Taking a good long look: disturbance, succession, landscape change and repeat photography in the upper Blakiston Valley, Waterton Lakes National Park

by

Graham Duff Watt-Gremm
B.A., University of Victoria, 2004
Dipl. RNS, University of Victoria, 2004

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Abstract

Understanding historical disturbance and succession is critical in park management and restoration. I examined successional patterns and disturbance dynamics in the Blakiston Valley, Waterton Lakes National Park, by analyzing changes in forest structure using field research and repeat photography. I sampled forest structural attributes in 23 stands and interpreted forest cover from oblique and aerial photographs from 1881, 1914, 1947 and 2004. I quantitatively compared the interpretation from oblique photographs to aerial photographs and geographic information system (GIS) data and related succession to environmental factors and historical disturbances.

Successional patterns were dominated by transitions from open meadows and shrublands to woodlands and closed forests, and were related to a small number of environment and disturbance variables, especially elevation, potential radiation, and time since last recorded fire. Accompanying these trends is a decline in landscape diversity.

These findings have implications for restoration and conservation of subalpine forests in the park and across the region. The GIS methods capture spatially approximate vegetation patterns from oblique photographs and show potential for further research, especially in combination with the photograph collection of the Mountain Legacy Project.

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Chapter 1 Introduction

1.1 Restoration ecology or ecological restoration?

I have been fascinated by ecological restoration ever since my father had me hacking gorse and transplanting tree seedlings in a neglected corner of our Saltspring Island farm. As he narrated the landscape with stories of tectonic uplift, glacial deposition, forest succession, and the agricultural clearing a century before, I gained an appreciation for the depth of time that prefaces all our present actions. Twenty years later, I continue to question how we know what to do when we set about restoring a place. A critical part of the answer is history (Higgs 2003): what was the landscape like in the past? What range of plant and animal communities occupied the land, and how did they shift with changing climates, disturbances, and human land management? For a restorationist, the attraction of analyzing ecological change is simple—finding out what *kind* of changes happened *where* in the landscape, can help us understand what to do, and what might happen, when we engage in ecological restoration. This thesis begins and ends with questions about ecological restoration, considering how concepts such as historical range of variation, ecological integrity, and landscape change apply to ecological dynamics in one subalpine watershed.

What is ecological restoration? The Society for Ecological Restoration International (2004, p. 3) defines ecological restoration as the "process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed." In turn, the sciences supporting and gaining knowledge from ecological restoration form the field of restoration ecology, which provides concepts, models and methods for restoration as well as contributing findings to ecosystem, community, and landscape ecology (Higgs 2003, SERI 2004). The suite of activities making up the science and practice of restoration are intentional and multidimensional. Thus restorationists need to address and incorporate a number of concerns, including the aspects of ecosystem health or integrity needing attention, the historical influences and trajectories of the ecosystem, and the manner in which we pay attention to and engage with the place and each other, what Higgs (2003) terms "focal restoration".

My quest to understand restoration in the context of landscape change has led me to explore some core concepts of restoration ecology: ecological integrity, historical range of variation, and reference landscapes. According to Parrish et al. (2003, p. 852), ecological integrity (EI) is an ecosystem's ability to support and maintain a community of organisms with species composition, biological diversity, and functional organization comparable to natural habitats in a region, or within natural ranges of variation. EI also implies the ability to "withstand and recover from most perturbations imposed by natural environmental dynamics or human disruptions" (Parrish et al. 2003, p. 852).

Defining ecological integrity requires framing current ecosystem conditions against the long-term variation in those conditions, or historical range of variation (HRV; Egan and Howell 2001). Essentially, HRV is a set of characteristic historical conditions in which the structure, composition, and functional dynamics of ecosystems are roughly stable or recurring at landscape scales, approximately bounded by climate and land use/management regimes. When land use, climate change, or other factors push ecosystems beyond these bounds, ecosystem conditions become unstable and may develop along novel trajectories towards "alternative stable states" outside the HRV (Turner et al. 1998, Jasinski and Payette 2005), making restoring towards historical conditions difficult or practically impossible.

Restorationists can use the conditions defined by the HRV as targets for restoration projects, based on the specific characteristics of ecosystems that are outside the HRV as compared to a model reference ecosystem or landscape. Reference ecosystems are places or descriptions that serve as models used in the planning and evaluation of restoration projects, allowing for the specification of restoration goals, benchmarks, and comparative evaluations (SERI 2004). References are composite models of multiple ecosystem components, describing the structure, composition, and functional complexity of ecosystems over time. Reference landscapes may be thought of as a collection of ecosystem types, defined by their vital ecosystem attributes and their interactions of metapopulations, disturbance processes, and land management regimes that maintain their ecosystem integrity (Aronson and LeFloch 1996, SERI 2004).

1.2 Promises and challenges of repeat photography

Defining ecological integrity, historical range of variation and reference ecosystems requires restorationists to draw on multiple lines of evidence of varying scale, resolution, and completeness (Egan and Howell 2001). There are a variety of techniques and resources available for historical analyses, including dendrochronology, charcoal studies, archaeological and oral history, and archival research of map and photographic records. For understanding recent landscape history, modern methods of GIS and remote sensing have enabled digital change detection (Coppin et al. 2004), which allows sophisticated analyses of land cover dynamics using air photos and satellite imagery. This may be extended for use with image data from other sources (Davis et al. 2002).

While aerial photography has often been used to interpret historical variation in vegetation cover, repeated historical ground photographs can extend the temporal depth and spatial resolution of analyses, especially when photographs are taken from promontories or show multiple perspectives of the landscape. This can provide valuable perspectives that give insight into particular social, historical, and ecological patterns and processes. There has been a steady interest in using repeat photography to document ecological dynamics since the publication of Hastings and Turner's classic study *The Changing Mile* (1965).

Researchers have applied quantitative and qualitative analyses of landscape change using repeat photography in a variety of settings. Some of the recent studies include glacier and forest cover change in Glacier National Park, Montana (Butler and DeChano 2001, Cerney and Butler 2004), aspen cover dynamics on the Rocky Mountain west slope in Colorado (Manier and Laven 2002), montane forest cover transitions in Jasper National Park, Alberta (Rhemtulla et al. 2002), riparian changes after damming of an Australian river (Start and Handasyde 2002), aspen/grassland ecotone dynamics in Waterton Lakes National Park (Levesque 2005), the distribution of forest types and forest structure in the San Juan Mountains of Colorado (Zier and Baker 2006), and treeline ecotones in Glacier National Park, Montana (Roush et al. 2007). Repeated historical photographs clearly have an important role to play in understanding vegetation and landscape change because of their significant advantages of time depth and image resolution relative to early aerial photos, which date from the 1920's and 1940's for mountainous areas, and the ability for researchers to quickly assess the nature and degree of landscape change from multiple viewing perspectives.

Despite these promising examples and the potential advantages of repeat photography, a number of constraints have prevented the images from being used in the same manner as satellite and aerial imagery. These limitations mean that only certain applications are appropriate and that special techniques must be developed and applied to obtain quantitative information from oblique photographs. Foremost is the problem of scale: ground oblique photographs have continuous and abrupt variation in the scale of objects, so most researchers have only reported quantifying relative, not spatially explicit, attributes (Rhemtulla 1999, Manier and Laven 2002, Pickard 2002).

A number of problems result from this scale variation. First, tree growth in the foreground has a similar effect on spatial estimates of cover as an actual increase of cover in the background (Manier and Laven 2002). Tree canopy cover becomes inflated as photograph scale declines (Fensham and Fairfax 2002), so structural interpretation of the foreground will show disproportionately more open canopies than the background; this is compounded by the difficulty of establishing a minimum size for mappable units in each photograph. Uncertainty also varies continuously across the image, so a line running from the foreground to the background could have the error associated with digitizing double along its length (Davis et al. 2002). This makes delineation of objects and polygons problematic, and means that estimates of uncertainty must be location-specific within the image (Davis et al. 2002). Oblique photographs also provide distorted views of stand shape and canopy structure, given much of the vegetation can be hidden behind tree canopy and topographic features.

Further issues arise when analyzing or classifying oblique images with remote sensing techniques. The overlap in spectral signatures of different classes between foreground and background causes extensive classification errors (Manier and Laven 2002), and the panchromatic range is often limited to simple (i.e. three class) classifications or textural analyses to define polygon boundaries (Hudak and Wessman 1998, Kadmon and Harari-Kremer 1999). With unknown dates and times of original photographs, seasonal phenological differences or tonal differences due to hour of day could show vast, but mistaken, changes in total cover. Differing light conditions also cause inconsistency in tone and contrast (Hinks and Cruden 2003).

Many of the historical photographs used in repeat photography projects are based on multiply-sourced archival collections and are selectively rephotographed, meaning they may be neither systematic nor random representations of the landscape (Pickard 2002). Furthermore, they may not actually represent the baseline that many suppose they do. For example, Hastings and Turner's (1965) original photographs were decades too late to record the massive changes in the landscape following colonization and the massive declines in First Nations populations (Pickard 2002). While ground photography is the oldest available image data other than paintings and drawings, it can only capture the variation within the last one to two centuries, which is relatively short when trying to understand landscape dynamics rooted in previous centuries. As such, repeat photography studies should be augmented with lines of evidence from other historical and ecological studies (Egan and Howell 2001). Finally, photograph collections often cover such a small area that results cannot be extrapolated to larger landscapes. As a result of these limitations, Pickard (2002) argues that most repeat photography studies have been less valuable for research than for education and rhetoric.

However, from the 1880's through the 1950's surveyors with the Geological Survey of Canada, the Department of the Interior's Dominion Land Survey, and other government departments deployed an effective method of surveying the mountains of Western Canada called phototopographic surveying. This work left a legacy of systematic photographs with nearly complete coverage of most mountainous areas. The photographs offer an unprecedented data set for historical researchers and repeat photographers, providing a comprehensive representation of landscape conditions during a period of intense development and ecological transitions (MacLaren et al. 2005).

The Mountain Legacy Project (MLP, formerly the Rocky Mountain Repeat Photography Project) is an ambitious interdisciplinary research project with collaborators from University of Victoria, University of Alberta, Parks Canada, Alberta Ministry of Sustainable Resource Development and Library and Archives Canada (http://mountainlegacy.ca). The researchers' principal aim is to use a combination of archival research, repeat photography, and scientific, historical, and cultural analyses of repeated historical survey photographs to assess landscape change in Canada's mountain landscapes over the last century. Project members have unearthed a vast collection of systematic phototopographic survey images, maps, and associated information dating back to the late 19th century, and have systematically re-photographed more than two thousand of these images since 1997. The photographs come from a series of surveys including MacArthur's 1888-1892 survey of Banff National Park, Bridgland's 1913-1914 survey of the Rocky Mountain Forest Reserve, and Wheeler and Cautley's 1913-1922 Interprovincial Boundary Survey. The Mountain Legacy Project is currently focusing on two key areas: the secure storage, digital reproduction and dissemination of archival photographs at Library and Archives Canada and University of Victoria, and the rephotography of images from Kootenay National Park (1922/1923), Crowsnest Pass (1913/14), and other areas (Pers. comm. E. Higgs 2007).

1.3 Landscape ecology and restoration of Rocky Mountain subalpine ecosystems

1.3.1 Ecology, conservation, and restoration

I first became acquainted with the work of the Mountain Legacy Project, then called the Rocky Mountain Repeat Photography Project, when visiting Waterton Lakes National Park (WLNP) in the summer of 2003. Having studied forest change and practiced restoration in urban protected areas, I was intrigued by the prospect of examining ecological changes at a much broader scale: entire valley landscapes in the Canadian Rocky Mountains.

Studying changes in a landscape requires setting them in context of the larger geographic and ecological regions. Two frameworks are helpful in contextualizing a study of disturbance and succession in the subalpine of WLNP. First, the broad geographical context of the park is well defined by the Nature Conservancy's Canadian Rocky Mountains (CRM) Ecoregion Assessment, which characterizes ecoregions as large areas that have similarities in faunal and floral composition due to large-scale, predictable patterns of solar radiation and moisture (Bailey 1995). Ecoregions have many common species, dynamics, and environmental conditions, and can "function together effectively as a conservation unit at global and continental scales" (NCC 2004, p. 17).

The CRM Ecoregion extends from the northern Columbia Mountains in BC south to western Montana and central Idaho, and includes the mountainous regions of southwestern Alberta and Montana's Glacier National Park. It is characterized by coniferous forests dominated by tree species common further west, for instance hemlocks (*Tsuga* spp.) and Larch (*Larix* spp.), as well as the lodgepole pine (*Pinus contorta* var. *latifolia*), spruce (*Picea* spp.), Douglas-fir (*Pseudotsuga menziezii*), and subalpine fir (*Abies lasiocarpa*). This region has sharp vertical zoning of vegetation and wildlife, associated with abrupt elevational gradients and secondary topographic and climatic effects (Peet 1981, Achuff 1992).

The second ecoregional framework demarcates the landscapes *within* the regions above according to climate and broad vegetation patterns. This approach is used by Parks Canada for ecological land classifications in a number of the mountain parks (Holland and Coen 1982, Achuff et al. 2002). The WLNP classification delineates four ecoregions: Foothills Parkland, Montane, Subalpine, and Alpine. The subalpine extends from the upper edge of montane forest to the lower edge of the treeless alpine, with the altitude of treeline locally depending on aspect. The subalpine is broadly uniform across the Rocky Mountains, dominated by forests of subalpine fir and Engelmann spruce (*Picea engelmanii*). Young montane and subalpine forests are usually composed of lodgepole pine and trembling aspen, depending on site conditions. Lodgepole pine forests typically form following fire when seed is available, forming dense, continuous forests with sparse to open understory, which gradually succeeds to subalpine fir and Engelmann spruce forests in most sites (Kershaw et al. 1998).

Across the CRM ecoregion there are significant populations of large carnivores and other important wildlife, including cougar, grizzly bears, wolves, wolverines, woodland caribou, mountain goat and mountain sheep, and moose (Ricketts et al. 1999, NCC 2004). The region has a large share of parks and protected areas, but industrial forestry, extensive rock and coal mining, oil and gas extraction, recreational and residential development, livestock grazing, and heavy recreational use increasingly threaten conservation values. Sources of habitat fragmentation also include highway and rail corridors, pipelines, and major mining sites (Harvey 1998, Ricketts et al. 1999, NCC 2004). Less immediately visible are threats from long-term and cumulative shifts in hydrology, fire regimes, and disturbance processes due to changing human influences locally, regionally and globally (NCC 2004).

The subalpine zone of WLNP and neighbouring lands (the "Crown of the Continent") shares many of the above threats to ecological integrity and wildlife diversity (Konrad et al. 1999). North of WLNP, the combination of large fires in the 1930's and 2003 with continued logging means that very little old-growth subalpine forest remains in the Castle-Carbondale area (Arc Wildlife Services Ltd. 2004). At the same time, fire exclusion has allowed forests to become more homogenous, which means less open or early successional fire-influenced habitat available for forage by moose (*Alces alces*) (Thompson and Stewart 1997) and grizzly bear (*Ursus arctos*) (Hamer et al. 1991), or open habitat favoured by bighorn sheep (*Ovis canadensis*) for predator/escape visibility (Shackleton et al. 1999).

Within WLNP, threats to biodiversity and ecological integrity are strongly related to the regional pressures and threats affecting individual species and vegetation communities. For instance, species such as grizzly bear or wolverine require ranges well beyond the Park border and are being affected or displaced by habitat fragmentation, resource extraction and industrial and recreational activity (Parks Canada Agency 2000b). Whitebark pine trees (*Pinus albicaulis*) have been decimated by white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (MPB, *Dendroctonus ponderosae*) throughout the region. Furthermore, fire exclusion may be causing successional displacement of whitebark pine by subalpine fir and a decrease in regeneration opportunities in some circumstances (Keane 2001). Decline of whitebark pine communities has serious impacts on wildlife habitat, biodiversity, and ecosystem processes (Keane et al. 2002).

Parks Canada (2000b) aims to protect ecological integrity and biodiversity in WLNP by maintaining or restoring ecological processes such as fire, especially where this can benefit habitat quality or regeneration of threatened species. They emphasize an ecosystem management approach that works with surrounding jurisdictions on habitat protection and wildlife conservation. The majority of active management such as prescribed fire is targeted for the aspen parkland and montane ecoregions (Parks Canada Agency 2000b).

1.3.2 Understanding subalpine landscape patterns in the Rocky Mountains

Restoration ecologists aim to provide guiding concepts and models for restoration and conservation planning and management, which need to be grounded in ecological processes (SERI 2004). In this section I will provide a review of major processes influencing the development of vegetation patterns in Canadian Rocky Mountain subalpine landscapes, focusing on successional models, disturbance processes, and environmental relationships.

Over the last several decades, researchers have developed an extensive literature about disturbance and succession in subalpine landscapes. There has been a gradual shift from simplistic models based on traditional assumptions about succession, towards a set of intersecting and diverging empirical studies, models, and narratives. I will address two long-running questions in this brief review – what models are appropriate for describing and predicting successional development in subalpine forest stands, and what are the most important determinants of vegetation structure in subalpine landscapes?

The conventional view of subalpine stand development was articulated from the 1950's through the 1970's (Day 1972, Coupe et al. 1991, Kipfmueller and Kupfer 2005), and continues to be narrated in popular books (Kershaw et al. 1998). The story begins with a mature forest stand undergoing an event that kills most or all of the trees (a stand-replacing disturbance such as fire). This disturbance releases growing space for seedling establishment, which is determined by the life histories of the trees present before the disturbance, seed source, type of disturbance, and environmental conditions (Oliver and Larson 1996). Usually, in a landscape dominated by Engelmann spruce and subalpine fir, a thick cohort of fire-adapted lodgepole pine establishes from the seed bank held in the serotinous cones, along with lesser amounts of fir and spruce. The pine dominates for 1-2 centuries until senescence, when the fir-spruce understory rises to the canopy and gradually produces a self-sustaining mixed-age stand.

This conceptual model has a number of variations. The classic equilibrium interpretation holds that forests will eventually return to a steady state climax with all-aged spruce and fir maintaining similar levels of dominance, if sufficient time since fire elapses. Aplet et al. (1988) argue that the nearly universal presence of minor to catastrophic disturbances means that all stands are in a process of progressive development, thus a steady-state equilibrium is likely to never occur. However, ecologists continue to document stands where disturbance has not been a critical structuring factor for centuries (Antos and Parish 2002). Under the non-equilibrium model, the high fecundity and shade tolerance of fir leads to eventual dominance by fir and decline of spruce (Day 1972, Peet 1981), but this has seen little empirical validation.

Aplet et al. (1988) illustrate a spruce-fir system where species respond differentially to changing stand conditions, suggesting that equilibrial and nonequilibrial processes operate at different times in stand development. In their model, fir and spruce seedlings both establish immediately in post-fire stands (colonization), but then spruce recruitment diminishes for one-to-two centuries while fir recruitment and growth continue, due to different responses to reduced light and growing space (spruce-exclusion phase). As the initial spruce and fir overstories start to die at 200-300 years, spruce recruitment increases (spruce reinitiation), joining with the multiple cohorts of fir. By the time the first generation fir and spruce trees have died, the forest matures into an open multi-aged stand of spruce and fir, with spruce recruitment depending on canopy openings during gap phase dynamics.

Seed and propagule availability strongly influences the abundance and dominance of trees and understory species following moderate severity and stand-replacing disturbances. In moderate and severely burned patches of a 1974 Wyoming fire, repeated sampling showed that all three common subalpine tree species (lodgepole pine, Engelmann spruce, and subalpine fir) established soon after the fire, with relative abundance being partly related to availability of seed sources (Doyle et al. 1998). The post-fire success of lodgepole pine is largely due to its seed bank of serotinous cones (seeds borne in cones that are kept closed on the tree until released by high heat), rapid growth and water use efficiency (Knapp and Smith 1981). However, post-fire pine density strongly depends on interactions between landscape variation in cone serotiny and historical variability in fire regimes, specifically the length of time between and since stand replacing fires (Schoennagel et al. 2003, Schoennagel et al. 2006).

Whatever successional models appear appropriate for a specific stand, the origin, development, and future of a forest landscape depend on and strongly interact with a number of biophysical, stochastic, and historical variables at stand and landscape scales

(Veblen et al. 1994, Oliver and Larson 1996). Many studies have focused on the importance of disturbance, especially fire, in structuring landscapes in subalpine ecoregions of the Rocky Mountains. While the influence of fire is not ubiquitous or permanent in subalpine ecosystems (Antos and Parish 2002), it is a good place to start in understanding subalpine disturbance regimes because of its spatial extent and lasting influences on vegetation structure.

Most fire studies attempt to characterize fire regime, which is a quantitative and qualitative description of the long-term presence of fire in the landscape, characterized by measures of extent, frequency, spatial pattern, severity, and seasonality (Agee 1993). Fire regimes in the Rocky Mountain subalpine have typically been described as mixed- to high-severity, stand replacing, infrequent (one to several century fire-return intervals), and extensive (Romme and Knight 1981, Romme 1982, Bigler et al. 2005, Dillon et al. 2005).

Many studies have attempted to characterize fire-return intervals in response to climate and weather (Collins et al. 2006) or fire management (Barrett et al. 1991). The long fire-return intervals of subalpine forests mean that they have been less affected by fire suppression and exclusion than lower elevation forests (Keane et al. 2002), though Barrett et al. (1991) and Rogeau (1996) recognize the prevalence of shifts to older age classes and the loss of younger forests. Fire occurrence in the mountains of western North America is strongly tied to interdecadal regional climate variability. In particular relationships between drought severity and area burned correspond well to the warm phase of the Pacific Decadal Oscillation (PDO) (Collins et al. 2006), and fire in cool and moist subalpine ecosystems is especially limited by sub-seasonal and annual variability in climate (Schoennagel et al. 2004).

