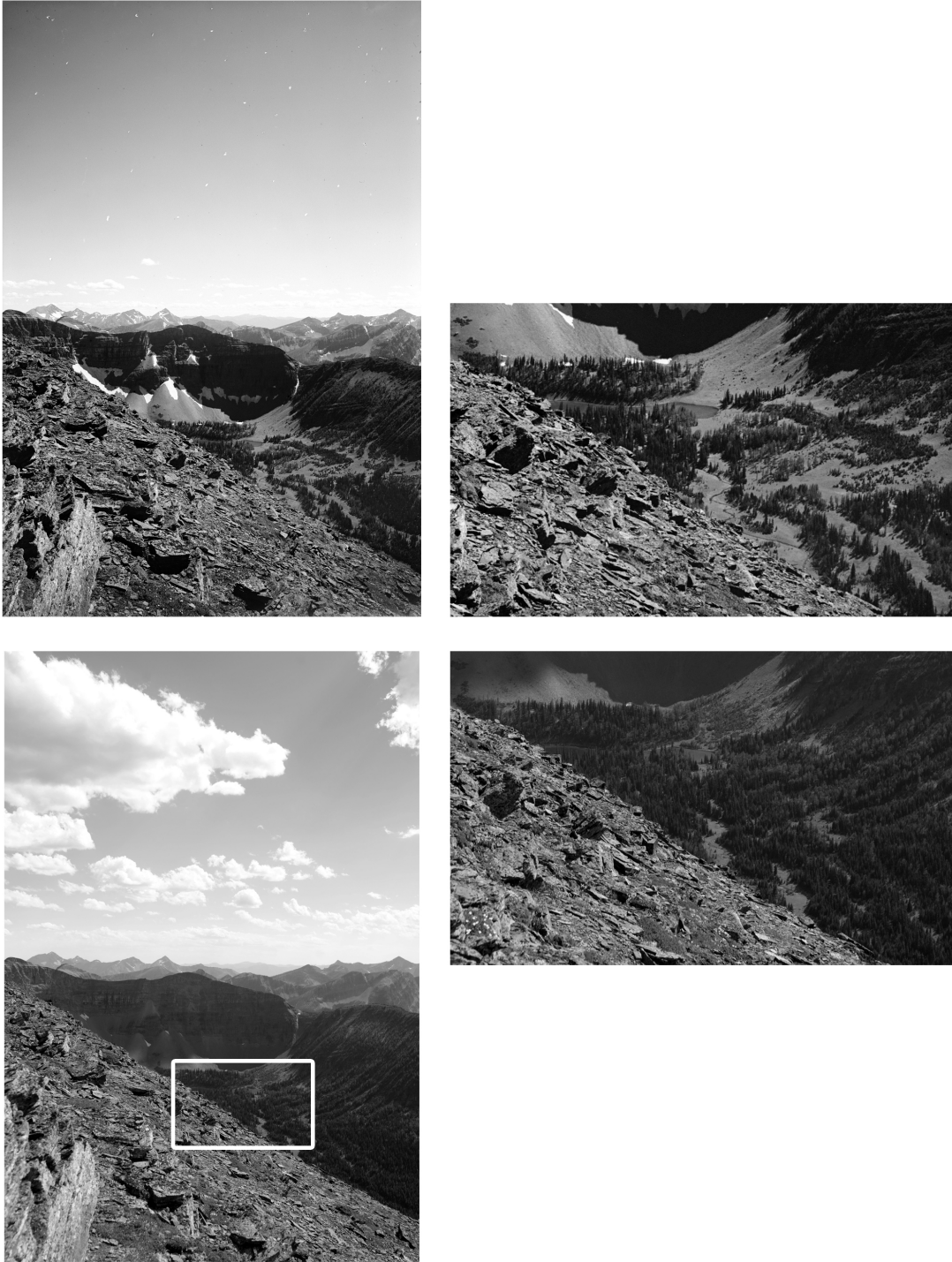


Figure 11: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2005. The meadow study site is Ruby, located in the Castle Special Management Area (CSMA), Alberta, Canada. The upper left photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The lower left photograph was taken in 2005 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The photographs on the right show Ruby meadow in 1914 (upper) and 2005 (lower). Ruby meadow is indicated by the white box in the landscape photograph.