A number of authors have argued that shifts in fire regimes over the last few centuries are more influenced by weather and climate than changing human land use and increased fire suppression (Keane et al. 2002). For instance, Bessie and Johnson (1995) demonstrate that fire severity is much more related to fire weather than fuel structure in subalpine landscapes, as fires occurring during extreme fire weather have the greatest area burned and burn through many vegetation types in spite of variations in fuel loading. However, local differences in severity, boundaries, and overall fire behavior depend on fuel loadings, especially where mixed-severity fire regimes have been important historically (Habeck and Mutch 1973, Barrett 1996, Keane et al. 2002).

Changes in biotic disturbance agents often accompany shifts in fire regimes. For instance, dwarf mistletoe (*Arceuthobium* spp.) and spruce budworm (*Choristoneura occidentalis*) increase as stands age with the absence of fire, or exotic diseases such as white pine blister rust kills whitebark pine, speeding succession to subalpine fir ecosystems (Keane et al. 2002). Barclay et al. (2005) found that susceptibility to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestation increased with the length of fire cycles and effectiveness of fire suppression, while timber harvest may decrease susceptibility and ability of the beetles to traverse stands.

There has been a small body of research documenting topographically mediated disturbances and interactions in subalpine landscapes, including wind (Baker et al. 2002, Kulakowski and Veblen 2002, Howe and Baker 2003), avalanches (Veblen et al. 1994, McClung 2003, Walsh et al. 2004), debris flows/rockfalls (Butler 2001), and fire—topography relationships (Suffling 1993). Sharp topographic gradients clearly influence what share these types of disturbances have on vegetation patterns, and how much they influence or mediate other disturbance patterns.

One key to understanding topographically mediated disturbances lies in gradient analysis, which is an approach in plant ecology that relates individual species responses to changes in abiotic environmental conditions (Whittaker 1967). Modern developments utilize new methods of terrain and multivariate analysis with ecologically meaningful explanatory variables, and allow insight into landscape vegetation structure in areas of steep environmental gradients (Urban et al. 2002, Lookingbill and Urban 2005, Pierce et al. 2005). The conventional characterization of vegetation by elevation and aspect has been refined by the use of indexes such as topographic moisture potential (Kipfmueller and Kupfer 2005), potential radiation (Donnegan and Rebertus 1999, Pierce et al. 2005), and other variables.

Studies of landscape change clearly need to address changes in vegetation patterns, disturbances interactions, and environmental gradients in concert (Veblen et al. 1991, Donnegan and Rebertus 1999, Kulakowski and Veblen 2003, Kipfmueller and Kupfer 2005). In the present study, I attempted to integrate elements of forest community and landscape ecology by addressing landscape and stand level successional patterns related to environmental and disturbance gradients. I utilized a variety of complementary data sources including historical oblique survey and aerial photographs, historical and modern vegetation maps, and forest stand age, composition and structural data.

1.4 From the first glimpse: research objectives and approaches

My study area introduced itself to me as soon as I saw the original and repeat photographs from the 2003 repeat photography field season. When I viewed the landscape from Mt. Blakiston, the highest point in WLNP, looking west towards South Kootenay Pass (Figure 1.1, larger photos in Appendix A), I was immediately taken with the complexity of changes in vegetation cover revealed by the photographs, and I became motivated to answer a basic question: what happened here? Some broad patterns could be distinguished in the pair of images. First, a large portion of the south aspect slope in the east-west valley consisted of meadow or shrub cover without evidence of snags or logs that could be expected to result from recent fires. In contrast, the north aspect slopes appeared to be covered with a thick canopy of lodgepole pine forest some decades in age. In the repeat image, canopy cover appeared relatively uniform across most of the valley, aside from an open forest/mixed herb and shrub complex across some of the upper south aspect slopes, and a series of avalanche paths persisted on most steep slopes. The

Figure 1.1 Oblique 1914 (left) and 2004 (right) view from Mt. Blakiston looking toward South Kootenay Pass.

photograph pair also revealed the role of geology and geomorphology in shaping the vegetation structure, displaying a thick band of limestone across the forests of the north side of the valley, abundant rock avalanches, and a braided stream along the valley floor.

Based on these observations, I formed two working hypotheses to help answer my initial question. First, I hypothesized that forests in the valley displayed complex successional trajectories from the early seral conditions following the fires of the 19th century to the continuous forest cover seen in the 2004 photographs. I expected these changes to be affected by topography, microclimate, site conditions, time since forest establishment, and interactions with other disturbances. Second, I noted the appearance and disappearance of avalanche paths in the valley and evidence of more localized disturbances such as insect and disease outbreaks and wind throws. These observations led to my hypothesis that as time since stand initiation increases, disturbances other than fire work to create heterogeneity that counters the effects of homogenizing successional trajectories.

To evaluate these hypotheses, I designed a study with two main components. In the field study (Section 2.2), I characterized the forest stand structure, composition, and conditions at a range of sites, seeking to understand the underlying environmental and disturbance factors that help explain the variation in forest structure. Specifically, I asked the following questions:

- How does forest structure and species composition vary among forest stands?
- What are the relationships between forest structure, community composition, and environmental variables among stands?

In the photograph and GIS analyses (Section 2.3), I developed an approach to quantify the kind and extent of vegetation cover transitions observed in the survey and aerial images (1881, 1914, and 2004 oblique views, and 1947, 1967, and 2005 orthophotos). I then related the observed trajectories to environmental variation within landscape and disturbance characteristics. I asked both methodological and exploratory questions:

- How do I relate quantitative information derived from horizontal oblique photographs to information in geographic projections (i.e. vegetation interpretation, land classifications)?

- What are the patterns of vegetation transitions (trajectories) between image years? How do these patterns relate to environmental and disturbance variables?
- What are the patterns of forest cover transitions at the study plots, and how do these patterns relate to forest structure, community composition, and environmental variables?

With my study design and approach to data analysis, I assert that multivariate ecological data are inherently *messy* (Legendre and Legendre 1998), especially when they represent several lines of evidence from varying sources and temporal periods. Any exploratory or predictive analyses should be robust under conditions of missing data, highly non-normal multivariate distributions, non-linear relationships among variables with high-order interactions and autocorrelation among predictor variables, and other problems that may plague conventional multivariate statistical methods in landscape change studies. Therefore I valued exploratory approaches that allow careful and circumspect examination of patterns, structures, and relationships, choosing methods appropriate for this study such as non-metric multidimensional scaling, Procrustes analysis, and classification and regression trees from methods layed out by Digby and Kempton (1987), Legendre and Legendre (1998), and De'ath and Fabricius (2000).

Chapter 2 Methods

2.1 Study area description

2.1.1 Biophysical setting

Waterton Lakes National Park (WLNP) is a protected area of about 525 km^2 at the southernmost extent of the Canadian Rocky Mountains in Alberta, Canada (49° to 49° 12' N, and 113° 40' to 114° 10' W) (Achuff et al. 2002) (Figure 2.1). WLNP forms part of the Waterton-Glacier International Peace Park, a designated World Heritage Site and IUCN biosphere reserve (Parks Canada Agency 2000b). WLNP is located within the Northern Continental Ecoregion and the Montane Cordillera Prairie Ecozones (Francis 1997). Ecological units can be broadly differentiated into Foothills Parkland, Montane, Subalpine and Alpine, with the subalpine divided into lower and upper regions by macroclimate (elevation and aspect) and vegetation characteristics (Achuff et al. 2002). This study focuses on the upper and lower subalpine ecoregion of the upper Blakiston Creek watershed in the northwest of WLNP, starting upstream of Blakiston Falls and extending towards South Kootenay Pass (SKP). The study area is approximately nine km long by three km wide (27 km^2), comprising nine percent of the subalpine area in the park and five percent of total park area.

The physiography of WLNP is characterized by older Paleozoic limestone forced over younger Mesozoic (Upper Cretaceous) rock by the Lewis Thrust. The steep ranges have since been influenced by glacial (Late-Wisconsonin - 70,000 - 50,000 ya), fluvial, and other geomorphological processes (Achuff et al. 2002). WLNP displays a remarkable diversity of ecosystems and vegetation, containing eighty-three “ecosites" based on vegetation, soil and landform, and over half of Alberta’s vascular plant species (Kuijt 1982). The study area includes thirty-two of these ecosites, including fluvial, morainal, colluvial, and bedrock landforms. Vegetation types in the study area include conifer, mixed conifer and aspen, meadow, and shrub communities (Achuff et al. 2002), roughly corresponding to the cooler and moister continental subzones of the Engelmann spruce-subalpine fir zone (ESSF) in the British Columbia Biogeoclimatic Ecosystem Classification (BEC) (Coupe et al. 1991). The topography of the study area is defined by the east-west drainage pattern,

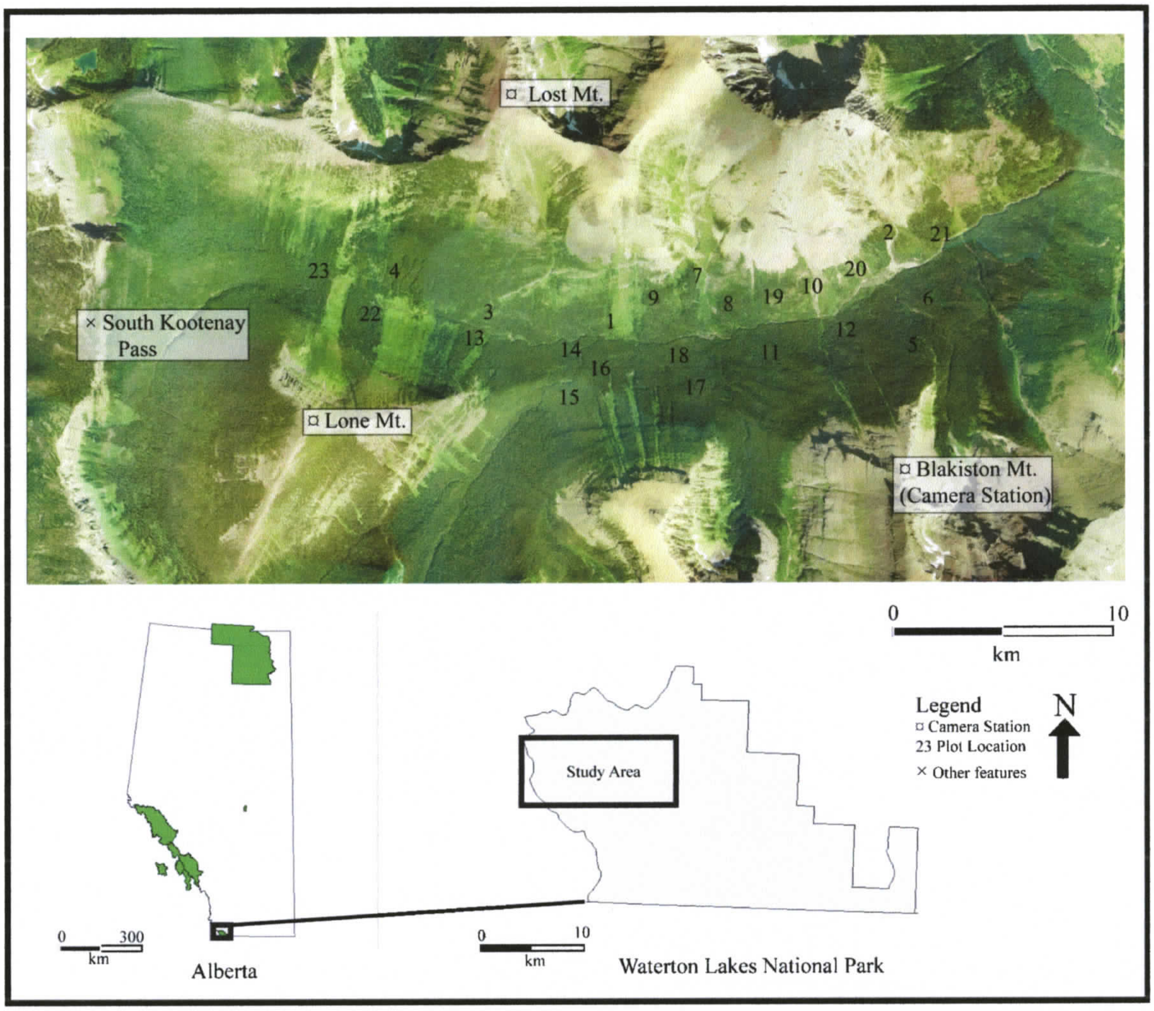

Figure 2.1 Study area map with plot locations. The orthophotograph area encompasses all oblique photograph views used and the outer boundary used in terrain analysis calculations.

gently sloping valley floor and steep north and south-aspect valley sides. Middle slopes feature prominent cliff bands, limestone scarps, avalanche tracks, rock avalanches and debris flows.

The macroclimate of the WLNP falls within the Boreal Southern Cordilleran and Subhumid Grassland Ecoclimatic Regions (Francis 1997). Mountainous portions are characterized by wet and cool summers with 50-100 frost-free days, cold winters, and high winds from the south and southwest occur at any time of the year (Poliquin 1973). Pacific Maritime and Arctic Continental air masses combine with complex topography to produce highly variable temperature and precipitation patterns. Higher elevations (Akamina Pass) have experienced an average total annual precipitation of 153 cm, and Poliquin (1973) described the Blakiston Valley area as having high to very high annual precipitation (150–175+ cm). However, characterizing the weather in the study area is difficult because of variable topography, limited data sets, and strong regional climatic variation (Poliquin 1973, Colenutt and Luckman 2000).

Holocene vegetation, fire and climate have been reconstructed regionally through palynological studies (Mandryk 1996, Hallett and Hills 2006, Power et al. 2006). The early Holocene (~10,000-8,000 yr BP) was distinguished by warm, dry summers, higher fire frequency and open juniper, pine and grassland parkland in upper montane valleys (Hallett and Walker 2000). After a 200 year cool period, fire frequency increased between ~8,000 and 4,000 yr BP, corresponding to the warm/dry Hypsithermal period in the Rocky Mountains, with increased proportions of *Picea, Betula, Alnus, Pseudotsuga* and *Larix* pollen in the palynological record (Hallett and Hills 2006). Cooler, wetter conditions prevailed during neoglacial advances ~4,000 yr BP, bringing a sharp decrease in fire frequency and the onset of *Picea/Abies/Pinus* forests common in the montane and subalpine forests of the region today, especially during the Little Ice Age (500-150 yr BP) (Hallett and Walker 2000, Power et al. 2006).

More recent climate history has been reconstructed using dendrochronology and instrumental records, which for southwestern Alberta effectively extend back to the 1600's and early 1900's, respectively (Colenutt and Luckman 2000). In general, the reconstructions show cooler than average (11.5 °C for Carway, Alberta, ~50 km SE of Waterton Townsite) conditions in the early 1600's, early 1700's, and much of the 1800's especially around 1850, 1875, and 1920. Warmer than average conditions prevailed in the late 1600's, 1770-1790 and the 1890's. There were several periods of drought between 1720-1735, during the 1850's, and 1920-1940, with wetter periods in the late 1600's, from 1790 through 1840, 1915, 1945-1960, the late 1960's, and 1987-1996 (Colenutt and Luckman 2000, Watson and Luckman 2004).

The diverse vegetation and topography of the northwest region of WLNP is associated with quality habitat and regional connectivity for large fauna. For instance, many grizzly bears in the region move in spring to the broad valleys of the Flathead (the drainage west of South Kootenay Pass), though others remain in the mountains for spring foods in avalanche chutes and meadows, and huckleberries and buffalo berries in burn sites and open areas (McLellan and Hovey 2001). In mild winters, moose may use the dense shrublands of lower avalanche paths for shelter; Langley (1993) reports that a number of moose travel to Alberta from the Flathead over South and Middle Kootenay passes.

2.1.2 Study area history

South Kootenay Pass was an important travel route before European contact and during trade and exploration periods, as it was the easiest and most direct route across the mountains in the region (Getty 1972). The Ktunaxa of the Flathead Valley and Nez Perce both used the pass to gain access to plains bison. Use continued during the early trade years, until the Blackfoot closed many of the trans-mountain trails circa 1810 to control arms exchanges (Getty 1972). The first recorded traverse of the Pass by Europeans was the Palliser Expedition (1857–1860) (Getty 1972).

Observations made during the early expeditions give insight into historical forest conditions. According to the 1876 report of Capt. S. Anderson, the astronomer for the North American Boundary Commission, old trails were blocked by timber and needed to be re-cut. Others noted the rough trail conditions due to undergrowth and the extensive burned areas. Dawson (1875), a geologist with the International Boundary Commission of 1872–1874, noted that buffalo remains were found in South Kootenay Pass on the east side of the watershed, signifying the importance of the route for people living west of the pass.

Dawson returned to southern Alberta in the early 1880's and detailed the geology east and west of the Pass, taking the first photographs of the valley in 1881 (Appendix A 8). He noted that August of that year was very dry in the lower pass, with considerable evidence of fire. Indeed, the young post-fire forests characterized the overall forest condition of the Waterton Lakes area at the turn of the last century (MacMillan 1909).

WLNP was incorporated as Kootenay Lakes Forest Park in 1895, with an area of 87 km^2. WLNP became a National Park in 1911, and the boundaries were temporarily expanded in 1914 to include much of the Castle River drainage to the north, before shrinking from the southern Castle drainage to the present boundary along the watershed boundaries of the Bauerman/Blakiston and Dungarvan Creek valleys in 1921 (Getty 1972).

As of the 1940's, fire suppression effort and effectiveness increased, with no substantial fires recorded in the northwest region of the park between 1940 and the late

1990's (Barrett 1996). The main trail above Blakiston Falls has been realigned a number of times (pers. comm. R. Watt 2004), but there has otherwise been little direct human modification of the study area aside from the camp and warden patrol cabin at Lone Lake.

2.2 Forest stand sampling & description

2.2.1 Sampling methods

Examination of the historical photographs reveals a range of seral to mature forest stand structures encompassing a variety of patterns of post-fire stand development after the major fires of the 1800's (Appendix A). Characterizing modern forest conditions requires examining both visual evidence and sampling stand attributes in the field. There are a number of approaches to sample and characterize forest vegetation stands at the landscape level (Barbour et al. 1999, Jennings et al. 2006). These include regular, random, stratified random, and preferential sampling designs. As my objective was to document a range of post-fire forest stand structures, I used preferential (purposive) sampling instead of other methods, so my selection of plots may show more bias than a random, stratified random, or systematic design. Additionally, as the intent of the field study was exploratory, the need to characterize particular responses to particular gradients was not a priority (Pers. comm. J. Antos 2004).

I selected plot locations by delineating regions of fairly uniform forest cover and structure on a 1999 orthophoto supplied by WLNP staff (Figure 2.1). For each day in the field I traversed a region and selected 1-2 stands that appeared representative of the dominant forest type for the area. I based this assessment on dominant species, differentiation of the canopy and the presence of multiple size classes. I placed 23 plots in the study area from July 3 to 23, 2004, during the peak of flowering for understory plants in the lower and middle subalpine.

At each site, I delineated a 20x20 m (400 m^2) plot with flagging stakes and tape, dividing it into four subsections to assist tallying vegetation cover. I recorded slope using a Suunto clinometer, aspect with a Suunto MC-2D compass, noted slope position, slope shape, and surface topography, recorded UTM coordinates and elevation (Zone 11, NAD83) using a Magellan GPS, and marked plot location on the orthophoto. I examined soil to depth of 25-50 cm using a soil auger, noting soil texture, humus form, colour, and coarse fragment content, then deduced moisture and nutrient regimes following Province of British Columbia (1998, p. 10-12). All site and vegetation data were recorded using Form FS882 (2) HRE 98/5 from Province of British Columbia (1998).

I noted all visible vascular plants in each plot with the aid of Kuijt (1982) and Kershaw et al. (1998), recording genus where I could not interpret species due to lack of flowers or other identifying characteristics. For each species I estimated abundance as percent cover by layer (tree layer >10 m, shrub <10 m, herb, and bryophyte/seedling).

For all standing dead and live trees and saplings within each plot, I recorded species, diameter at breast height (DBH, 1.3 m), and possible cause of mortality based on visual inspection for fire or impact scars, beetle bore holes, or snapped boles. I measured all coarse woody debris (CWD, defined as dead woody material located above the soil surface and larger than 7.5 cm diameter, (Province of British Columbia 1998) at the bole base using DBH tape, recording only logs with the bole base in the plot. Unlike methods designed to estimate CWD volume, this measure only allows comparison between plots using basal area calculations.

To obtain an estimate of stand age I used an increment borer to collect 2-3 samples per species from 5–8 dominant trees per stand. As lodgepole pine and Engelmann spruce often establish immediately after fire when there is a seed source present (Aplet et al. 1988), I cored pines and spruce trees preferentially over co-dominant fir trees. I sampled 193 cores in total, keeping 166 for analysis as some were inferior duplicates (12) or too rotten to use (15). I took the cores as close to the ground as possible, angling towards the root collar, and counted the annual rings at the University of Victoria Tree-Ring Laboratory using a stereomicroscope. I assumed the oldest core taken from each stand represents the approximate minimum time since establishment, which does not account for remnant trees belonging to cohorts established in previous fires. However, this cannot be taken to mean time since disturbance or stand initiation as regeneration was clearly delayed in a number of sites, which is a phenomenon long associated with high-elevation fires (Stahelin 1943).

2.2.2 Data analysis

In order to explore relationships between stand structure and terrain, I developed a number of terrain layers based on a 20 m digital elevation model (DEM) and sampled each at site coordinates using GRASS GIS version 6.1 (GRASS Development Team 2006). I computed elevation and slope directly from the DEM, and used two ecologically meaningful proxies for soil moisture and solar radiation: Topographic Convergence Index (TCI) (Beven and Kirkby 1979, Wolock and McCabe 1995, Arge et al. 2003), and growing-season potential relative radiation (PRR) (Hofierka and Sùri 2005, Pierce et al. 2005). Using GRASS I computed PRR and TCI with the modules r.terraflow and r.sun, using a section of the DEM sufficiently larger than the study area to account for shading effects and upstream flow accumulation.

The Topographic Convergence Index assesses topographic effects on drainage with the formula:

$$TCI = \ln\left[\frac{\alpha}{\tan(\beta)}\right]$$

where α is the upslope contributing area, β is the local slope angle, and ln is the Napierian logarithm (Wolock and McCabe 1995). Flow directions can be steepest (converging) or multiple (diverging and converging); I selected the steepest converging flow direction (SFD) as there was no difference between the results for the DEM data set. This index is well correlated with soil moisture, with highest TCI occurring at the wettest sites (Taverna et al. 2004). PRR is a measure of Watt-hours per square metre (Wh/m^2), summed over one day from each month of the growing season (June–September, following Pierce et al. 2005); the algorithm incorporates hill slope shading effects and monthly variation in solar insolation (Hofierka and Sùri 2005, Institute for Environment and Sustainability 2005).

I provided a summary of the tree species and basal area data within and between plots using importance value (IV) (Barbour et al. 1999), which is the sum of the proportions relative basal area, relative density, and relative frequency (ranges from 0–300). I prepared tables of recorded abiotic and biotic site variables, and explored these values using simple correlation analysis and scatterplots.

To assess differences in plant species composition among plots I used non-metric multidimensional scaling (NMDS) on plant cover data (tree species were included and plant cover was summed across layers). NMDS is a highly robust ordination method that represents the ordering relationships among objects but does not assume linear relationships between variables as do simpler ordination methods (i.e. principal components analysis, correspondence analysis, or principal coordinates analysis) (Digby and Kempton 1987, Legendre and Legendre 1998). An ordination is a multivariate technique that reduces a large number of observations (i.e. species abundances) taken from a set of objects (i.e. vegetation plots), to a smaller number of dimensions (axes). This can be very useful for interpreting differences between sites. For NMDS the relative placement of the plots on the configuration closely represents the actual rank differences among the objects based on the observations (Digby and Kempton 1987, Legendre and Legendre 1998). I chose to use just two axes for ease of interpretation.

NMDS ordinations have a wide variety of options that strongly affect the resulting visual configuration. I selected the species transformation and dissimilarity measure that are best suited to vegetation data with moderate variation in species composition between sites (Legendre and Legendre 1998). Using the function metaMDS from the R (version 2.3.1) (R Development Core Team 2006) package Vegan (version 1.8-2) (Oksanen et al. 2005), species data were transformed using square root and Wisconsin double standardizations before computing the Bray-Curtis dissimilarity matrix, a distance measure that is appropriate for species composition data (Oksanen 2006).

The NMDS algorithm repeatedly places sites randomly on the plot and iteratively moves the site positions on the plot to minimize stress, which is a monotonic step regression comparing the configured inter-site euclidean dissimilarities ($d_{\bar{hi}}$) and the original dissimilarity matrix (d_{hi}):

$$STRESS = \sqrt{\frac{\sum(d_{\bar{hi}} - \hat{d}_{\bar{hi}})^2}{\sum d_{\bar{hi}}{}^2}}$$

where $\hat{d}_{\bar{hi}}$ are the predicted dissimilarities (Quinn and Keough 2002). The algorithm performs a number of random starts, stopping when the attempts converge on a configuration with the lowest stress. The resulting NMDS plot is scaled and rotated so Axis 1 contains the largest amount of variation in vegetation data and separation between sites indicates differences in species composition and cover. Species scores are scaled to a weighted average of site scores for display, meaning that species names are displayed near the sites containing them in greatest abundance.

There are a variety of approaches available to test the concordance of species composition data to environmental factors (Jackson 1995, Legendre and Legendre 1998, Quinn and Keough 2002). The simplest approach is to assemble a set of correlations of all possible species and environment variables, but this increases the likelihood of Type I errors. Multivariate techniques such as correspondence analysis or principal components analysis summarize variation in species data into a limited number of axes, allowing interpretation of these axes by correlation with environmental variables, though this can still result in many individual correlations (Jackson 1995). More sophisticated techniques such as canonical correlation analysis and redundancy analysis may still assume linear relationships between variables. The matrix comparison Mantel test (Mantel 1967) may be used to test correlation between matrices using randomization, though the results may be difficult to interpret as there is only one universal statistic.

A robust alternative is Procrustes analysis. This method rotates and stretches two configurations of points (from previously conducted ordinations) to minimize squared differences, then assesses the resulting fit as the minimization of the residual sum of squares between the points for each observation (Peres-Neto and Jackson 2001).[1] The relative relationships of the objects in the ordinations are preserved for further visual inspection, which can be useful for assessing which sites have the greatest agreement or difference between species composition and environmental factors.

I selected the biotic and abiotic variables for Procrustes analysis of vegetation/environment relationships from the NMDS using the R function envfit (Oksanen et al. 2005) from the Vegan package, which fits explanatory stand structural and environmental variables onto an ordination with significance tests based on permutation. Permutation or randomization tests (Manly 1997) estimate the significance of an observed statistic relative to a large number of values for the same statistic generated by randomly permuting (reshuffling) the original data set and recording the correspondence of the randomized data set to the original data. The shuffling is repeated many times, creating a distribution of values that represent a random association between the matrices, and the proportion of randomized statistics that have a residual sum of squares smaller than or equal to the observed statistic.

I used the subset of variables that explained the highest proportion of the variation in vegetation composition for interpreting the NMDS configuration. I then used Procrustes

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[1] Procrustes was the gruesome innkeeper of Greek mythology who had but one bed so he stretched or chopped his guests to fit (Legendre and Legendre 1998).

analysis to test the fit of the comparison between the NMDS configuration among sites using species composition and two separate NMDS configurations using (1) stand structure (maximum age, basal area, and shrub and herb diversity) and (2) environment variables (slope, PRR, and elevation) (Peres-Neto and Jackson 2001, Oksanen et al. 2005).

2.3 Photo interpretation and GIS analysis

2.3.1 Data sources and preparation

The challenge of understanding and modeling historical successional dynamics and ecosystem trajectories is both helped and hindered by the availability of such rich and varied imagery and GIS data. The variety of data helps by offering greater time depth and multiple variables to use in analyses, and hinders by introducing data integration challenges and spatial and thematic uncertainty. I initially chose the study area based on the excellent phototopographic survey coverage from the 1914 Rocky Mountain Forest Reserve survey, which is accompanied by the repeat images from the 2004 Mountain Legacy Project field season. There are three survey stations with several overlapping views of the main valley – Mt. Blakiston, Lone Mt., and Lost Mt. (Figure 2.2).

This study utilizes a set of images of a subalpine valley in Waterton Lakes National Park originally taken by M.P. Bridgland in 1914 and rephotographed by the Trudi Smith and Eric Higgs in 2004. The original photographs are high resolution (scanned from medium-format glass plate negatives) and provide systematic coverage of the landscape, while the repeat photographs are high-resolution medium format digital images taken with a Hasselblad H1 with an Imacon iExpress 16 megapixel digital back; the photographs are displayed in Appendix A. WLNP staff provided a series of 1881 photographs taken by George Dawson (Appendix A 8 and 9), one of which the Mountain Legacy Project was able to retake, and scanned aerial photographs from 1947, 1967, and 1999. WLNP also furnished a 2005 orthophoto (NAD 83, UTM zone 12), a 20 m digital elevation model (DEM), draft vegetation polygons from the 2005 vegetation mapping project, and GIS layers from the 2002 Ecological Land Classification (ELC) (Achuff et al. 2002). These included polygons from the 1967 forest cover interpretation (Lopoukhine 1970), the digital Phase 3 forest cover interpretation as used in Barrett's (1996) fire history study, and land classification maps with vegetation, terrain, and soil components.

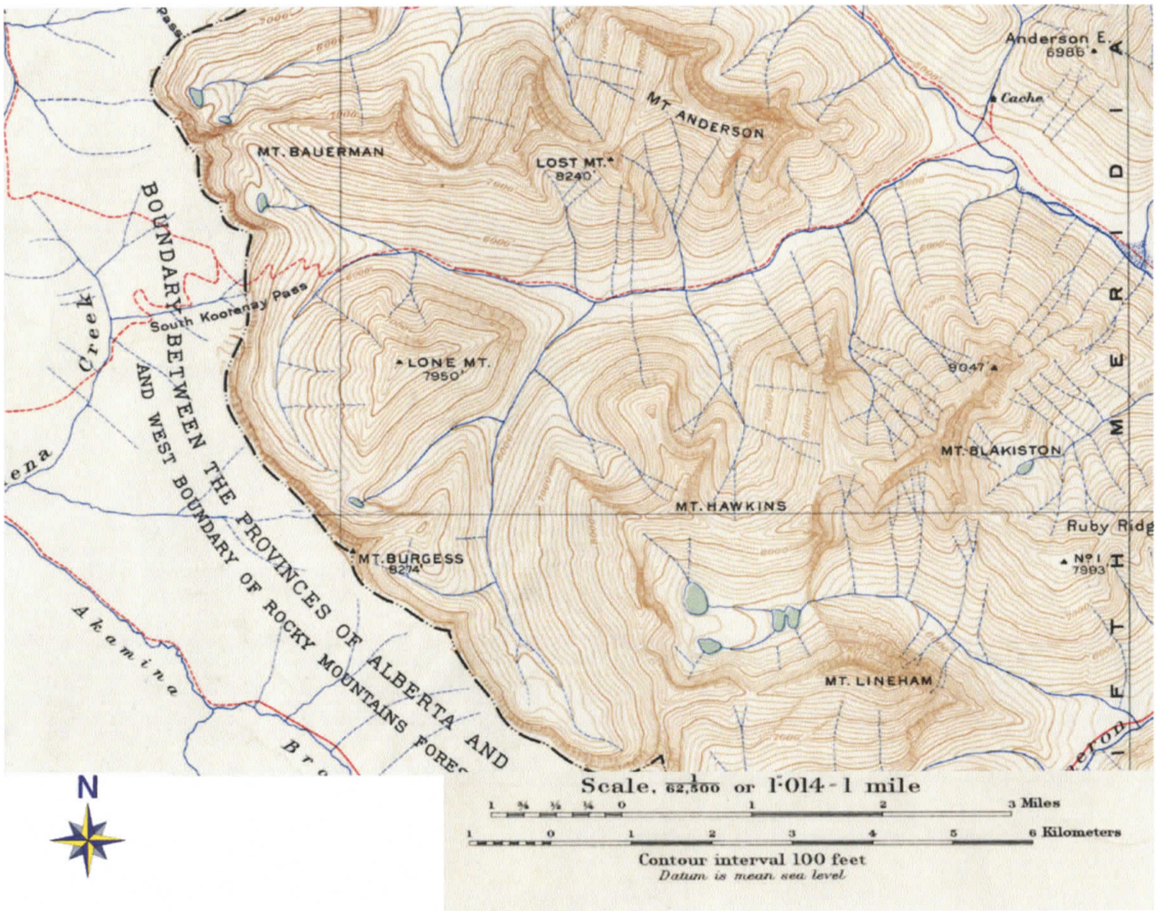

Figure 2.2 Detail from map sheet 5 from M.P. Bridgland and A.E. Hyatt's 1913–1914 survey of the Rocky Mountain Forest Reserve, showing survey camera stations with triangles and elevation marks. The three stations providing images of the study area are Mt. Blakiston, Lone Mt., and Lost Mt. Ottawa: Dept. of the Interior, 1915.

In addition, I developed three map layers representing influence of disturbance agents for use in multivariate analyses. The MPB layer is a presence/absence map of the MPB infestation in 1981–1983 (map on file at WLNP warden office), the avalanche layer indicates presence of avalanche path vegetation types or disturbance modifiers in 1914, 1947, 2004, and 2005 vegetation polygons, and the geomorphological disturbance layer indicates presence of geomorphic process modifiers (i.e. debris flows or braided streams, extracted from my photo interpretation and the ELC).

I prepared photograph mosaics from 1947 (47WL5W257, 47WL5W258, and 47WL5W259) and 1967 (142, 144, and 106) aerial photographs using GRASS GIS. The 1947 mosaic fits the 2005 orthophoto with reasonable accuracy, but the larger scale of the 1967 photographs made it difficult to assemble an accurate orthophoto so I used the 1967 forest cover interpretations rather than interpreting the photographs myself. The 1967 cover interpretations had an unknown projection that was significantly distorted from the 2005 orthophoto; I registered it to the orthophoto using control points from peaks, ridges, lakes, rivers, and roads, using a second order affine transformation. The ELC polygons also needed to be adjusted 105 m west and 6 m north to exactly match the features on the 2005 orthophoto.

2.3.2 Photo interpretation methods

To interpret the 1881, 1914, 1947 and 2004 oblique and aerial photographs, I adapted the 2005 cover classification scheme of the WLNP/Glacier National Park (GNP) vegetation project by generalizing it to a level that preserved stand structural characteristics but omitted species (Appendix B). I did this because tree species were difficult to discern in historical photographs. For the purposes of my study this system is appropriate because it is directly comparable to the current WLNP and GNP vegetation classification, but is generalized to the extent that its results could be translated to BC and Alberta vegetation classification systems used in similar studies (i.e. Rhemtulla 1999).

I interpreted the photograph layers (oblique and aerial) onscreen in GRASS, creating maps of vegetation cover with an eight-class vegetation cover scheme. After the interpretation, I simplified the eight-class scheme to a five-point scheme (Appendix B) to enable better comparisons between my interpretations and the 1967 and 2005 interpretations, and to make transition analyses easier to interpret. This simplification reduced the possible permutations of transitions from 56 to 20, but meant that I lost the ability to detect subtler variations in vegetation cover and transition patterns. To relate transition patterns to stand structure and site environmental factors, I also interpreted cover at the 23 field study plot locations using the five-point scheme on 1947 and 2005 orthophotos.

2.3.3 Spatial approximation methods

Obtaining spatially explicit measures of land cover has emerged as one of the most difficult and important challenges for researchers using data derived or interpreted from historical oblique photographs (Pickard 2002). A small selection of GIS and remote sensing techniques could prove to be useful in overcoming this challenge. One approach is to rectify the photographs to a digital elevation model (DEM), using control points identifiable in both the oblique images and an orthophoto (pers. comm. P. Keller 2004). In an initial pilot study, I attempted this with three images. However, I found the results were highly distorted and difficult to interpret due to the lack of definite control points in the forested terrain. A colleague with the MLP tried to overcome this problem by placing ground control points (GCP's) in the landscape using flags and a GPS, though placing sufficient points was highly time-consuming (pers. comm. W. Roush 2006). Corripio (2002) also used GCP's, translating surface snow reflectance values to a GIS with a function that maps each pixel of the oblique image to each DEM pixel.

Some researchers have adapted orthorectification software to register high-oblique images from aircraft to digital terrain data (Neteler et al. 2004). This requires the nadir point (image centre) and horizontal fiducial marks to be below the horizon (pers. comm. M. Neteler Nov. 2005), which is not the case for the majority of images in this study. Davis et al. (2002, 2004) used image fusion techniques to combine oblique videos with rendered perspectives of the DEM and forest inventory data, on which they were able to directly digitize new vectors.

Aside from the image fusion approach of Davis et al. (2002, 2004), the above methods seemed inappropriate for working with multiple photographs across a large landscape. In the end I adapted an approach used by M.P. Bridgland, the surveyor who mapped much of the mountains of Western Canada (MacLaren et al. 2005) and took the 1914 images from my study area. To make maps from photographs and survey instrument measurements, Bridgland and other surveyors defined the spatial location of many features in the images using a grid system referred to as the picture plane, or "perspectrometer", then translated features to the topographic maps (MacLaren et al. 2005) (Figure 2.3).

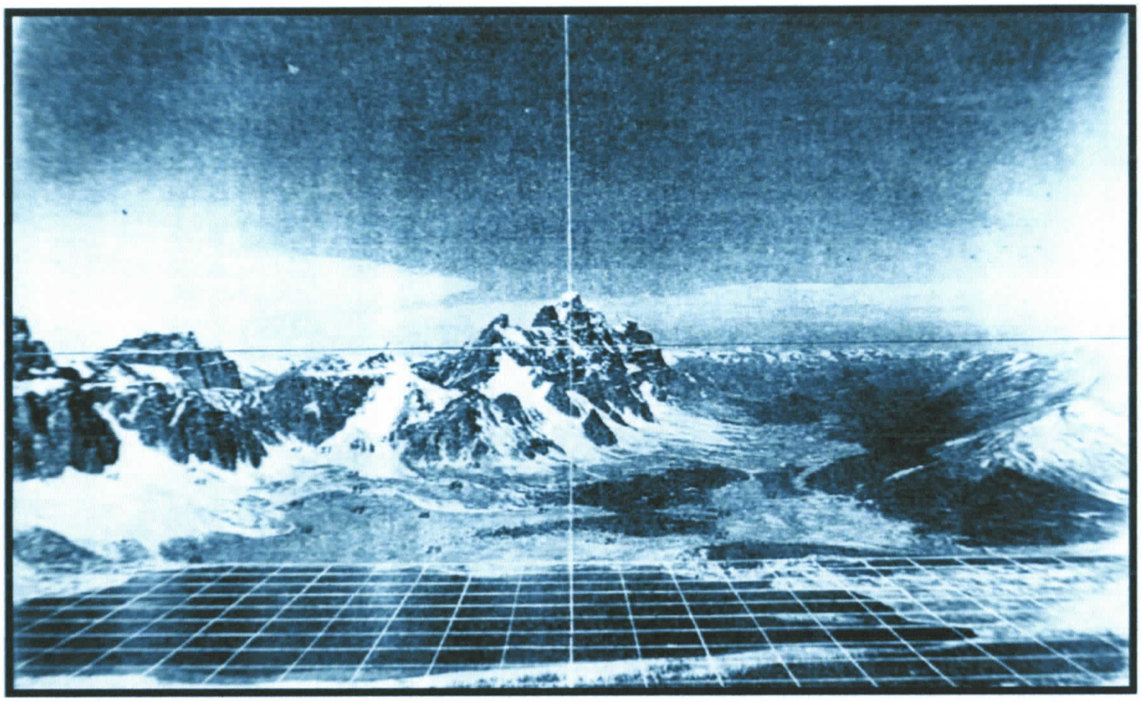

Figure 2.3 Phototopographic image plane (perspectometer) of the Tonquin Valley, Jasper National Park (from Bridgland 1924).

Bridgland's phototopographic methods inspired me to experiment with using a grid to define a basic spatial unit (BSU) in order to translate data between oblique and aerial views, thus allowing a spatially approximate comparison between the different views of the same areas. The idea was to create a grid in the GIS, view it draped (overlaid) on a projected image of the landscape in terrain visualization software, fit it to the photographs, then manually register the projected grid to the original grid and use GIS and database operations to relate data interpreted from the oblique photographs to GIS data sets.

To choose a grid size that would minimize both effort and spatial uncertainty, I created one ha and four ha vector maps of grid squares in GRASS to entirely cover the study area. I then applied a random colour table to visually differentiate and identify grid cells, and worked through the workflows outlined below. In the image pair I evaluated (Appendix A4), I found that the four ha grid took one-quarter of the time of the one ha grid to register, and for areas of undulating terrain the interpreted features could “shift" by at least 100 m, so I selected the four ha grid size. This resulted in a grid of 1296 cells, or 5184 ha.

The spatial approximation workflow has two main components. In the scene selection and data preparation workflow (Figure 2.4), I selected the images that best represented my study region (Appendix A), and overlaid, scaled and rotated the photograph pairs to fit using ridgelines, rivers, and other stable features, in Adobe Photoshop 7.0. Next, I used a smooth interpolation method (regularized spline with tension) to resample the 20 m DEM to 3 m in order to make the orthophoto drape visually appealing, which I prepared with the GRASS terrain visualization module NVIZ. I obtained approximate image centre coordinates by rendering the terrain model to resemble the repeat photograph view, then fine-tuned the perspective by adjusting the coordinates of the image centre and viewpoint and the field of view, until the NVIZ representation closely resembled the repeat photograph. I then exported a screen view of the NVIZ scene to Adobe Photoshop (Version 7.0) to verify matching of ridgelines, water courses, and vegetation, and repeated fine tuning in NVIZ if needed. Finally, I overlaid the colourized raster grid and a binary grid defined by the vector grid lines on the scene in NVIZ, and exported the orthophoto scene and grids to overlay on the repeat photograph in Photoshop.