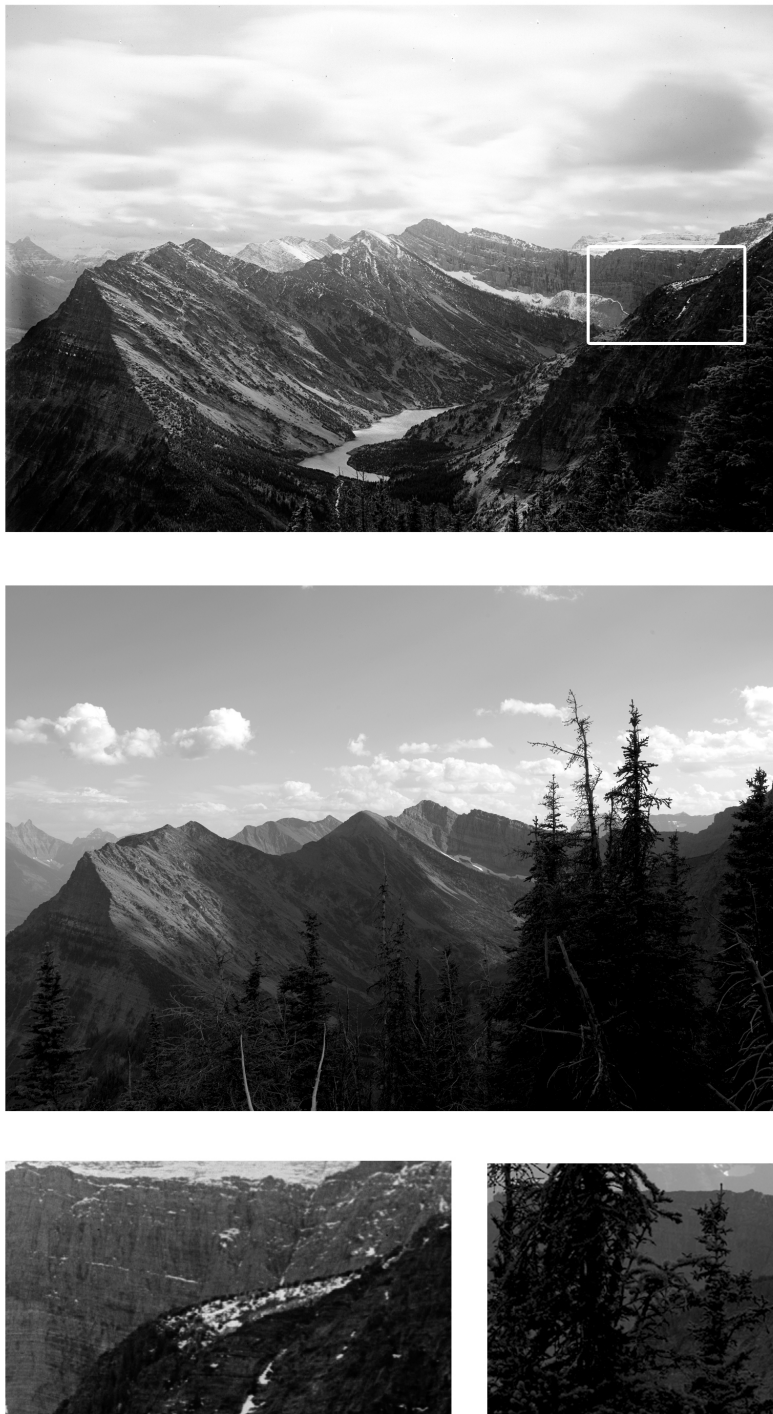


Figure 12: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Bertha, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The centre photograph was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Bertha meadow in 1914 (left) and 2004 (right). Bertha meadow is indicated by the white box in the landscape photograph.