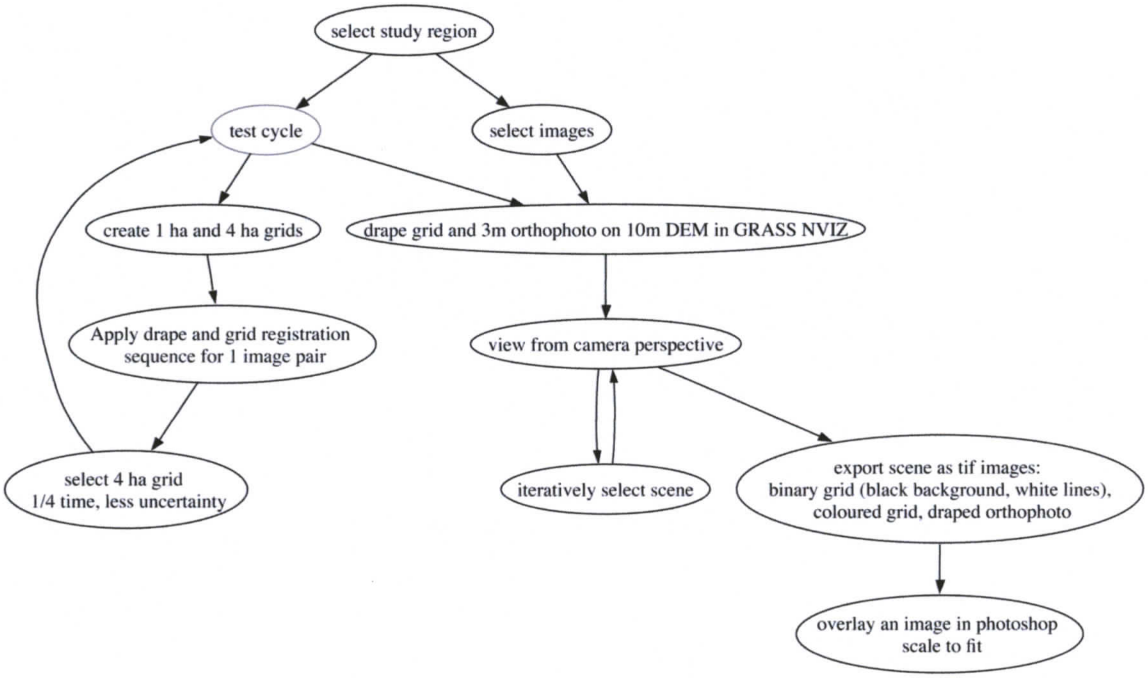

Figure 2.4 Scene selection and image data preparation.

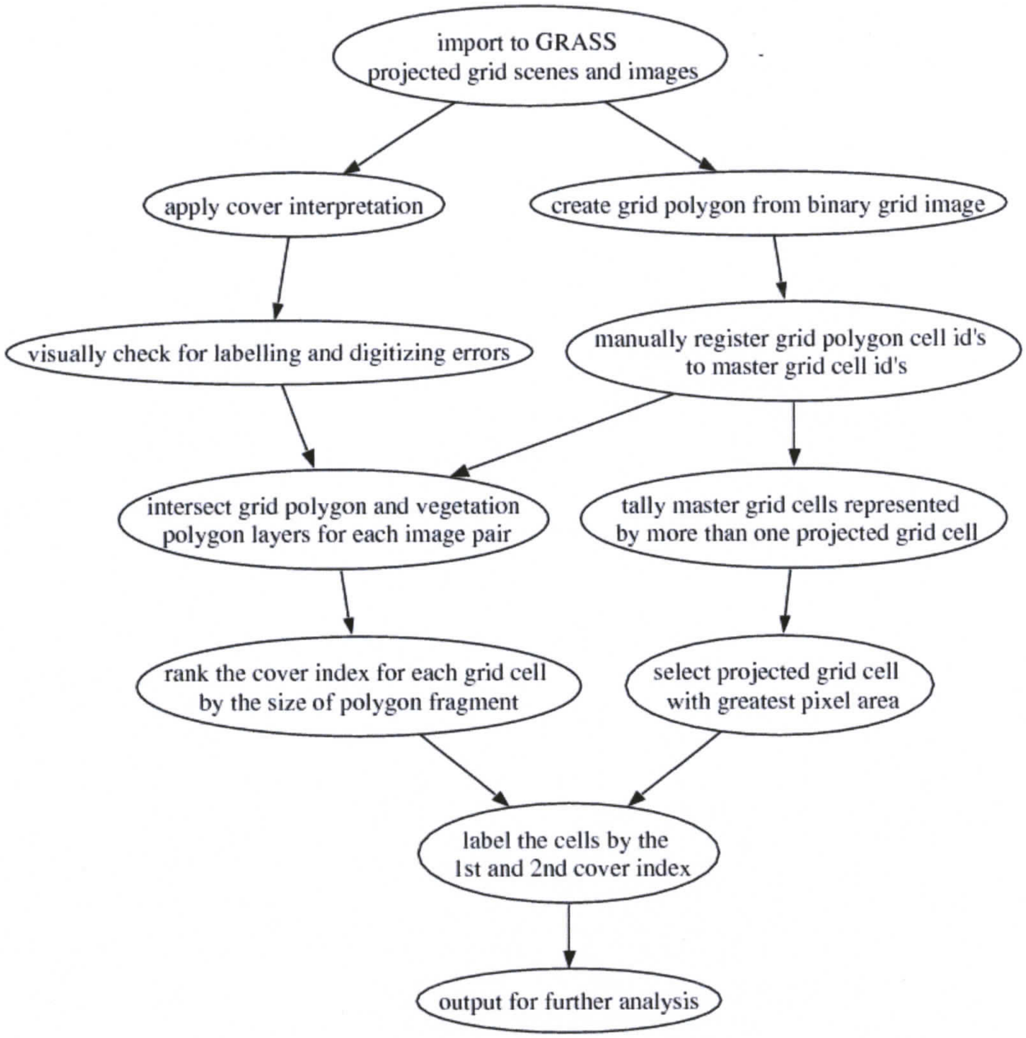

Figure 2.5 Grid registration, photo interpretation, and spatial approximation workflow.

In the second component of the workflow (Figure 2.5), I imported into GRASS each of the layers for each photo (original and repeat photos, colour grid, and binary grid lines). I converted the binary grid raster image to vector format by clumping contiguous white areas (the cells) then filtering the lines before converting them to vector format. Next, I identified and numbered the projected grid cells to correspond with the original grid using the colour grid layer as a visual aid to identification, then referenced oblique grid cells to the master grid table in a database (PostgreSQL version 7.3, The PostgreSQL Global Development Group, 2005). The photographs have overlapping spatial coverage, so multiple oblique cells reference each master grid cell. Therefore I uploaded the pixel area of the cells from the oblique view to the database then selected the oblique view with the greatest pixel area for each cell (Figure 2.6). To visualize the varying scale of the selected oblique views, I represented the pixel area for each selected cell with a circle, the diameter of which corresponds to the scale of the selected grid square relative to the other cells in the figure.

I performed an intersection on each of the interpreted vegetation layers with the grid cell layers in GRASS, then ranked each cover type within each grid cell by the sum of the polygon fragment sizes of that type. I labeled each cell by the highest rank cover type within the cell, and also recorded the 2nd cover type if it was >15 % of the cell area. I also produced an array of the number of intersected cover types within each cell to represent forest cover polygon complexity, following Zhang and Bradfield (2000). I prepared maps of polygon complexity to accompany maps of primary forest cover for each year of photograph coverage. I also prepared transition tables and pathway diagrams to illustrate the patterns of forest transitions, and prepared a density plot of 2004–2005 cover interpretations to convey classification uncertainty due to differences in interpretation.

I recognize that the spatial translation approach presented here introduces a number of sources of uncertainty that confound the analysis. First, there is an unknown difference in focal length between the camera and the NVIZ scene used to create the approximation grid. Second, errors and uncertainty in the DEM, photo interpretation, and supplementary GIS layers are propagated through all phases of terrain analysis, re-projection and subsequent statistical analysis; this has unknown consequences on the overall validity and reliability of the resulting maps and models. For the purposes of this study I maintain the naïve assumption that these uncertainties to some extent cancel each other out, and do not substantially alter the overall results. I recognize that analyzing the spatial component of these problems may help address some of the thematic and spatial uncertainty, and may help extend our understanding of the patterns and processes contained in these images and related data sets, but this was beyond the scope of my study.

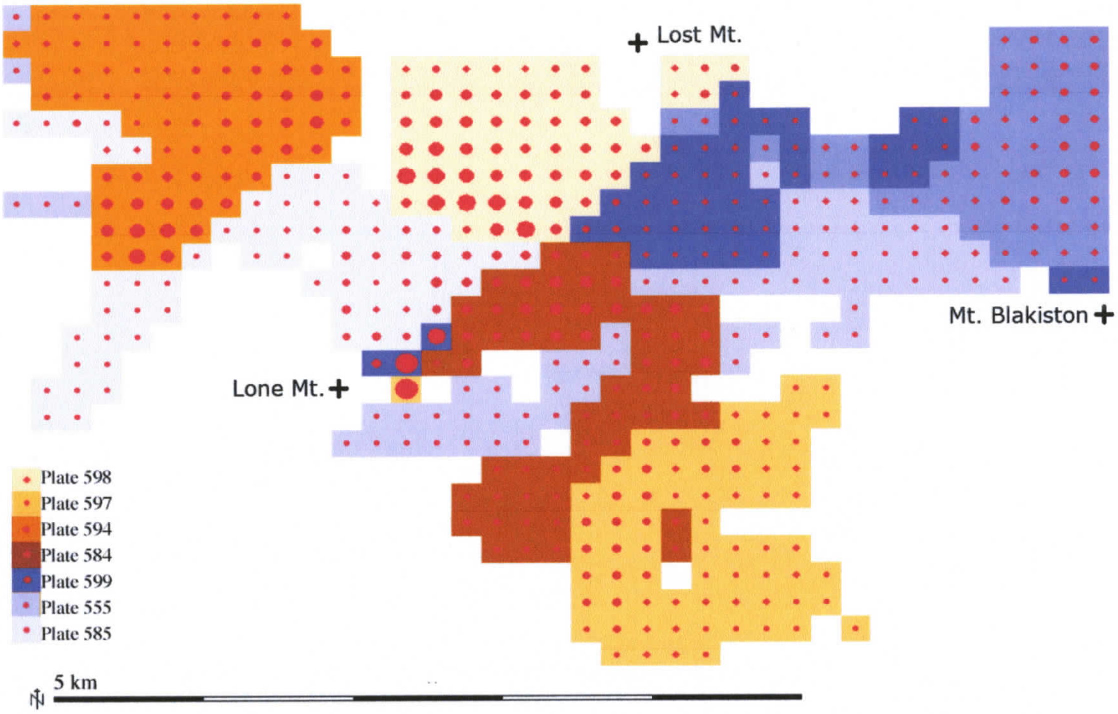

Figure 2.6 View selection from 1914/2004 survey views with camera stations noted. Photograph views overlap in spatial coverage, so the grid cells are coloured according to the view that has the greatest pixel area among those that overlap. Blank cells are either not visible in the photograph views or were not interpretable because of the viewing angle to the landscape. Red circles show the scale of the selected grid square relative to the other cells in the figure.

2.3.4 Analyzing cover transitions

To understand potential influences of environmental and disturbance history variables on forest cover transitions, I built classification tree diagrams for cover transitions at individual sites (1947–2005) and grid cells (1914–2004 and 1947–2005) using R library MVPART (De'ath et al. 2004). This method is an adaptation of the proprietary classification and regression tree (CART) algorithm developed by Breiman (1984), which splits the data set into increasingly homogeneous groupings of the response variable, labeling each node with the explanatory variable which accounts for the greatest decrease of impurity or deviance, and labeling each leaf by the response variable with the greatest frequency for that leaf (Ripley 1996, De'ath and Fabricius 2000). The classification tree method is particularly good at interpreting relationships between variables involving high-order interactions and strong non-linearity, where the data are complex, unbalanced, contain missing values, and break the normality assumptions of conventional approaches (De'ath and Fabricius 2000). The algorithm cross-validates accuracy with training and test data, picks the tree with the lowest predictive error, then “prunes" the tree back to balance group homogeneity with parsimony (De'ath et al. 2004). For each of the tree models, I specified the explanatory data set to include the full range of environmental and disturbance variables collected; the algorithm only selects those that best explain the variation at each of the branches and leaves in the tree.

The environmental data used as inputs to the classification trees include the plot data, point sampling of the GIS layers, and the grid-cell averaged terrain variables of elevation, slope, PRR and TCI. I also obtained soil texture and terrain surface data from the site description for sites and from the ELC polygon layer for grid cells, using the same ranking query used in the grid cell cover selection procedure.

Although I would have liked to include distance to nearest older forest patches to incorporate seed dispersal and the influence of remnant patches on patterns of tree invasion (Kipfmueller and Kupfer 2005), it was not possible to interpret species with certainty in the oblique photos, and the other available layers with species information (2005 and 1967 vegetation interpretations) contained too much temporal, thematic, or spatial uncertainty to be useful.

Chapter 3 Results and interpretation

3.1 Site conditions, stand structure and diversity

The sampled stands represent a variety of forest site conditions across the lower and middle subalpine of the upper Blakiston watershed. Sites range from steep mid-slope south- and north-aspect stands with well-drained soil (i.e. plots 9, 11, 12, 19, 20), to moist lower slope and valley floor forests (i.e. 2, 3, and 15) and mid-slope moisture-receiving conditions (2). South aspect stands in the eastern part of the study area have the highest potential relative radiation (2, 7, 10, 19, 20), while the shadiest stands are mid-slope on the south side of the valley (5, 12, 17, 22). The sites with the greatest topographic moisture potential (convergence) are plots 1, 6, 8, 16, 18, and the sites with the lowest are 5, 7, 12, 14, and 17 (Table 3.1).

Table 3.1 Summary of terrain environmental characteristics for all study area plots, including UTM (zone 11) easting and northing, elevation, slope, aspect, potential relative radiation, and topographic convergence index.

Plot	East (UTM)	North (UTM)	Elevation (MASL)	Slope (%)	Aspect	Potential Radiation	Topographic convergence
1	274525	5444594	1606	13	253	4596	7.00
2	276973	5445392	1643	36	331	4811	5.59
3	273556	5444720	1684	22	280	4712	6.73
4	272676	5444974	1720	13	272	4629	6.11
5	277318	5444396	1826	26	118	3586	4.48
6	277345	5444774	1649	18	140	3932	9.80
7	275325	5445079	1738	31	298	4812	4.77
8	275585	5444747	1592	11	306	4529	7.81
9	274938	5444836	1671	23	283	4761	6.28
10	276283	5444984	1657	39	325	4789	5.28
11	276069	5444411	1636	16	102	3841	6.38
12	276663	5444504	1624	32	91	3343	4.76
13	273316	5444400	1780	31	57	3669	5.32
14	274127	5444374	1652	13	78	3919	4.92
15	274166	5443992	1669	15	51	3981	6.72
16	274489	5444226	1643	8	37	4164	12.43
17	275271	5444046	1725	24	103	3570	2.77
18	275199	5444334	1604	10	91	4006	7.18
19	275980	5444824	1628	27	269	4836	5.65
20	276654	5445115	1633	30	295	4788	5.43
21	277363	5445402	1549	17	322	4645	5.83
22	272500	5444634	1776	24	64	3766	6.64
23	271965	5445139	1737	6	299	4460	6.80

Table 3.2 Summary of stand structural conditions. Basal area and density are for live trees only; total species richness includes species from all layers.

Plot	Basal Area (m^2/ha)	Density (stems/ha)	% Dead Trees	Herb Richness	Shrub Richness	Total Richness	CWD basal area (m^2/ha)
1	34.11	1475	22	6	12	22	4.20
2	40.09	525	29	14	8	25	3.30
3	35.23	1100	30	7	6	17	7.64
4	54.39	2425	3	12	6	21	0.78
5	65.75	2575	19	3	6	12	3.71
6	26.89	2325	27	10	10	23	2.89
7	44.31	2075	20	10	7	21	2.25
8	23.39	800	34	21	6	32	1.13
9	25.02	1050	5	13	8	25	0.00
10	41.81	575	52	9	6	18	5.40
11	41.56	1725	14	6	6	15	3.27
12	31.89	1525	16	9	11	23	7.10
13	51.49	1550	35	7	7	17	4.10
14	37.89	3050	27	4	7	14	1.92
15	14.79	2900	43	2	3	8	2.42
16	54.62	3550	29	5	4	12	1.37
17	143.19	7000	9	8	7	18	106.85
18	41.85	2250	37	11	7	21	8.84
19	21.58	1825	30	16	7	27	5.98
20	12.22	375	13	9	10	22	0.00
21	30.61	500	5	11	11	23	0.00
22	36.70	2500	46	10	7	19	2.74
23	35.90	1275	10	14	5	21	16.69

These stands show a variety of forest structures, ranging from dense, transitional lodgepole pine-Engelmann spruce-subalpine fir stands (plot 17, Figure 3.1A) to sparse sub-climax spruce-fir (20, Figure 3.1B) and mature fir-spruce (9). Tree density ranges from very low (375 stems/ha and 500 stems/ha for plots 20 and 21) to very high (plot 17) (Table 3.2). Proportion of live trees and coarse woody debris (CWD) also varies widely; the plots (10, 22, 15) with highest proportions of standing dead trees had low amounts of CWD, while the plot with the most CWD (17) had relatively low proportion of dead trees (9%). Stand density (for live and dead trees) and understory plant species richness have a negative relationship (Figure 3.2, $\rho = -0.59$). Most of the sites with over 2500 stems/ha had fewer than 15 species, while sparse, open stands tended to have greater than 23 species. One very dense site with medium species richness (plot 17) suffered a MPB outbreak in the early 1980's and has a high volume of standing dead pine as well as thick regeneration of spruce and fir.

Figure 3.1 Photographs of selected stands. A) Impenetrable lodgepole pine CWD in plot 17; B) open forest in south-aspect plot 20; C) dry, mid-slope Douglas-fir stand (plot 2); D) sparse understory in spruce forest (plot 5); E) impact scars from falling trees in plot 17; F) charred snag in plot 15; G) moist, rich Douglas-fir/subalpine fir stand (plot 10).

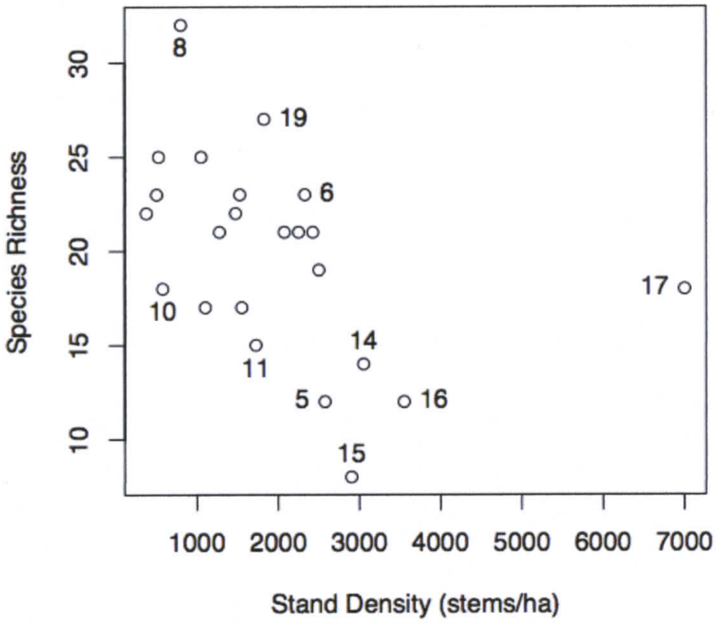

Figure 3.2 Relationship of total species richness (including tree species) to tree density (selected plots identified).

The most abundant and dominant tree species in the study area are subalpine fir, lodgepole pine, and Engelmann spruce (across-site importance value (IV) = 137, 125, and 99). Other tree species include whitebark pine, cottonwood, trembling aspen, and Douglas-fir (IV = 9, 14, 10, and 14). Within the plots, the relative importance of tree species varied (Table 3.1), with subalpine fir and Engelmann spruce sharing greater importance when lodgepole pine is less important. Deciduous trees never attained more than minor importance, and were only present in four plots. I recorded no measurable CWD in three of the plots (9, 20 and 21), which had little else in common besides their southern exposure.

The plots with the lowest minimum and median ring counts are plots are 1, 4, 7, and 20 (Figure 3.3A), while the oldest trees are 10 and 14 (each with trees ~200 years). However, most of the ring counts in these stands are between 100 and 120, which could indicate the older trees may be remnant survivors of the 19th century fires. The majority of median stand ages are between 80 and 140, which corresponds to the distribution of ring count data across the study area (Figure 3.3B). There is no relationship between diameter and approximate age (Figure 3.3C), meaning size structure of the stand cannot be used to infer stand age structure or stand age.

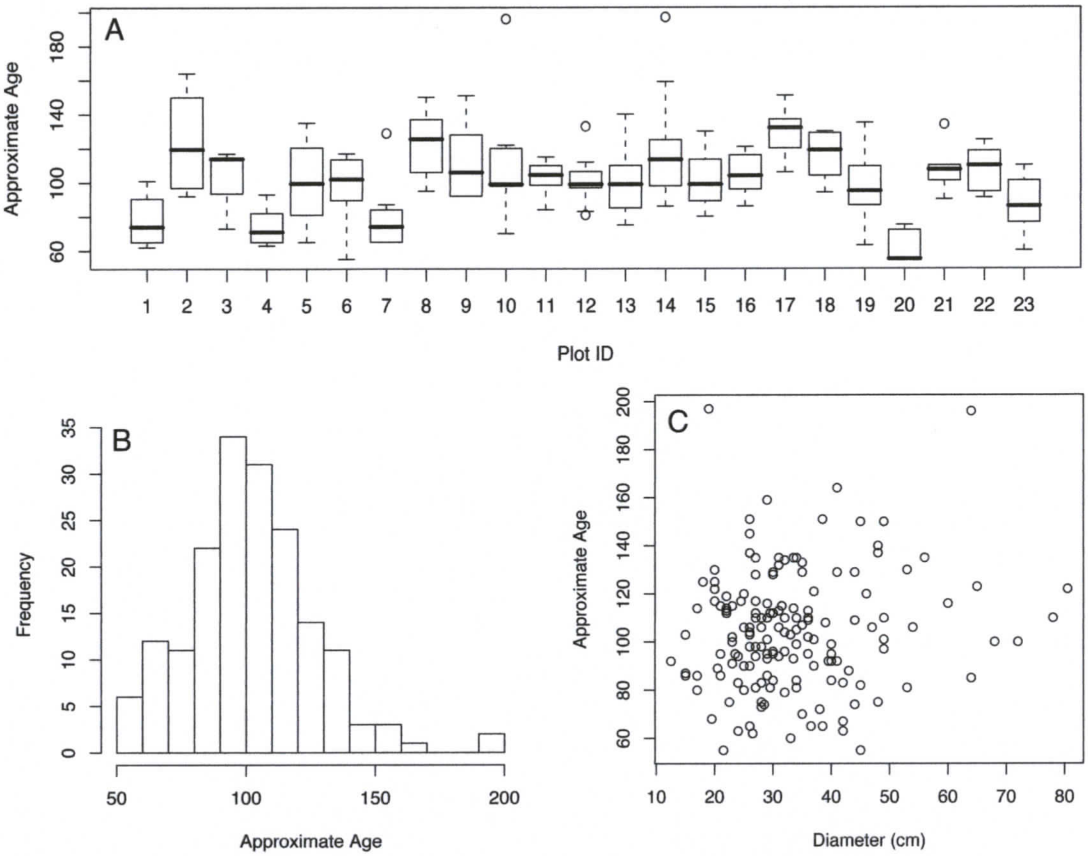

Figure 3.3 Tree ring counts within and across study area plots. A) Variation in tree ring counts (approximate ages) by plot number; B) distribution of ring counts across all plots; and C) relationship between tree diameter at core height (DCH) and ring count.

Forest stands in the study area show evidence of a number of disturbances of low to high severity over the last century. In a stand originating in the 1880's, a circa 1942 fire (Barrett 1996) killed individual trees while leaving a number of pine trees scarred and the canopy largely intact (plot 15, Figure 3.1F). Avalanches uprooted trees adjacent to plot 8, a 140-150 year old stand, opening the canopy and altering understory conditions. Evidence of the extensive MPB outbreak of the early 1980's can be seen in plots 5, 12, and 17 (~140, 130, and 150 years old), where the number of downed trees made traversing the slope difficult (Figure 3.1A). Still, canopy cover is quite high with mature dominant and sub-dominant spruce and fir. These stands also show a minor secondary disturbance related to the MPB outbreak where impacts from falling pine on the boles of other small and mature may have increased tree mortality in the years after the outbreak

(Figure 3.1E). While most of the stands I sampled were below the elevation limit of whitebark pine, plots 7 and 16 (90 and 120 years old) had some remnant whitebark pine that were dying or killed from white pine blister rust. None of the plots I sampled had noticeable windfall, though some of the mid-slope regions in the western part of the study area displayed directionally patterned CWD that may have been caused by wind disturbance.

Simple exploratory analysis reveals several distinctive relationships. For instance, as stand age increases, there tends to be a lesser proportion of live trees (Spearman's ρ = -0.26). There is a positive relationship between slope (0.37) and aspect value (0.39) and maximum age, so steeper sites on north aspects with lower TCI tend to be older (-0.46). There is lower diversity of trees (-0.5), shrubs (-0.24), and herbs (-0.34) on north aspect sites, greater tree and herb diversity where potential solar radiation is higher (0.4 and 0.5), less shrub species at higher elevations and where basal area is higher (-0.39 and -0.35), and more shrub species with higher slopes and percentage live trees (0.37 and 0.28).

3.2 Forest structure, plant species, and environment relations

Forest stands in the upper Blakiston Valley vary widely according to plant community composition. The NMDS analysis reveals a number of distinctions among sites based on species diversity and abundance. In the upper left quadrant of Figure 3.4, plots 19 and 21 share similar abundances of *Amalanchier alnifolia*, *Clematis columbiana*, *Sheperdia canadensis*, and *Erigeron species*, with a similar Axis 1 position to plots 7 and 2, the latter being associated with *Fragaria virginiana*, *Smilacina stellata*, *Mahonia repens*, and *Senecio* species. Plot 20 is associated with *Arctostaphylos uva ursi*, *Potentilla fruticosa*, *Juniperus horizontalis*, and *Allium* and unidentified grass species, while closer to the midline of axis 1 *Linnaea borealis*, *Aquilegia* spp., and *Pinus latifolia* distinguish plot 6. In the upper left quadrant, plots 3, 5, 12, 14, 15, 16, and 17 are associated with *Pinus latifolia*, *Arnica cordifolia*, *Menziesia ferrugina*, *Vaccinium scoparium*, *Alnus viridis*, and *Pyrola asarifolia*. In the upper lower right quadrant, plots 18 and 22 share similar abundance of *Picea engelmannii*, *Clintonia uniflora*, *Tiarella trifoliata* and *Disporum* spp., while closer to the centre of axis 1 plot 4 is related to *Abies lasiocarpa*

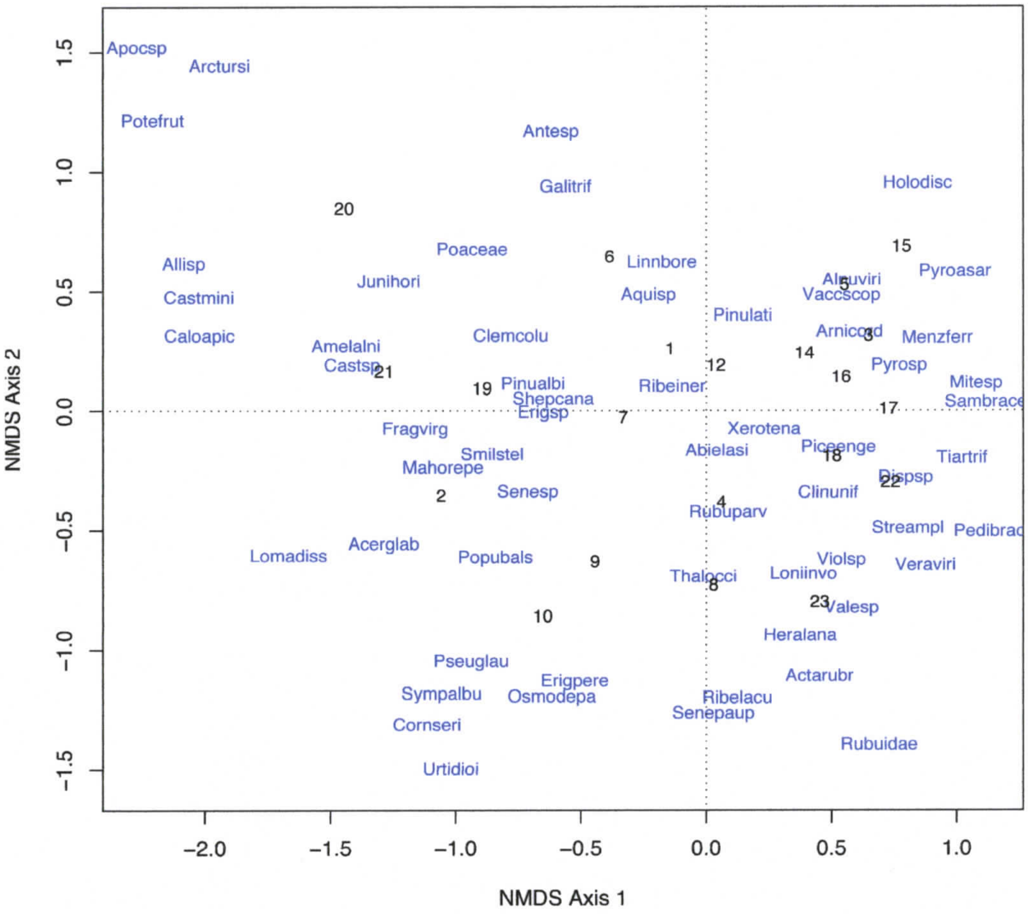

Figure 3.4 Non-metric multidimensional scaling (NMDS) of vegetation cover, displaying only non-overlapping species scores (display priority given to most abundant) and site scores (priority given to further separated sites). Species labels are an eight-letter abbreviation of the species name; corresponding species and common names are in Table C.4.1.

and *Rubus parviflorus*. Plots 8 and 23 share similar abundance of *Thalictrum occidentale*, *Lonicera involucrata*, *Heracleum lanatum*, *Actea rubra*, *Ribes lacustre*, and *Valeriana* and *Viola* spp., while lower on axis 1 in the lower left quadrant plots 9 and 10 are distinguished by *Populus balsamifera*, *Pseudotsuga menziesii*, *Symphoricarpos albus*, *Erigeron peregrinus*, and *Osmorhiza depauperata*. Appendix C.4.1 lists plant species across the study area.

The two-axes NMDS configuration explained 87–97% of the variation in Bray-Curtis dissimilarity between plots based on vegetation composition and abundance (Figure 3.5). The fit had a stress value of 16.5, which satisfies Clarke's (1993) suggested constraint of only interpreting NMDS configurations with a stress value below 20. The variables with the strongest relationship with the NMDS configuration are herb layer species richness (R^2 =0.59, P=<0.01) and potential relative radiation (PRR, 0.54, <0.01) (Table 3.3). Other variables that contribute significantly include shrub layer richness and elevation, with a small contribution from basal area. Herb richness and PRR were strongly associated with plots 2, 9 and 10 (the lower left quadrant), while increasing shrub diversity is associated with plots 21, 19, and 6 (Figure 3.7). Elevation and slope appear to have opposite relationships along axis 1, though slope explains little of the variation and is not significant. Note that these arrows imply linear relationships between explanatory variables and vegetation composition and abundance; Oksanen (2006) warns that ordinations relying on ordinal dissimilarity measures may violate this assumption.

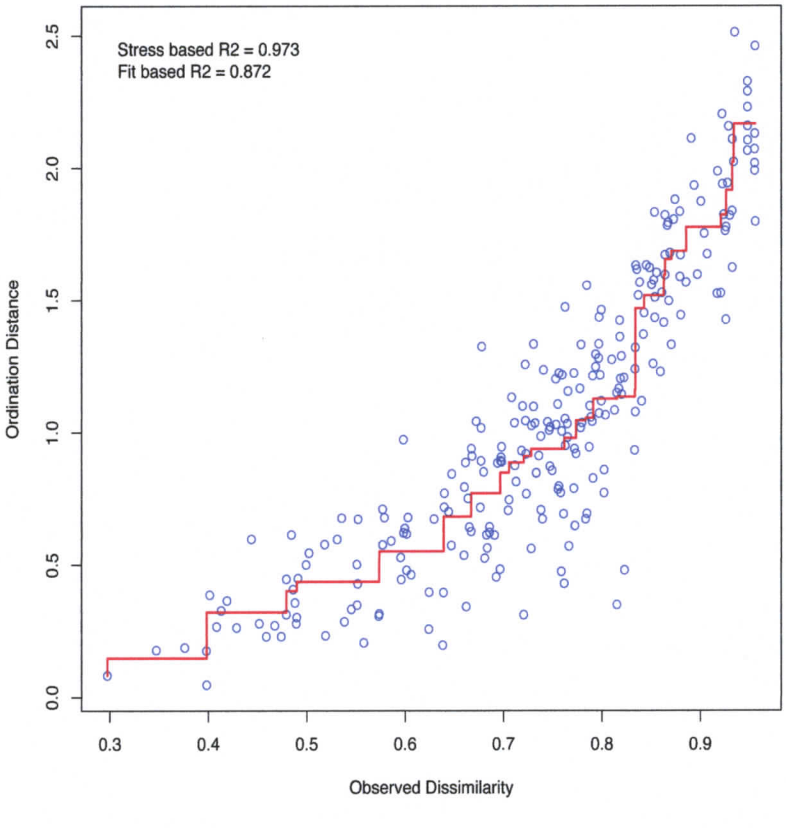

Figure 3.5 Shepard plot comparing ordination distances to empirical distances based on species data. Goodness of fit (GOF) statistics shown are stress-based R^2 (1-stress) and fit based R^2, the correlation between fitted values and the community distance matrix.

The relationship between species composition and stand structure ordinations was somewhat strong (r=0.69) and highly significant (p<0.001), requiring a small rotation to match the species configuration (root mean square error (RMSE)=0.15, Figure 3.6). On

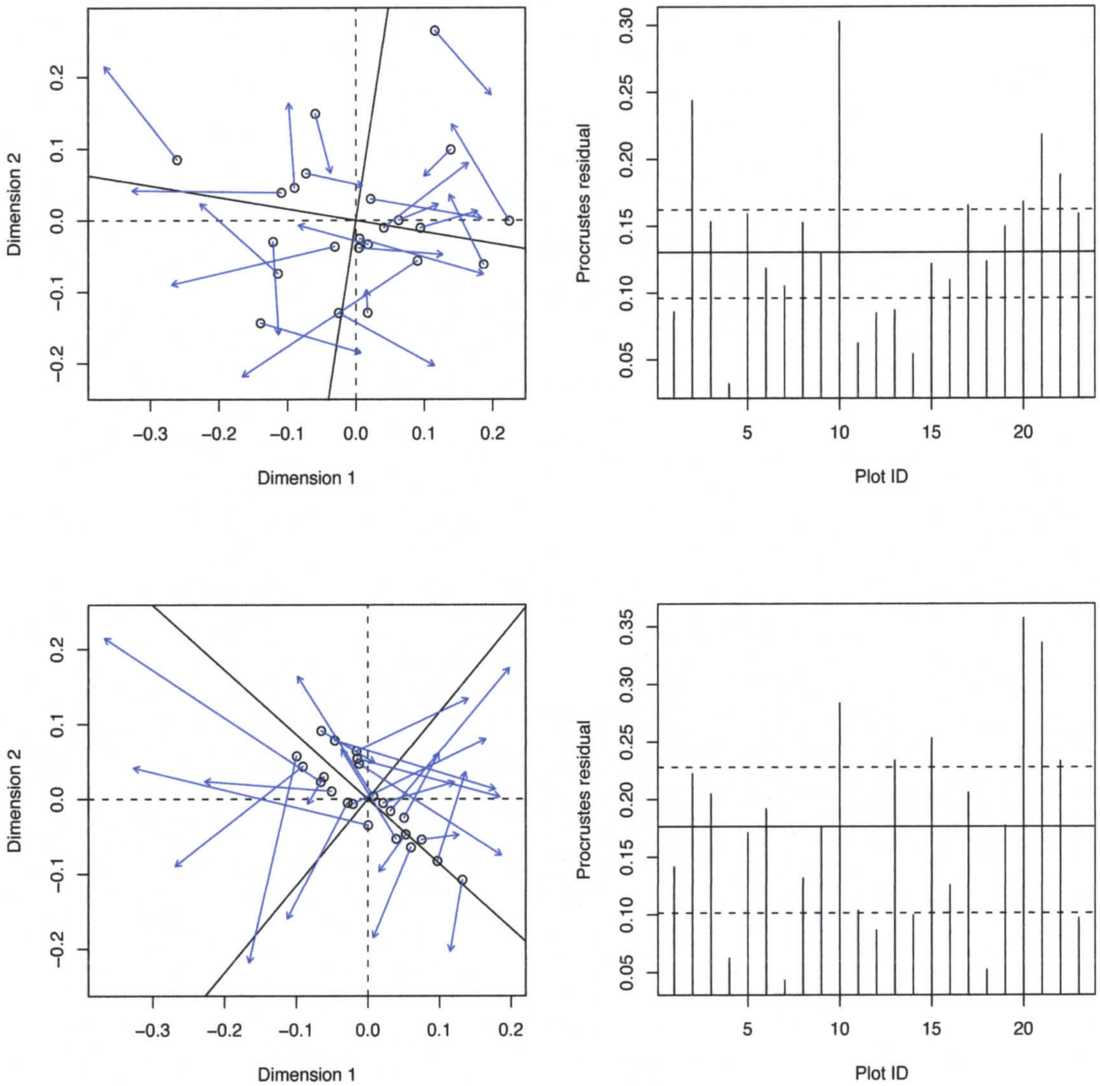

Figure 3.6 Procrustes analysis of stand structure–vegetation (top) and environment–vegetation (bottom) relationships for plot vegetation data. On the left the original NMDS plot vegetation configuration (dashed grid lines and arrowheads) is juxtaposed with the rotated and scaled environment or stand structure ordination (solid grid lines and circles). The length of the arrows indicates the residual of the fit between the two ordinations for each site; the arrow direction indicates the change in relationship to the axes (dimensions) needed to relate the object in the second configuration to the original. Residuals for individual plots are shown on the right, with median and 1st and 3rd quantiles of Procrustes errors shown with solid and dashed lines, respectively.

the other hand, the relationship between species composition and environment ordinations was weaker (r=0.38) and less significant (p=0.068), requiring a greater rotation to match the species configuration (RMSE=0.19). Examining the residual error from the Procrustes test reveals which stands have the closest relationships between species composition and stand structure or environment. For stand structure relationships, plots 4, 11, and 14 showed the lowest residual error, while plots 2, 10, and 21 show the greatest error. Similarly, plots 4, 7 and 18 show strong species–environment relationships, while plots 10, 20 and 21 have a high proportion of the residual error.

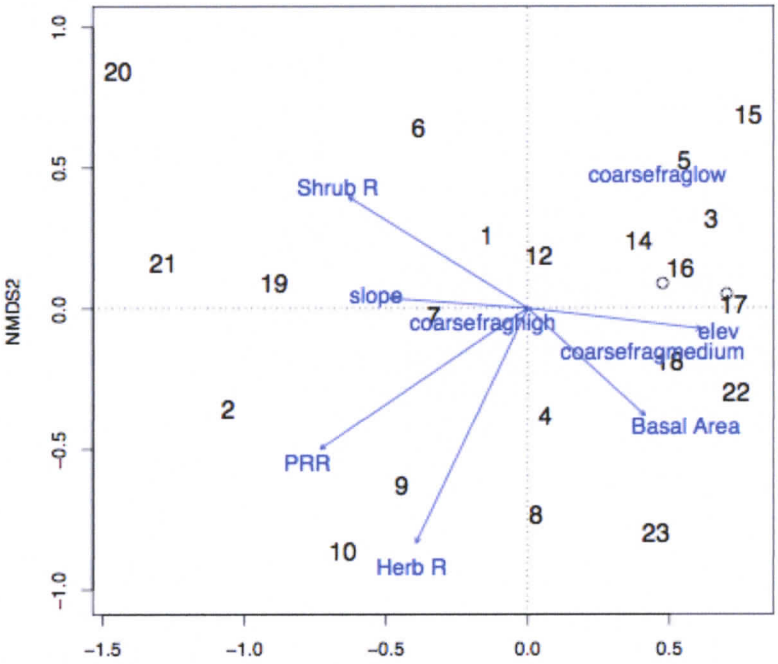

Figure 3.7 Interpretation of relationships between NMDS ordination and stand structure and environmental variables for plant species data. The arrow points in the direction of most rapid change in the explanatory variable, and the length of the arrow is proportional to the correlation between the ordination configuration and the variable. Factor variables are plotted in the centroid of each level. R^2 and significance values are given in; only variables with significance of 0.2 or better are plotted.

Table 3.3 Weighted fitting of environmental and stand variables on NMDS ordination scores, with P values based on 1000 permutations. Relationships of variables to axes scores are displayed in Figure 3.7.

Variable	R^2	P
Oldest tree	0.15	0.21
Percent alive	0.06	0.58
Basal Area/ha	0.22	0.09
Tree richness	0.01	0.93
Shrub richness	0.38	0.01
Herb richness	0.59	<0.01
CWD/ha	0.08	0.48
Slope	0.16	0.16
Potential radiation	0.54	<0.01
Elevation	0.26	0.05
Slope position	0.05	0.93
Moisture regime	0.08	0.53
Nutrient regime	0.02	0.95
Coarse fragment	0.16	0.13

3.3 Cover transitions

Overall, increasing forest cover dominates the transitions observed from 1881 to 2005 in the oblique and aerial photographs (Figure 3.9). In 1881, most of the grid cells were interpreted as herb or shrub, with a large patch of forest at the far west end of the study area. In 1914, patches of shrub and woodland appear across the valley floor and on the north aspect slopes, and the effects of a previously undocumented fire (circa 1890) can be seen where the far west end of the valley was forest in 1881 but was herb, shrub, and woodland in 1914. While the boundaries are difficult to determine, this event may be reflected in the difference in ring counts between plot 22 (~130 years) and plots 4 and 23 (~80-100 years; see Figure 3.3), which are in similar landscape position to plot 22 but appear as recent regeneration in 1914 in plates 555 and 585 (Appendix A).

By 1947, forest cover appears to dominate the south side of the valley, with shrub, herb and woodland patches across the north side. Age data supports this interpretation, with forests 30-40 years older on some north side plots (7 and 20) than south side plots (5 and 17). However, there appears to be greater spread in age data for some south aspect and mid-valley plots (2, 10, and 14), which could reflect fire boundaries or refugia seen right midground of plate 555 (Appendix A 1). There is a deviation in 1967 grid cover types where woodland is present in many sites that were forest in 1947; this is likely due to spatial errors in the 1967 data set, re-coding of the different cover interpretations, and data aggregation, themes which I will cover in more depth in Section 4.2. By 2004, herb and shrub communities are mainly found on steep slopes and upper slope positions, and forest carpets most of the valley floor except in avalanche run-outs.

When all of the years with available photograph coverage are counted together, restricted to cells with coverage in 1914/2004, the cover transitions become less clear (Table 3.4). For instance, forest cover appears to peak in 1967 (568 ha), but declines in 2004/2005. Woodland communities dominate 1947 and 2004, but shrub communities dominate 1914 interpretations. These discrepancies are likely due to the differences among classification schemes and the aggregation of cover types within grid cells.