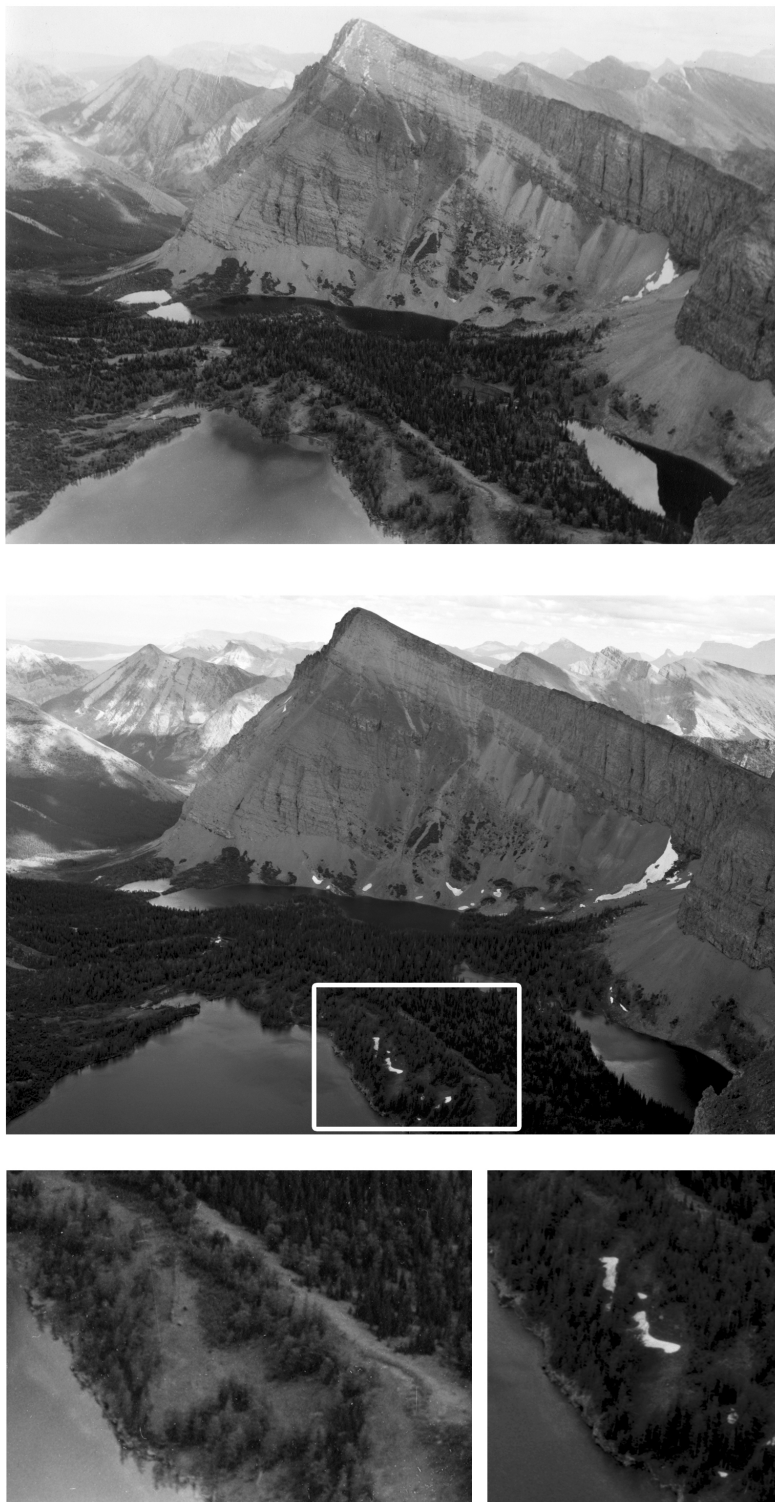


Figure 13: Repeat photograph showing conifer encroachment in subalpine meadows from the 1930s to 2007. The meadow study site is Lineham, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The top photograph was taken in the 1930s by A. Riggall, a horse outfitter (courtesy of the Whyte Museum). The centre photograph was taken in 2007 by Trudi Smith. The lower photographs show Lineham meadow in the 1930s (left) and 2007 (right). Lineham meadow is indicated by the white box in the landscape photograph.



Figure 14: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Vimy, located in Waterton Lakes National Park (WLNP), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The photograph second from the top was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Vimy meadow in 1914 (upper) and 2004 (lower). Vimy meadow is indicated by the white box in the landscape photograph.