There are a number of minor differences between my interpretations of the 2004 photograph and the 2005 vegetation map, which can be visualized as deviations from the diagonal line in a bivariate density surface (Figure 3.8). These are mainly seen on ridges and upper slopes where I interpreted sparse vegetation as bare while the vegetation map classified it as sparse herb or shrub communities, possibly due to the use of colour, colour infrared, and thermal channels during photo interpretation.

Table 3.4 Summary of area (hectares) in each simplified cover type for each year interpreted, restricted to the grid cells selected for approximation from 1914 and 2004 photographs. See Appendix B for cover type definitions.

Year	Bare	Herb	Shrub	Woodland	Forest	Total
1881	20	20	316	48	96	500
1914	396	52	492	492	320	1752
1947	352	88	372	440	500	1752
1967	896	0	128	420	308	1752
2004	376	8	132	468	768	1752
2005	88	4	316	772	572	1752

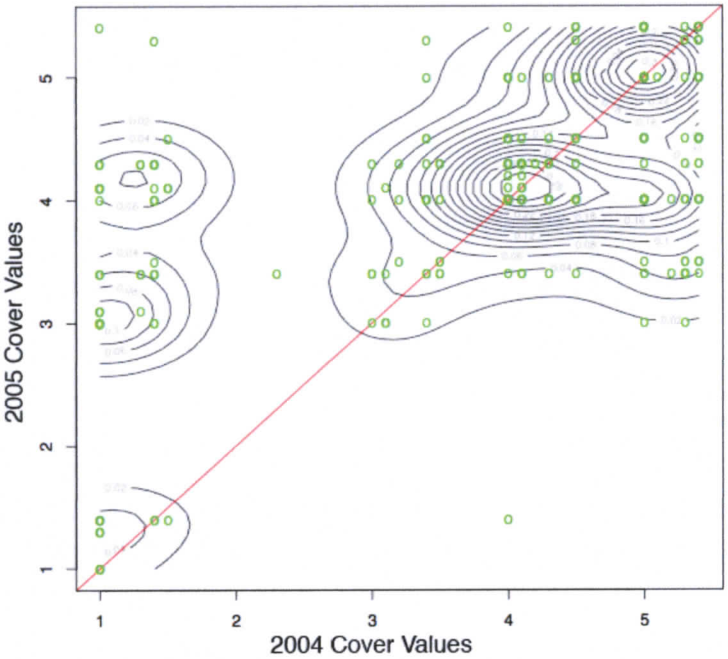

Figure 3.8 Bivariate density surface for 2 digit cover classes comparing 2004 (oblique) and 2005 (aerial) interpretations. Numbers correspond to cover types: 1=bare, 2=herb, 3=shrub, 4=woodland, 5=forest. Higher cover classes in the graph overall and in each cluster indicate greater cover of trees. Each cluster of points within the graph displays the concordance of the two dates for the primary (1:5) and secondary (x.1:x.5) cover classes in each 4 ha grid cell. A major cluster to the left of the diagonal indicates the majority cell was more open (less vegetated) in the aerial than the oblique set, while a major cluster below the diagonal means the cell was less open in the aerial. Conversely, a major cluster above or to the right of the diagonal indicates the cell was less or more vegetated, respectively.

The pattern of increasing forest cover between 1914 and 2004 can also be seen in the diagram detailing transition pathways (Figure 3.10). Among stable sites, 65 cells remained bare, 12 shrub, 65 woodland, and 46 forest, but greater numbers of cells succeeded towards forest than decreased in cover. Shrub⇒forest, woodland⇒forest, and shrub⇒woodland were the most frequent transitions (68, 50, and 28 cells), with 10 `forward' and 6 `backward' pathways identified overall.

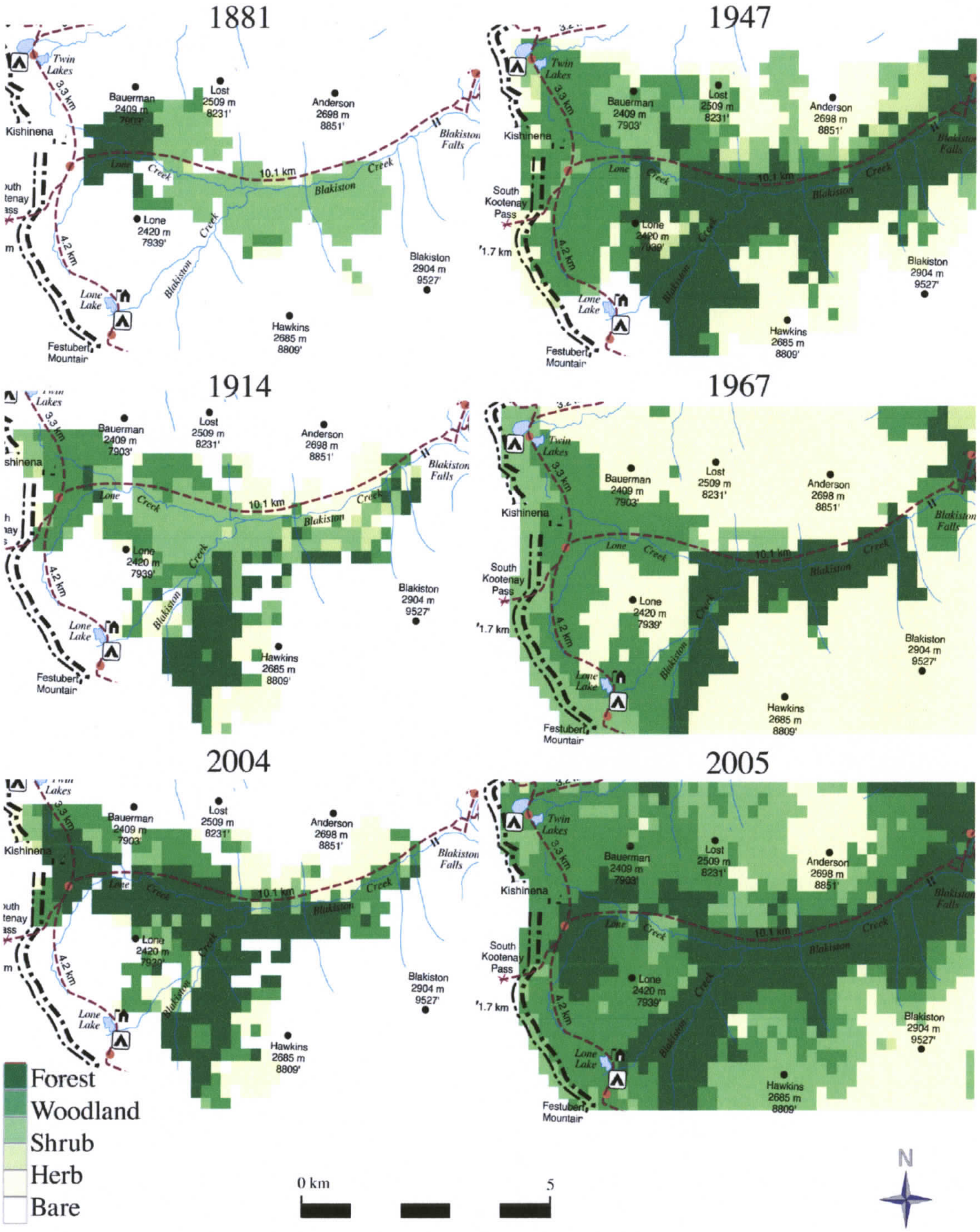

Figure 3.9 Vegetation cover for grid cells interpreted from oblique (left) and aerial (right) photographs. Vegetation cover shows the modal class from the interpreted vegetation polygons each grid cell intersects. The map overlay shows location of geographical features and trails in the study area.

When the secondary component of cover data (vegetation cover value composing between 15 and 49% of each cell) is taken into account there is greater variation in transitions (Table 3.5) than shown in the simple pathway diagram (Figure 3.10) alone. Cells that appeared stable show an appearance, disappearance, or change in second cover class, especially in the shrub, woodland, and forest sub-classes.

Table 3.5 Frequency of cover type transitions between 1914 and 2004 across all oblique photograph views. The integer portion of the cover class shows the primary (majority) cover type for each cell, and the decimal portion represents the secondary portion (between 15 and 49%). 1=bare, 2=herb, 3=shrub, 4=woodland, and 5=forest.

	2004 Cover																			
1914 Cover	1	1.3	1.4	1.5	2.3	3	3.1	3.2	3.4	3.5	4	4.1	4.2	4.3	4.5	5	5.1	5.2	5.3	5.4
1	43	2	2	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-
1.3	1	1	2	2	-	-	1	-	-	1	-	2	-	1	-	-	-	-	-	-
1.4	2	-	12	3	-	-	1	-	2	-	1	4	-	-	-	2	-	-	-	-
1.5	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2.1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
2.3	-	-	-	-	1	-	-	1	2	-	-	1	-	1	-	1	-	-	1	-
2.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-
3	-	-	-	-	-	3	-	1	2	1	5	1	-	-	4	32	-	-	4	11
3.1	-	1	-	-	-	-	1	-	-	-	1	2	-	-	-	-	-	-	1	1
3.2	-	-	-	-	-	-	1	1	-	2	-	1	-	-	3	1	1	1	1	3
3.4	-	-	1	-	-	1	1	-	1	1	3	2	-	1	2	3	-	-	5	4
3.5	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-
4	-	-	-	-	-	-	-	-	4	-	16	3	-	7	4	24	-	-	-	5
4.1	2	-	1	-	-	-	-	-	-	-	6	10	-	-	1	2	-	1	-	-
4.2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	1	-
4.3	-	-	1	-	-	1	-	-	-	1	6	-	-	2	3	5	-	-	-	4
4.5	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1	4	-	-	-	3
5	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	32	-	-	-	2
5.1	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
5.3	-	-	-	-	-	-	-	-	1	-	1	1	-	1	-	3	-	-	-	2
5.4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	4	-	-	-	3

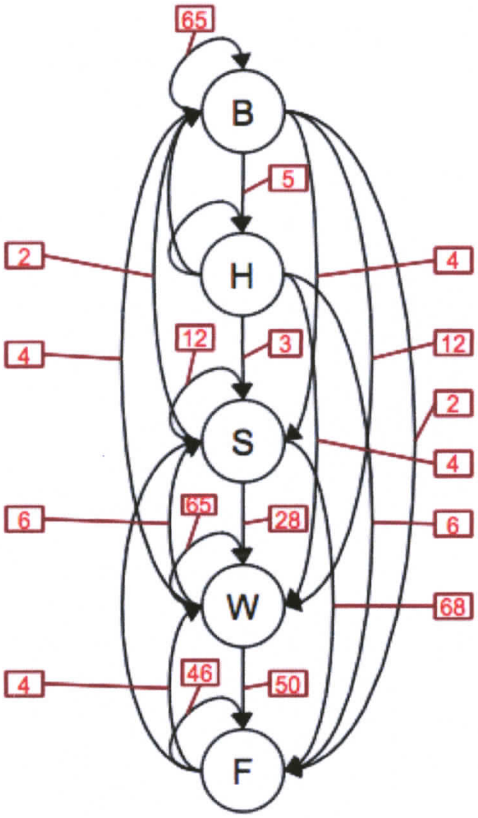

Figure 3.10 Transition pathways between 1914 and 2004 across all photograph views, simple cover classes only. Numbers within the circles represent the dominant cover type (B bare/non-vegetated, H herbaceous, S shrub land, W woodland, F forest) for each grid cell, and line labels (in red) show the number of grid cells having the transition indicated by the line (grid cells equal 4 ha). Transitions of only one cell are unlabeled. "Stable" cells are shown with a loop, while cells with an increasing cover type are drawn downward on the right and those with decreasing cover type are on the left.

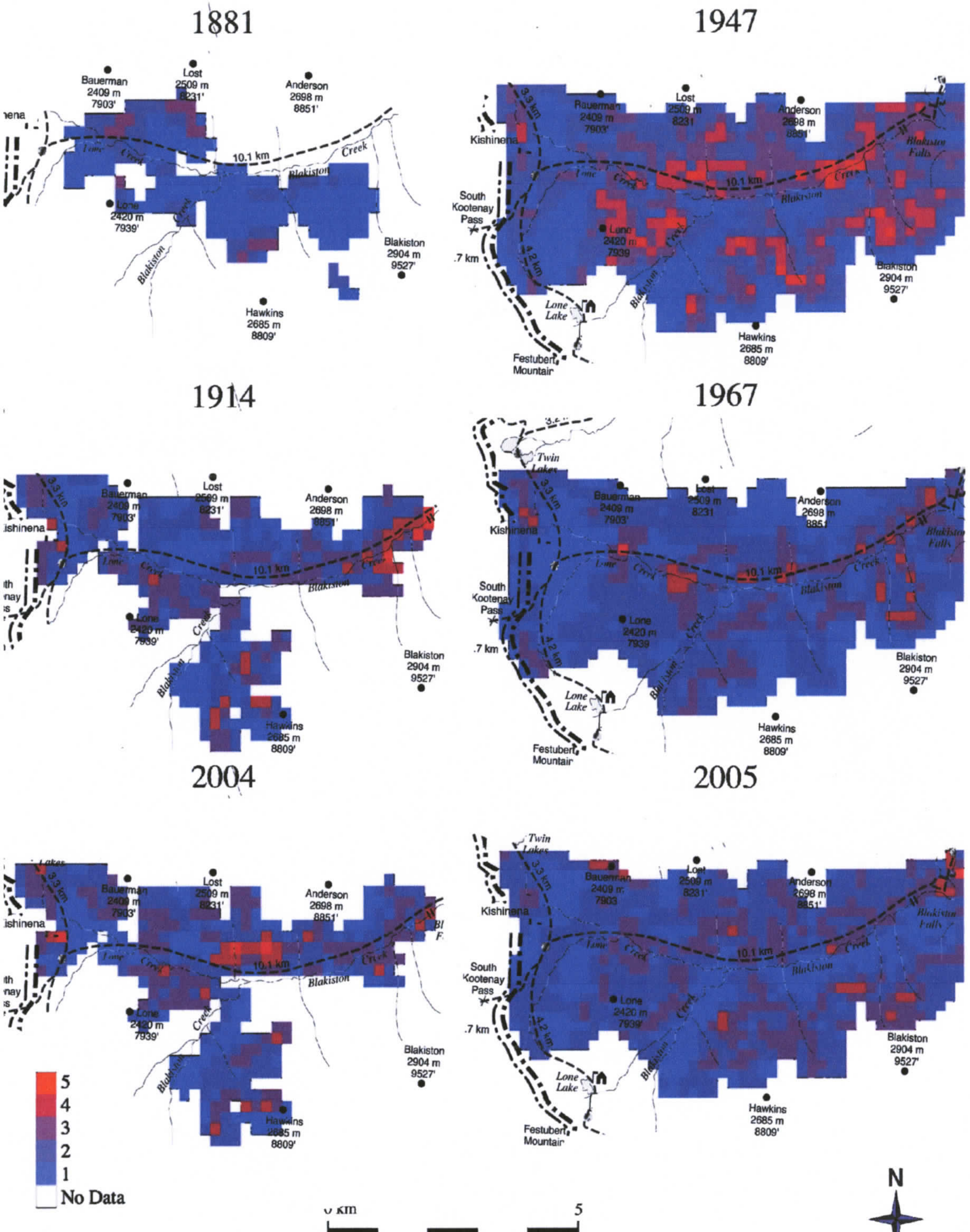

Figure 3.11 Vegetation polygon complexity across all photograph views from oblique (left) and aerial (right) photographs. Cell colour shows the number of cover types from the polygons intersected by each grid cell, with red being the maximum complexity. Map overlay shows locations of geographical features for reference.

In the map of polygon complexity (Figure 3.11), a decline of structural heterogeneity can be seen in the eastern end of the study area where the forest had been patchy due to wind-falls early in the 1900's (Lopoukhine 1970), but an increase is evident in the centre of the valley in the 2004 photographs at the intersection of avalanche run-outs, open woodlands, and riparian areas. The orthophoto sequence shows the diminishing complexity of the post-fire regeneration mosaic still visible in the 1947 photos; the main areas of higher complexity in 2005 are around timberline, in avalanche run-outs, and in some of the active rockfall and floodplain areas in the east-central part of the valley. Examining the number of cover classes contained in the polygons intersected by each grid cell also reveals a pattern of declining structural diversity, with more cells losing than gaining diversity of cover classes (moving from 2–1, 3–1, 4–3 and 5–4) between 1914 and 2004.

Forest cover transitions from 1947 to 2005 at site locations (n=23) are best explained by potential relative radiation (PRR), topographic cumulation index (TCI), and elevation (Figure 3.12). Sites with PRR<4312 were predominantly stable forest (n=12) with minor amounts of shrub⇒forest and stable woodland, while sites with higher PRR and TCI >6 showed woodland⇒forest and stable forest transitions. In sites with lower TCI, higher elevation sites (>1638) were stable forest while lower elevations were a mix of herb⇒woodland, shrub⇒woodland and stable woodland. The classification tree model excluded slope, stand age, surface texture and soil, and other site variables.

For grid cell transitions recorded from the oblique photographs (1914–2004, n=335)(Figure 3.13), the tree model selected elevation, fire class, and the presence of MPB (in decreasing order of importance). For instance, at higher elevations (>2061m), transitions were predominantly stable woodland (WW), with a minor component of bare⇒woodland (BW). At lower elevations, for years of fire between 1667 and 1844 and with the presence of MPB, transitions were mostly woodland⇒forest (WF), while cells without MPB were stable forest. When the fire class was 1844–1900 or unknown, cells were predominantly shrub⇒forest, with components of shrub⇒woodland, woodland⇒forest, and stable woodland.

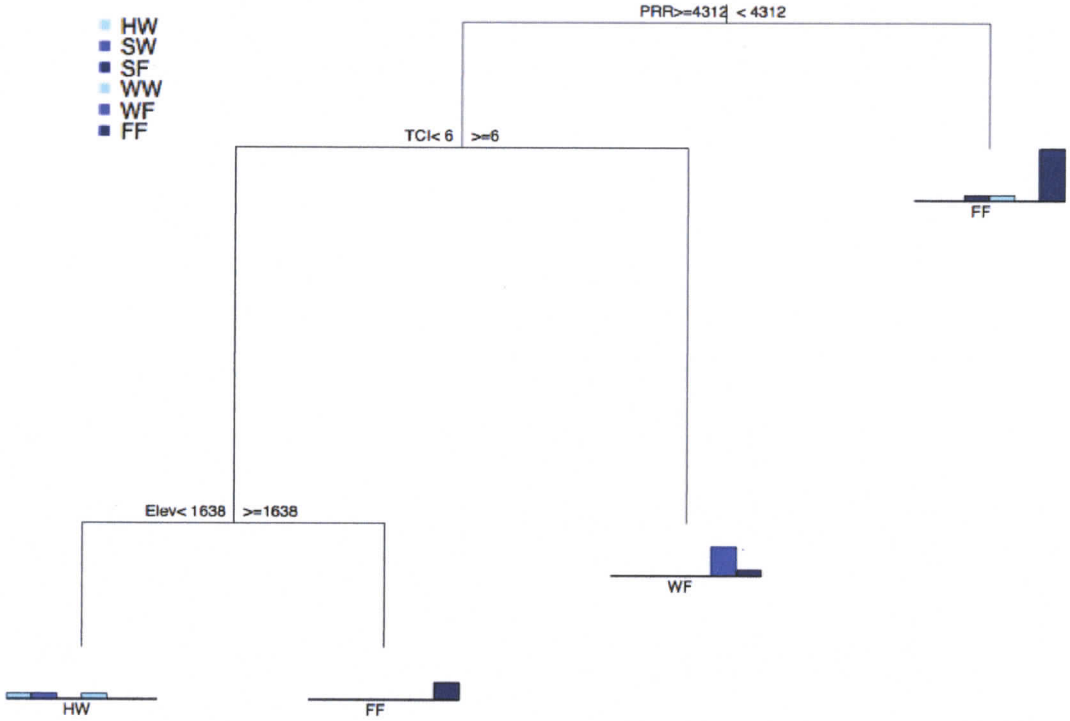

Figure 3.12 Classification tree for interpreting site cover transitions measured at plot locations on 1947 and 2005 orthophotos. Starting at the root of the tree (the top), the cases are split into decreasingly heterogeneous groups, with the branches holding the largest number of cases per node placed on the right. Each group (node) is labeled according to the response (transition class) with the highest number of cases, and shows the number of cases in each class within that group (L-R, along the sequence defined in the legend). The vertical length of the tree branches corresponds to the relative proportion of variation explained by that split.