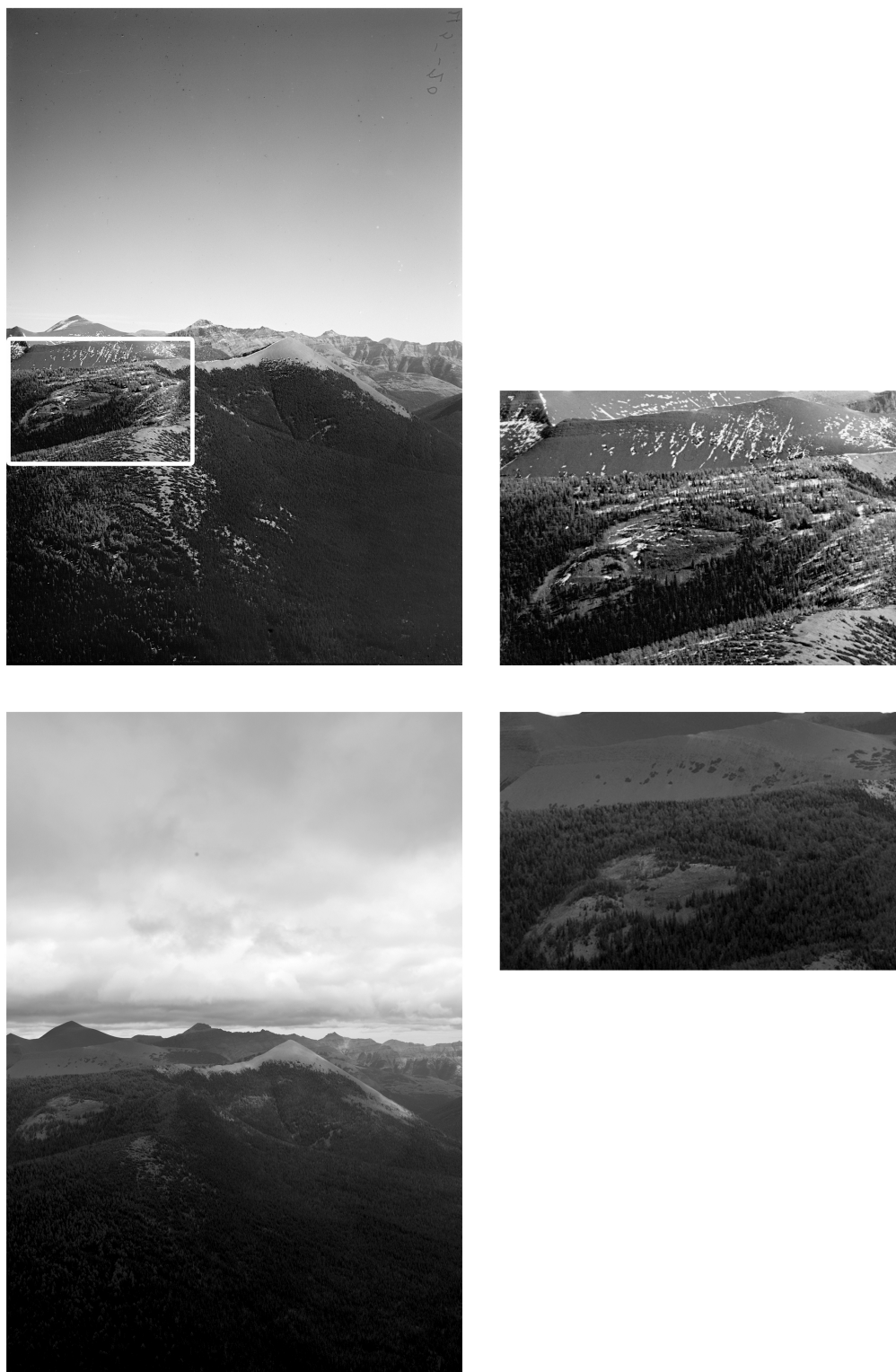


Figure 15: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Avion, located in the Castle Special Management Area (CSMA), Alberta, Canada. The upper left photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The lower left photograph was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The photographs on the right show Avion meadow in 1914 (upper) and 2004 (lower). Avion meadow is indicated by the white box in the landscape photograph.



Figure 16: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2006. The meadow study site is Barnaby, located in the Castle Special Management Area (CSMA), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The centre photograph was taken in 2006 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Barnaby meadow in 1914 (left) and 2006 (right). Barnaby meadow is indicated by the white box in the landscape photograph.