In contrast, for transitions recorded from the orthophoto mosaics (1947 and 2005 only, n=884), the tree model used elevation, fire class, PRR, and slope (Figure 3.12). Elevation was the most important predictor of cover transitions, accounting for over half of the variation in the model; for lower elevation cells (<1891 m), lower PRR corresponded to stable forests, while higher PRR interacted with fire class to produce a mix of transitions. At higher elevations, cells with stand origins of 1667–1900 were predominantly stable woodland where PRR is high (>4104), and a mix of stable forest and other transitions with lower PRR. Where the fire class is unknown, higher elevation cells (>2245 m) likely succeeded from bare to shrub. Elevations between 1891 and 2245 m interacted with slope and PRR, for instance leading to stable woodland or shrub⇒woodland with slopes <24 and high PRR, and were more likely bare⇒shrub or

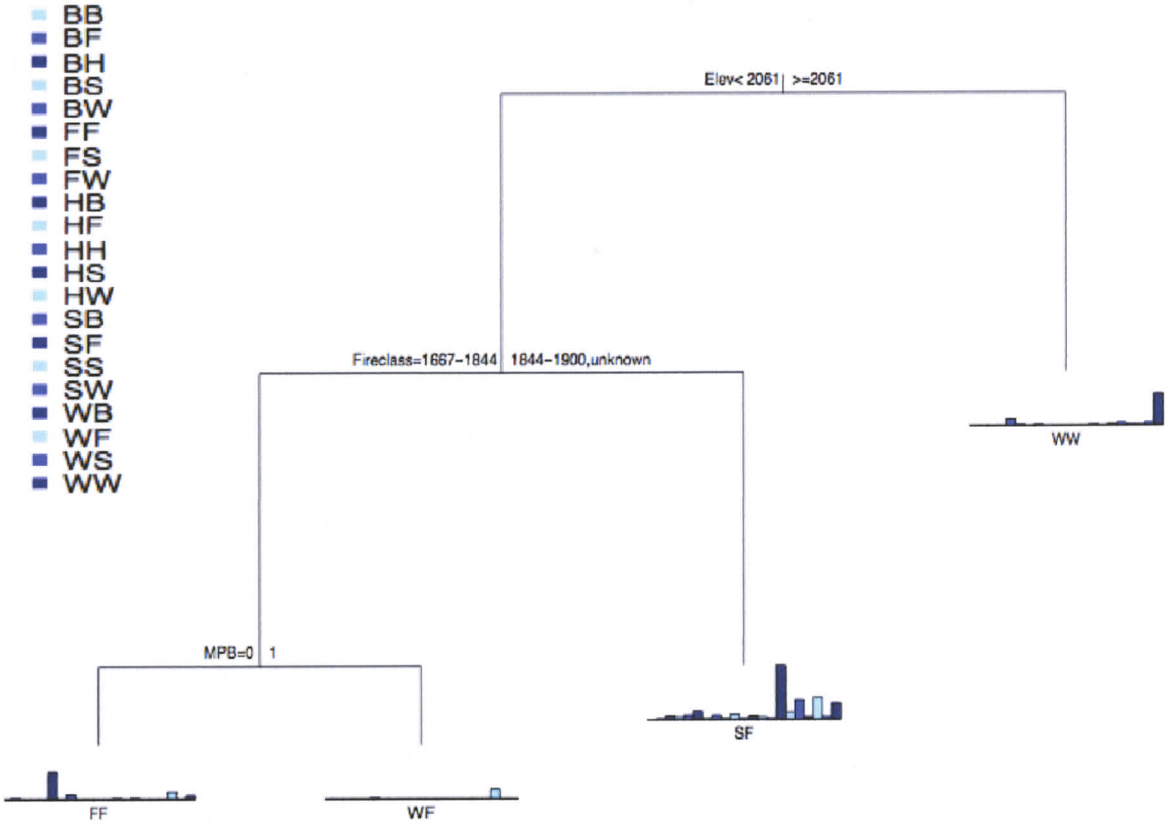

Figure 3.13 Classification tree for simple cover transitions (1914-2004), excluding bare to bare. Figure interpretation corresponds to Figure 3.12.

bare⇒woodland where slopes are steeper and PRR was medium–high. Aside from the fact the orthophoto sequence started 33 years after the oblique sequence, the other major difference is that it covers a greater proportion of the terrain in the study area, with more high elevation polygons in sharp terrain.

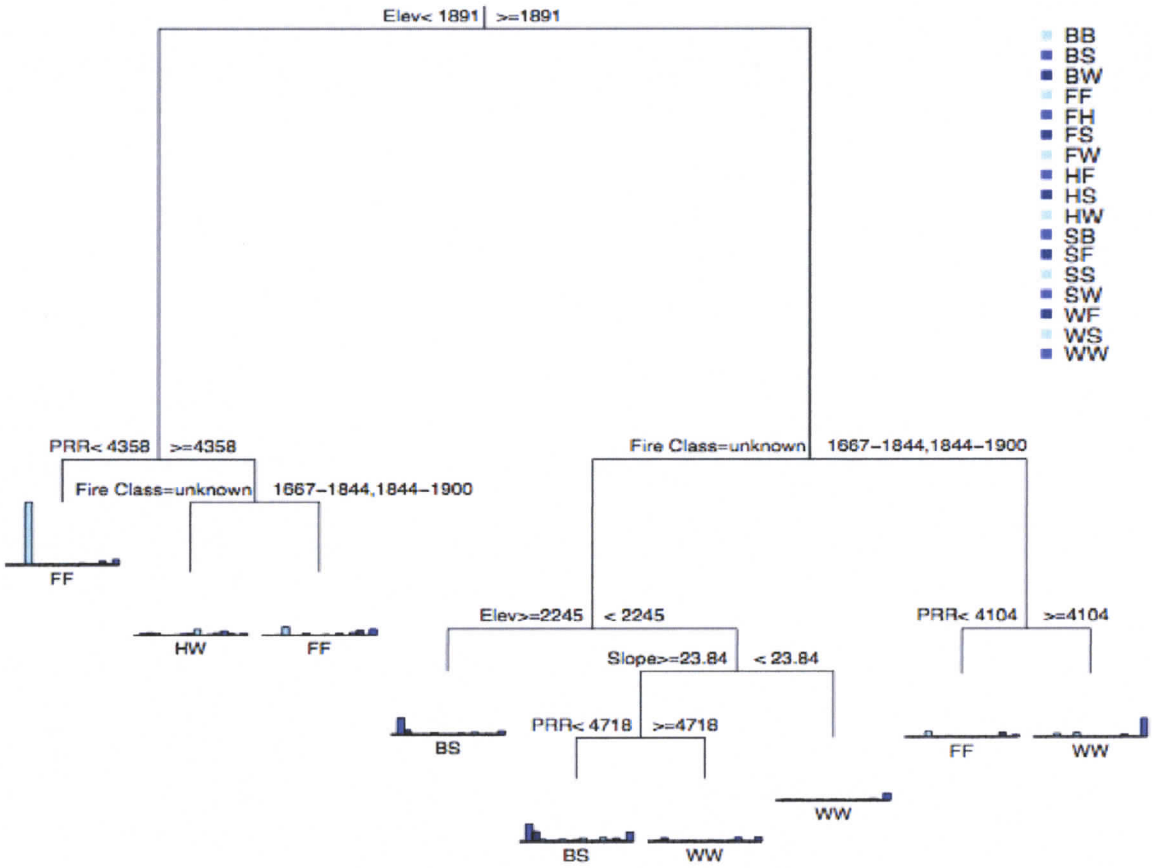

Figure 3.14 Classification tree for simple cover transitions (1947-2005), excluding bare-bare transitions. Interpretation corresponds to Figure 3.12.

Chapter 4 Discussion

4.1 Forest succession patterns across time and space

The forests of the upper Blakiston Valley display wide variation in species composition and stand structure, as is expected for a subalpine valley with a large species pool, diverse disturbance history, and sharp topographic gradients. Overall, lodgepole pine, Engelmann spruce, and subalpine fir dominate the stands recovering from the fires of the middle and late 1800's, aside from the mid-slope stands where Douglas-fir survived previous fires. The forest landscape is characteristic of topographically diverse watersheds in the Canadian Rocky Mountains, sharing many of the disturbances processes and stand development patterns noted by Suffling (1993), Veblen et al. (1994) and Kipfmueller (2005).

The twenty-three sampled stands have a diverse species composition, with as many as twenty-six different vascular plants in one plot and 109 species observed overall. Though species richness depends on the size of the plot, the intensity of sampling, and the season of sampling (Coulloudon et al. 1999), species richness is comparable to studies of greater sampling intensity in subalpine forests. For instance, Bottorff (2001) noted 149 vascular plants in an intensive transect study in the foothills–subalpine region of west-central Alberta. A lodgepole pine chronosequence study in the same region (Bainbridge and Strong 2005) found 135 vascular plants from 167 stands, using a much higher sampling effort than this study.

Plant community composition tended to vary most with the physical variables of potential radiation, elevation and slope and the forest structure variables of herb and shrub species richness and basal area. In a study of early post-disturbance succession, Rydgren et al. (2004) found that composition was strongly dependent on degree of disturbance, propagule availability and response to disturbance, and initial environmental conditions of canopy cover and soil moisture.

The successional pattern most apparent in the photographs is the slow regeneration of forests in south aspect stands as compared to north aspect stands. This pattern was somewhat corroborated by tree ring-count data (Figure 3.3); plots 4, 7, 19, and 20 have substantially lower minimum ages than most north aspect stands.

When sufficient time elapses between subsequent fires in mesic subalpine forests, maturing seral lodgepole pine stands succeed to Engelmann spruce–subalpine fir stands, and subsequent regeneration from major stand-replacing fires may have limited pine (Campbell and Antos 2003). Sufficiently severe or successive fires in such stands may exclude seed sources for any of the dominant, wind-dispersed trees in the area (spruce, fir, and Douglas-fir), therefore favouring only slower, patchy regeneration from sprouting aspen or bird-dispersed whitebark pine (Howard 2002) until favourable conditions trigger pulses of regeneration where seed is available (Anderson 2003). Given that the fire-return interval for stand replacing fires was long prior to the 1800's (Hallett and Walker 2000, Power et al. 2006), the exclusion of seed sources by successive fires could help explain the pattern of very slow regeneration on the south aspect stands (Veblen et al. 1991). Alternatively, harsh conditions on exposed south aspect sites or competition by quick-establishing graminoid and herb species may allow persistence of shade-intolerant species for decades (Stahelin 1943, Selmants and Knight 2003).

Tree establishment patterns are also related to weather and climatic conditions, although the temporal resolution of the photographs and the uncertainty of the age data I collected makes it difficult to observe general patterns here. On Mt. Rainier, warm, dry springs with lower snow pack and moist, cool summers favoured tree establishment, especially near favourable microsites (Little et al. 1994). In the Cascades, trees established along north slopes during regional warm-dry periods and on south slopes during cooler and moister periods (Miller and Halpern 1998), suggesting that establishment history is closely tied to topographic interactions with climate as was suggested by the classification and regression tree analysis.

The ability of lodgepole pine to produce seed quickly after fire means that successive fires with sufficient time between them can produce pure pine stands with few other species, which only succeed to spruce and fir after long periods of time (Anderson 2003). There is only one (nearly) pure lodgepole pine stand in the study area, but the high density of pine (Table 3.2) and the greater approximate age in a number of north aspect stands (Figure 3.4) corresponds with rapid pine regeneration following fire. This stand structure corresponds to lower species diversity (Figure 3.2); Haeussler et al. (1999) also noted a significant negative correlation between pine stem volume and understory species richness and diversity.

Fire history, which was coded as the period of last known fire, was an important variable in the cover transition classification trees. It accounted about one third of the variation in 1914–2004 transitions and about one fifth of the 1947–2005 transitions. Fire's influence on succession is related to the dependence of post-fire regeneration on the pattern, sequence and timing of previous fires and other disturbances, both in terms of the effect of fires on plant propagule sources and on microclimate and soil moisture and nutrient conditions (Howe and Baker 2003, Kipfmueller 2003, Schulte and Mladenoff 2005).

Based on qualitative analysis of the photographs and field observations, disturbances other than fire are clearly important in structuring vegetation and affecting successional trajectories, including shifts in avalanche paths and widespread mortality of lodgepole and white bark pine from MPB and blister rust. However, the only non-fire disturbance variable with any explanatory power in the classification tree analysis was MPB disturbance, appearing only once in the 1914–2004 model. The few areas of increasing polygon complexity (Figure 3.11) may be related to shifts and reappearances of defined avalanche paths (as opposed to open shrub land and meadow across the north side of the valley). These observations support the hypothesis that as time since stand initiation increases, multiple disturbances and interactions come to affect vegetation structure and increase landscape heterogeneity. Similarly, Veblen et al. (1991) noted that windstorms disturb stands during synchronous medium-intensity events, but only after enough trees are old enough to be susceptible to wind disturbance. Windthrows could then increase the likelihood of spruce-beetle outbreak or other pests (Veblen et al. 1991).

4.1.1 Restoring the subalpine landscape?

The findings from this study are relevant for the management and restoration of subalpine landscapes in WLNP and surrounding regions. This study provides a century-long characterization of forest cover dynamics in a large subalpine valley. Such a characterization useful in developing a reference landscape for restoration projects in the area, and can be assessed against or used in the development of models to predict disturbance and succession in mountainous landscapes (Keane et al. 1996, Cary et al. 2006).

Analysis of the photographs shows a dramatic transition from a mosaic of early, mid, and late seral forests to a landscape dominated by closed-canopy, maturing and late seral forests. This decline in landscape diversity is of concern for the conservation of biodiversity in the region and the maintenance of ecological integrity within WLNP. In particular, Parks Canada (2000) recognizes that fire protection impacts natural processes, as decreases in the number and size of fires allows forests to grow older and more homogenous with accompanying fuel accumulation and habitat loss.

Large fires burned through upper Blakiston Valley in the 1840's, 1880's, and other periods of the 1800's (Barrett 1996), creating a mosaic of regenerating and recently burned forest by the turn of the 20th century. The valley exhibits both stand-replacing and mixed-severity fires, with two to three major fire periods evident in the photos in addition to the small burn noted in the vicinity of plot 15. Extensive fires were common in the 18th and 19th century in subalpine landscapes of the region (Day 1972, Barrett et al. 1991), coinciding with regional droughts connected to decadal climatic variations (Kipfmueller 2003, Schoennagel et al. 2005) and increased fires from mineral exploration, railroads, and other settler activity (Murphy 1985). Barrett (1996) suggests fire-scarred lodgepole pine usually indicates a margin of a more severe fire, but there is only evidence of a small low-intensity fire in the 1940's in this area. The survival of mature Engelmann spruce and subalpine fir in low-intensity fires has also been noted by Campbell and Antos (2003).

More contested is the role of First Nations in subalpine fire regimes, who certainly used fire in the region to open travel routes, increase game, forage and berry production, and drive game during hunts, among other uses (Barrett 1982, Turner 1994, Peacock and Turner 2000, Heitzmann 2001, Baker 2002). Kay et al. (1999) claim that human activity has been the dominant factor controlling fire regimes, especially on the east slopes and valley floors of the Rockies where fires may be otherwise limited by lightning frequency that is lower than the west slope of the Rockies (Wierzchowski et al. 2002). Others argue it is difficult to partition the human influence on fire regimes over the last five centuries from climate shifts (Johnson et al. 1990, Masters 1990, Johnson and Larsen 1991, Rogeau 1996, Baker 2002), even though there appears to be little correlation between fire frequency and climate change (Luckman and Seed 1995, Heitzmann 2001). Johnson and Larson (1991) also argue that it is unlikely first peoples frequented subalpine habitats or burned them enough to alter fire regimes. As Heitzmann notes,

> Whether native people had a significant role in igniting fires is a critical issue for mountain national parks because evidence of when, where and how native peoples conducted burning could become a model for intervention in ecosystems today (Heitzmann 2001, p. 169).

For South Kootenay Pass the importance of the valley as a travel route (Getty 1972) and the lower occurrence of lightning strikes in the area than in surrounding regions (Barrett 1993) make it very likely that human-ignited fires influenced the fire regimes and vegetation patterns prior to human population declines resulting from disease. Stand age data for the north west part of the park supports this notion: the neighbouring Bauerman Valley, of similar size and orientation to the study area but without importance as a travel route, has a far greater proportion of old age classes than the upper Blakiston Valley (Barrett 1993). However, this cannot be taken as conclusive because there is insufficient replication, and many the fires of the mid 19th century burned after active travel and trading over the passes had ceased (Getty 1972).

The consequences of excluding fire over many decades are numerous, and interact with landscape processes, habitat loss, and climate change to have pronounced effects on biodiversity (Keane et al. 2002). Old, multistoried forests have cover value for some ungulates, but forage values are far lower than in open areas, late seral and beetle-affected pine stands may be difficult to traverse, and the loss of open habitat adversely affects Bighorn sheep (Gruell, Freedman and Habeck 1985, Peek et al. 1985, Heitzmann 2001). Fire-adapted ecosystems support a number of keystone plants (i.e. whitebark pine and aspen) that decline in the absence of fire (Keane et al. 2002 p. 260), and post-fire and early seral communities provide critical habitat for many rodent, insect, and bird communities (Higgins et al. 1989, Hutto 1995). Finally, fire exclusion is related to heightened insect and disease outbreaks due to plant competition, declining tree vigor (McHugh et al. 2003), and increased patch contagion (likelihood of similar patches being close together, allowing easier spread of insects, disease, and fire) (Hessburg 1994, Wilson and Tkacz 1996).

In WLNP, fire exclusion has potentially allowed much of the montane and subalpine landscape to shift from a combination of mixed-severity and stand-replacing fire regime to a long fire-interval stand replacing fire regime, with dramatic effects on forest structure, composition, and disturbance interactions (Barrett 1996). Mixed-severity fire regimes have fires of varying severity with a fire-return interval of 30-100 years that kill many of the trees and leave a mosaic of underburned live trees and dead trees. Stand-replacing fire regimes have longer fire-return intervals with high-severity fires that kill the trees across most of the burn area while leaving lightly burned trees in patches and along burn margins (Barrett 1996, Arno et al. 2000). Barrett et al. (1991) showed fire suppression is most effective in areas previously having mixed-severity regime, and much less so in areas of stand-replacing regime.

In the upper Blakiston Valley, evidence for the role of mixed-severity fires can be found in the small burn of 1940 near the junction of Blakiston Creek and Lone Creek and in the prevalence of Douglas-fir stands and open meadows along the south slope of Mt. Anderson. Overall, about 1/3 of subalpine stands sampled by Barrett (1996) show a mixed-severity fire regime, with an overall subalpine mean fire-return interval (MFI) of 98 years, among the shortest documented. However, since fire suppression became effective (circa 1940), there has been only one small fire in the subalpine of WLNP (Barrett 1996), giving a fire-free interval nearly twice as long as any in the historical record and a MFI nearly nine times the length of the historical MFI.

Parks Canada has identified broad management objectives that address this shift, namely to "maintain biological diversity at broad landscape and community scales, including ecological processes", and to "ensure that natural disturbances… and their effects function unhindered" (Parks Canada 2000, p. 13). They aim to use prescribed fire to return fifty percent of the natural fire cycle, giving priority to foothills parkland on montane ecoregions. However, Parks Canada has opted to suppress all lightning-caused fires in the park due to its small size and east-west orientation of major valleys (pers. comm. R. Watt, 2007). Even if lightning fires were allowed to spread under prescribed conditions, lightning alone may not provide enough ignitions to restore the historical fire cycle in subalpine areas, especially in major valleys along travel routes where First Nations burning was likely important. If Parks Canada does not pursue restoration of the fire cycle in the subalpine, there could be increased risk of losing biodiversity of valley side aspen, whitebark pine, and Douglas-fir stands, and increased fuel loading and continuity which could allow stand replacing fires to spread more easily (Barrett 1996).

If low and medium severity fires are seen to be an important part of the disturbance regime in subalpine valleys in WLNP, Parks Canada has a few options to consider. Management staff could do nothing, continuing a policy of suppressing lightning fire. They could re-initiate prescribed natural fire under prescribed conditions, though this may not produced sufficient fires to restore the natural fire cycle. Managers might also prescribe re-ignition of suppressed natural fires from current or previous years under certain conditions, though Arno et al. (2000) notes this will have different results than the unsuppressed lightning fires. Parks Canada should consider at least two scenarios where prescribed fire can play a role in maintaining landscape diversity. First, as a complement to stand thinning in whitebark pine ecosystem restoration, prescribed fire has a great deal of potential. However, remote, high-elevation sites may be problematic for thinning and fire control access, and ideal conditions for burning stands at higher elevations rarely occur (Keane 2001). Second, prescribed fire could be used in valley floor and lower slope areas in carefully planned, late-season burns to open habitat and provide fuel breaks and habitat refuges in the event of large stand-replacing fires. These could be placed adjacent existing natural fuel breaks such as avalanche paths (Suffling 1993).

Before engaging in active fire restoration in the subalpine, however, it is important to clarify in what sense fire cycle restoration might be needed. First, is the landscape outside of the historical range of variation? Considering that major stand-replacing fires occur every one to several centuries in Canadian Rocky Mountain subalpine landscapes (Romme and Knight 1981, Romme 1982, Bigler et al. 2005, Dillon et al. 2005), and that the small lower and medium severity fires have less impact on landscape-scale stand structure than large fires (Johnson et al. 1990, Bessie and Johnson 1995), some would argue the upper Blakiston Valley is within the HRV. However, given the landscape context of industrial forestry, fire suppression, mining, intensive recreation, and residential development of the surrounding landscapes (Arc Wildlife Services Ltd. 2004), the increasing rarity of subalpine landscapes exhibiting ecological integrity (NCC 2004), and the mandate of Parks Canada to manage for ecological integrity and representative ecosystems and processes (Parks Canada Agency 2000a, 2000a), there is a clear need to examine carefully the consequences of fire suppression and the potential for restoration within subalpine ecosystems of the Park.

4.2 Spatial approximation and oblique photographs: Promises and Uncertainty

The methods I used to reveal successional trajectories are novel in their attempt to directly compare patterns of forest cover interpreted from oblique photographs to those interpreted from aerial photographs. The spatial approximation method references the interpreted pixels to spatially-defined ground area instead of relative to picture area (Manier and Laven 2002, Rhemtulla et al. 2002). It also extends multivariate analyses and interpretation of cover transitions decades earlier than possible with aerial photos. This method introduces a number of uncertainties that bear careful consideration, but also opens the way for further studies using other spatial translation, approximation, or rectification approaches.