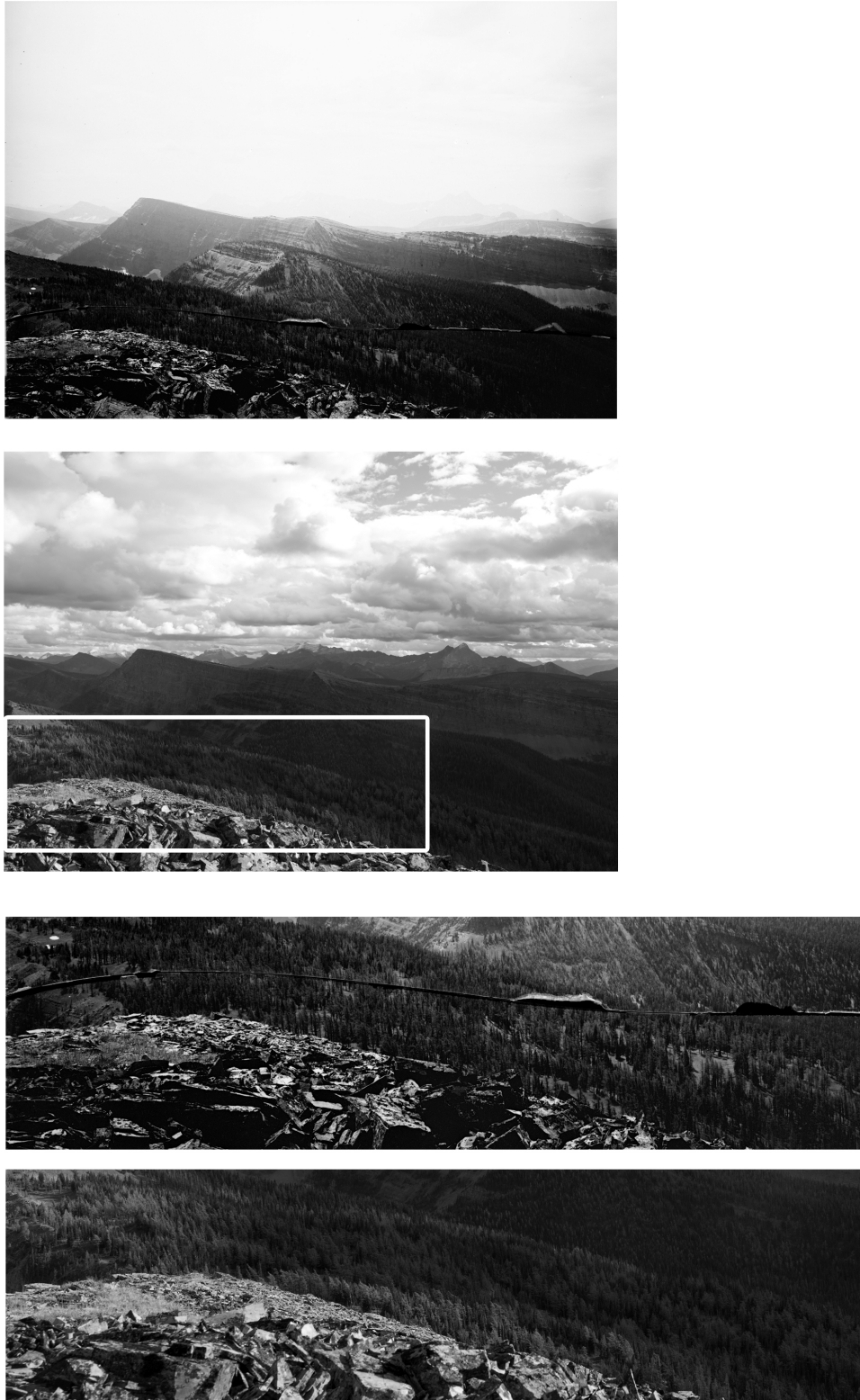


Figure 17: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2004. The meadow study site is Sage, located in the Castle Special Management Area (CSMA), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The photograph second from the top was taken in 2004 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Sage meadow in 1914 (upper) and 2004 (lower). Sage meadow is indicated by the white box in the landscape photograph.



Figure 18: Repeat photograph showing conifer encroachment in subalpine meadows from 1914 to 2005. The meadow study site is Windsor, located in the Castle Special Management Area (CSMA), Alberta, Canada. The top photograph was taken in 1914 by M.P. Bridgeland, a Dominion Land Surveyor (courtesy of Library and Archives Canada). The photograph second from the top was taken in 2005 by members of the Mountain Legacy Project (www.mountainlegacy.ca). The lower photographs show Windsor meadow in 1914 (upper) and 2005 (lower). Windsor meadow is indicated by the white box in the landscape photograph.