While I did not attempt formal accuracy assessments, I believe reflecting on the sources and implications of uncertainty in the analysis will help guide future studies using spatial approximation from oblique photographs. What are the sources of uncertainty (spatial, thematic, and temporal) in the spatial approximation and analyses procedures? How do these issues affect the potential uses of the data source and the interpretation and application of the results? And finally, what are some ways that error and uncertainty could be better assessed and quantified?

The cover data displayed in the maps may be seen as resulting from multiple interacting processes—the geological and geomorphological processes that shaped the landforms of the valley, the climatological processes that shaped hydrology and broad-scale vegetation patterns, disturbance (from glaciers to gaps) that have created and renewed growing spaces for plants (Oliver and Larson 1996), plant dispersal and succession, animal-habitat relationships, human influences, among others. Each of these processes contains both stochastic and predictable variation that affects the patterns observed in the photographs, some of which can be addressed through integrating ecological gradients and disturbance processes in successional studies (Wimberly and Spies 2001, Kipfmueller and Kupfer 2005).

Another set of variations called spatial and thematic uncertainty, introduces troubling issues that confound attempts to attribute patterns to the processes mentioned above (Hunsaker et al. 2001). These include the spatial variation and discontinuity of the photograph views, photographic flaws, image quality variation within photographs and between original and repeat photos, photo interpretation bias and error, error introduced or propagated through the spatial referencing process, thematic generalization and spatial aggregation, and comparison errors between photographs and between different data sources (Congalton and Green 1999, Edwards and Fortin 2001, Stine and Hunsaker 2001).

A loss of information due to the thematic aggregation is revealed when secondary components of vegetation cover are displayed (Table 3.5). If I had just displayed the aggregated classes I would have obscured the variation in numbers of cover types. However, I included only the simple cover classes in subsequent analyses and so could be missing critical elements in the interpretation of the data. There may be more sophisticated methods for dealing with these data (e.g., asymmetry analysis, Digby 1987).

At least three of these sources of uncertainty could account for the patterns observed in Figure 3.8. First, there is difference between my interpretation and that of the 2005 photo interpreters. For example, I tended to interpret sparsely vegetated sites as less vegetated (i.e. bare as opposed to herb or shrub, indicated by the two clusters on the left of Figure 3.8, and often interpreted forest and woodland stands as more closed than the aerial interpretation. The first of these tendencies may be explained by interpreter error, or different understandings of the classification system, and together can be considered thematic uncertainty (Congalton and Green 1999). The second source of uncertainty is caused by viewing the landscape from oblique angles, which obscures smaller canopy openings and decreases the area interpreted as open because intervening landscape features or forest canopy hide the near edge of openings. Viewing the landscape from oblique angles causes the images to have a continuously varying spatial scale and angle of incidence from the viewer to the landscape, meaning that the foreground may be better represented than the background, and that portions of the landscape that face the viewer are easier to interpret accurately than areas that slope gently or severely away from the viewer (Aschenwald et al. 2001). The varying spatial scale also relates to varying image quality as haze or smoke increases with distance from the camera. This set of problems could help explain the difference in sparsely vegetated sites noted above.

A third and potentially more troubling cause of the differences between 2004 and 2005 is related the effects of delineating boundaries and aggregating data, together known as the modifiable areal unit problem (MAUP) (Openshaw 1984, Jelinski and Wu 1996). When spatial data are delineated into map units, the placement of boundaries affects the amount of variation within and among polygons. This issue has been addressed in a number of settings. For instance, Edwards and Lowell (1996) demonstrated that when different interpreters delineate vegetation polygons, different boundaries result, giving a large zone of uncertainty that can gulf the area within the polygon and directly affect the area of cover types determined by interpretation (Edwards and Fortin 2001).

This problem means that some of the primary cover transitions shown in Figure 3.9 could be replaced with the secondary cover types listed in Table 3.3 if the placement of the cell boundary changed, or if the size of the cells were different. Furthermore, it may not be valid to assume that the 4 hectare cell accurately represents the interpreted space it overlays because (at least for larger polygons) the interpretation may ignore areas of slight, but locally important variation, and the cover class selection procedure excludes the small polygons and fragments that the grid cell intersects. Indeed, Fotheringham and Wong warn that MAUP is

> …essentially unpredictable in its intensity and effects in multivariate statistical analysis and is therefore a much greater problem than in univariate or bivariate analysis. The results of this analysis are rather depressing in that they provide strong evidence of the unreliability of any multivariate analysis undertaken with data from areal units (Fotheringham and Wong 1991, p. 1025).

One way of accounting for some of the spatial uncertainty due to the grid approximation method would be to repeat the intersection of vegetation polygons with a range of grid cell sizes and offsets, then examine the distribution of vegetation or transition classes that result in order to find the configuration that maximizes the explained variation and minimizes the spatial and thematic uncertainty (Dungan et al. 2002). Jordan et al. (2005) combined raster (fuzzy set) and vector (boundary membership) methods of uncertainty analysis in a study of historical fire boundaries. Combining the two approaches partitioned the spatial autocorrelation in the data sets, providing complementary information about fire history in riparian and upland areas.

Dealing with MAUP and scale issues is just one step in partitioning the uncertainty from the interpretation, approximation method, overlay analyses, and aggregation steps. There are also issues of validity of terrain variables and moisture and radiation proxies, which could have missed local terrain features such as drainage. Proxies could be validated using more direct measurements (Lookingbill and Urban 2005), but this effort was beyond the scope of this study.

4.2.1 Future directions in spatial approximation

While the spatial approximation approach used in this study provided rich data and expanded research in repeat photography and landscape change, the manual, labour-intensive process limits the number of scenes that can be analyzed in a given study, constrains the resolution of the translated data sets, and introduces a number of spatial and thematic uncertainties (as discussed in the previous section). Automating the rectification or translation process could resolve these problems and allow greater research into new applications; promising leads emerge from the work of Corripio (2002), Davis et al. (2002), and Honda and Nagai (2002).

After the analyst selects the view in the terrain visualization system, enters the photograph orientation parameters and confirms the fit to the photo, the ideal program would automatically register the oblique projection to the aerial by recording the correspondence between the spatial coordinates of the draped scene and the X-Y coordinates of the visualized window/photograph (similar to Aschenwald et al. 2001). This correspondence would then be used to rectify the oblique images, interpretations and classifications, or point-sample measurements (Corripio 2002), image clustering results, or spatial pattern metrics (Perry et al. 2002) from the oblique image pairs.

There are a number of ways available to carry out this translation. For instance, Corripio (2002) first masked areas of the scene not visible from the camera perspective using viewshed analysis, then geometrically transformed pixel coordinates from the DEM to the oblique photo with an algorithm that accounts for camera focal length, tilt, and radiometric differences. Aschenwald (2001) implemented a similar approach, though the algorithm is not as transparent and is more difficult to implement (pers. comm. W. Roush 2006). Honda and Nagai's (2002) approach of automatically matching skylines between the DEM and the oblique view may be useful in mountainous terrain, because few or no ground control points (GCPs) need to be established.

Once it has been calibrated and tested, automatic image registration would likely have greater speed, higher accuracy and precision, and greater extensibility than the manual method I used. In order to properly assess the accuracy of interpretation and remote sensing change detection techniques on the oblique photos, I recommend trying to characterize the effect of slope, aspect, and viewing angle on classification accuracy, using suitable data from fieldwork and aerial/satellite imagery. Corripio (2002) found that errors were introduced by displacements between the DEM and the photograph, especially where an abrupt change of slope was not represented in the DEM. This may be corrected by the production of a greater number of precisely georeferenced GCP's and the use of a higher-resolution DEM of greater currency, for instance using Heimsath and Farid's (2002) method of developing DEM's from multiple oblique photographs. Corripio dealt with errors due to low angles of incidence to the landscape by taking images with greater angle to the terrain. However, almost all of the images taken for the historical surveys used by the RMRPP are taken at or near an elevation angle of 0°, meaning that that for much of the gently undulating topography of the foothills and Rocky Mountain east slope rectifying the images using Corripio's method could introduce unacceptably high levels of uncertainty.

One other approach bears consideration here. One could select optimal study areas within the photographs to reduce variation in angle of incidence, or at least characterize the distribution of error in the image (Aschenwald et al. 2001, Davis et al. 2002). Given this knowledge and the use of a DEM one could also estimate the ground resolution for each pixel for more spatially precise estimates of land cover without the need for translation.

These approaches could be combined with stratified or systematic point-based sampling (i.e. Fensham et al. 2002) for the estimation of structural attributes, especially canopy structure, crown closure, and percent live crown, which can be identified in the photographs given an appropriate angle of incidence and local resolution. It also may be possible to measure height of trees or shrubs with distinct crowns if the local pixel resolution and slope, aspect and the camera angle of elevation are known, or to digitize new features to update forest inventory data in specific locations (Davis et al. 2002). These techniques could be useful in applications such as monitoring plant demography, growth and vigor, hill slope erosion and revegetation, and other factors important in park management and forest landscape restoration (Kullman 1987, Clay and Marsh 2001, Davis et al. 2002). For example, Aschenwald et al. (2001) developed a rectified time-series of oblique photographs to measure spatial and temporal variation in snow depth in the Italian Alps, and Barker et al. (1997) measured river bank erosion using terrestrial photographs.

4.3 Conclusion

Characterizing historical patterns of disturbance and succession requires integrating multiple sources of ecological information, including field data, historical imagery, and map and GIS data (Egan and Howell 2001). The field and GIS methods I used provided a basis for understanding contemporary patterns of forest structure in light of historical disturbance and succession dynamics and other ecological factors. Moreover, the spatial approximation methods represent a novel and promising approach to interpreting and analyzing repeated oblique photographs, notwithstanding the negative effects of spatial and thematic uncertainty. There is clearly much more work required to effectively use and analyze the extensive survey photograph collections of the Mountain Legacy Project.

The results of my study contribute observations and insight useful in developing conceptual models of historical forest dynamics for use in managing and restoring subalpine landscapes. In the near absence of fire this century, the forests of the upper Blakiston Creek have undergone substantial changes. Forest cover has increased dramatically at the expense of herbaceous and shrub communities, with an associated decrease in landscape heterogeneity. This trend is concerning because it represents a decline in important wildlife habitat and keystone ecological processes in protected areas within a region where industrial forest management, residential expansion, recreation and other land uses are increasingly degrading the ecological integrity of entire landscapes.

Clearly, the cross-boundary nature of these problems requires improving the capacity for ecosystem management through interjurisdictional cooperation, cross-boundary research, and the development of a comprehensive cumulative-effects model (Pedynowski 2003). Park and forest managers have the ability to respond in a limited way to the changing fire regimes and loss of landscape heterogeneity by restoring mixed-severity fire regimes to ecosystems. However, restoring ecological integrity to the greater landscape will require going beyond fire to consider multiple interacting disturbance processes, ecological influences, historical legacies, and the changing effects of human activities locally, regionally, and globally.

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Appendix A Historical and repeat photographs

Historical photos were taken by M.P. Bridgland, Dominion Land Survey, unless otherwise noted. Repeat photos were taken by Trudi Smith, Eric Higgs and Adrienne Shaw during the 2004 and 2005 field seasons. Historical images courtesy Library and Archives Canada and Waterton Lakes National Park; Repeat images copyright Eric Higgs, 2004-2006.

Appendix A 1 View west (plate 555) toward South Kootenay Pass from Mt. Blakiston (2748 m at camera station) in 1914 (left) and 2005 (right).

Appendix A 2 View south (plate 584) toward Mt. Festubert from Lost Mt. (2471 m) in 1914 (left) and 2004 (right).

Appendix A 3 View south west (plate 585) toward South Kootenay Pass from Lost Mt. (2471 m) in 1914 (left) and 2004 (right).

Appendix A 4 View northwest (plate 594) along the continental divide from Lone Mt. (2413 m) in 1914 (top) and 2005 (bottom).

Appendix A 5 View northwest (plate 597) west toward Mt. Hawkins and Mt. Festubert from Lone Mt. (2413 m) in 1914 (top) and 2004 (bottom).

Appendix A 6 View north (plate 598) toward Lost Mt. from Lone Mt. (2413 m) in 1914 (left) and 2004 (right).

Appendix A 7 View east (plate 599) toward Anderson Mt. and Red Rock Canyon Parkway from Lone Mt. (2413 m) in 1914 (left) and 2004 (right).

Appendix A 8 1881 (top) and 2005 (bottom) view from the upper Blakiston Valley (elevation 1750 m) east toward Mt. Blakiston, G.M. Dawson, 1881 and Trudi Smith, 2005. Note the extent and severity of the fire, extending into the alpine larch woodland on Mt. Hawkins (upper right), and possibly extinguishing in an avalanche path in the foreground.

Appendix A 9 1881 view from the Blakiston Valley (1680 m) southwest toward Mt. Festubert (top, A.S. Hill Glenbow NA-2592-1) and 1881 view of Mt. Blakiston from the South Kootenay Pass (2050 m), G.M. Dawson.

Appendix B Vegetation cover interpretation

The WLNP vegetation codes and criteria were obtained from Cyndi Smith (Park Ecologist, WLNP); additional criteria were adapted from Rhemtulla (1999). I generalized the classification schema at the intermediate level because the colour, quality, and resolution constraints of the original aerial and oblique views, the lack of stereoscopic pairs, and the lack of colour infrared film. I interpreted the photos using the intermediate scheme and physiognomic class with modifiers (below), then aggregated data to the final classification for the spatial translation and analyses.

Class	Physiognomic Code	Vegetation Class	WLNP Vegetation codes	Criteria / notes
Bare (B)	7 – rock 8 – sand/gravel	VCT	VCT – cliff and talus sparse vascular	Vegetation cover 0-10%
	8 – sand/gravel	VSL	VSL – Exposed lake or stream deposits	
	6 – water 9 – anthropogenic		N – non vegetated	Snow patches, water
Herbaceous (H)	5 – herbaceous	H	HGL – grassland, HWM – wet meadow	Difficult to distinguish
Shrubland {S)	4 – shrub-dominated	SAD	SAD – deciduous shrubland avalanche / snow burial	Shrub layer > 25% cover; tree layer < 25% cover
	4	SAM	SAM – mixed Engelmann spruce / subalpine fir / deciduous avalanche path shrubland	Both spruce-fir and decidous > 25%
	4	DS	D – dwarf shrubland, C – shrub/herbaceous complex	Difficult to distinguish
	3	SD	SDS – decidous shrubland, SWL – riparian willow shrubland	Sometimes
	3 – sapling/young tree growth	SMR	SMR – shrubby mixed regeneration / early regeneration following fire, blowdown, other disturbance	
Woodland (W)	2 – open forest / woodland	WC – conifer	WLP, WLM, WWB, WDF, WFS, WSL	Tree height < 25%, <10m, rules as below
		WM – mixed WD – decid.	WEP	
Forest (F)	1 – closed forest	FC	F, FLP, FDF, FFS, FSP	Tree cover > 60%, conifer trees > 66% relative cover
		FM	FSW, FEP	Conifer and deciduous each > 25% cover
		FD	FAP, FCW	Deciduous > 66% cover

Cover class modifiers

Seral Stage
- YS – young seral
- MS – maturing seral
- M – mature/old growth

Stand Structure
- S – single story
- X – multiple stories

Disturbance
1. Fire
2. Avalanche
3. Wind
4. Insect/disease
5. Unknown

Vegetation Cover Density
1. Closed canopy/continuous (60—100% cover)
2. Open canopy/discontinuous (25—60% cover)
3. Dispersed/sparse canopy (10—25% cover)

Vegetation Cover Pattern
1. Evenly dispersed
2. Clumped/bunched
3. Gradational/transitional
4. Regularly alternating

Appendix C Additional summary tables

Table C.4.1 Species list with English names, abbreviated names (used in Figure 3.4), and frequency of occurrence in study plots.

Species	English Name	Short Name	Frequency
Abies lasiocarpa	subalpine fir	Abielasi	22
Acer glabrum	Douglas maple	Acerglab	7
Achillea millefolium	yarrow	Achimill	2
Actaea rubra	baneberry	Actarubr	6
Allium sp.	onion	Allisp	2
Alnus viridis	green alder	Alnuviri	11
Amelanchier alnifolia	saskatoon	Amelalni	6
Anemone patens	prairie crocus	Anempate	1
Angelica arguta	sharptooth angelica	Angeargu	1
Angelica sp.	angelica	Angesp	1
Antennaria sp.	pussytoes	Antesp	1
Apocynum sp.	dogbane	Apocsp	1
Aquilegia flavescens	yellow columbine	Aquiflav	2
Aquilegia sp.	columbine	Aquisp	2
Arctostaphylos uva-ursi	kinnikinnick	Arctursi	2
Arnica cordifolia	heart-leaved arnica	Arnicord	18
Artemisia sp.	sagewort or wormwood	Artesp	1
Astragalus sp.	milk-vetch	Astrsp	4
Balsamorhiza sagittata	arrowleaf balsamroot	Balssagi	1
Brassica sp.	mustard	Brassp	1
Calochortus apiculatus	three-spot mariposa lily	Caloapic	1
Carex sp.	Sedge	Caresp	1
Caryophyllaceae	pink	Cryphyll	1
Castilleja miniata	scarlet paintbrush	Castmini	4
Castilleja sp.	paintbrush	Castsp	1
Chimaphila umbellata	princes pine	Chimumbe	10
Cirsium hookerianum	Hooker's thistle	Cirshook	1
Clematis columbiana	blue clematis	Clemcolu	9
Clintonia uniflora	Queen's cup	Clinunif	6
Collinsia parviflora	Small-flowered blue-eyed Mary	Collparv	1
Cornus canadensis	bunchberry	Corncana	2
Cornus sericea	red-osier dogwood	Cornseri	2
Disporum sp.	fairybells	Dispsp	2
Disporum trachycarpum	fairybells	Disptrac	1
Epilobium angustifolium	fireweed	Epilangu	9
Epilobium sp.	willowherb	Epilsp	2
Equisetum sp.	horsetail	Equisp	1
Erigeron peregrinus	subalpine daisy	Erigpere	2
Erigeron sp.	fleabane	Erigsp	9
Fragaria virginiana	wild strawberry	Fragvirg	8
Galium sp.	bedstraw	Galisp	2
Galium trifidum	Small bedstraw	Galitrif	2
Galium triflorum	Sweet-scented bedstraw	Galitrif.1	1

Geranium viscosissimum	Sticky purple geranium	Geravisc	2
Goodyera oblongifolia	rattlesnake-plantain	Goodoblo	11
Heracleum lanatum	cow-parsnip	Heralana	5
Holodiscus discolor	oceanspray	Holodisc	1
Juniperus communis	common juniper	Junicomm	1
Juniperus horizontalis	creeping juniper	Junihori	6
Linnaea borealis	twinflower	Linnbore	2
Linum lewisii ssp. *lewisii*	western blue flax	Linulewi	1
Listera cordata	heart-leaved twayblade	Listcord	1
Lomatium dissectum	fern-leaved desert-parsley	Lomadiss	1
Lonicera involucrata	black twinberry	Loniinvo	3
Mahonia repens	creeping Oregon-grape	Mahorepe	9
Menziesia ferruginea	false azalea	Menzferr	12
Mitella sp.	mitrewort	Mitesp	1
Mitella trifida	three-toothed mitrewort	Mitetrif	1
Monarda fistulosa	wild bergamot	Monafist	1
Orchidaceae	orchid	Orchidac	1
Osmorhiza depauperata	blunt-fruited sweet-cicely	Osmodepa	4
Parnassia sp.	grass-of-Parnassus	Parnsp	2
Pedicularis bracteosa	bracted lousewort	Pedibrac	1
Pedicularis sp.	lousewort	Pedisp	1
Penstemon lyallii	Lyall's penstemon	Penslyal	1
Picea engelmannii	Engelmann spruce	Piceenge	18
Pinus albicaulis	whitebark pine	Pinualbi	2
Pinus contorta var. *latifolia*	lodgepole pine	Pinulati	18
Platanthera orbiculata	large round-leaved rein orchid	Platorbi	1
Poaceae	Grass species	Poaceae	7
Populus balsamifera	balsam poplar	Popubals	3
Populus tremuloides	trembling aspen	Poputrem	4
Potentilla fruticosa	shrubby cinquefoil	Potefrut	2
Potentilla sp.	cinquefoil	Potesp	1
Prunus sp.	cherry	Prunsp	1
Pseudoroegneria spicata	bluebunch wheatgrass	Pseuspic	1
Pseudotsuga menziesii var. glauca	Rocky Mountain Douglas-fir	Pseuglau	5
Pyrola asarifolia	pink wintergreen	Pyroasar	1
Pyrola sp.	wintergreen	Pyrosp	11
Ribes inerme	white-stemmed gooseberry	Ribeiner	2
Ribes lacustre	black gooseberry	Ribelacu	5
Ribes sp.	currant or gooseberry	Ribesp	4
Rosa acicularis	prickly rose	Rosaacic	7
Rubus idaeus	red raspberry	Rubuidae	1
Rubus parviflorus	thimbleberry	Rubuparv	15
Salix sp.	willow	Salisp	1
Sambucus racemosa	elderberry	Sambrace	1
Sedum lanceolatum	lance-leaved stonecrop	Sedulanc	1
Sedum sp.	sedum species	Sedusp	1
Senecio pauperculus	Canadian butterweed	Senepaup	1
Senecio sp.	groundsel species	Senesp	2

Shepherdia canadensis	soopolallie	Shepcana	7
Smilacina stellata	star-flowered false Solomon`s-seal	Smilstel	9
Sorbus sp.	mountain ash	Sorbsp	9
Spiraea betulifolia ssp. *lucida*	birch-leaved spirea	Spirluci	7
Stellaria crassifolia	thick-leaved starwort	Stelcras	1
Streptopus amplexifolius	clasping twistedstalk	Streampl	3
Symphoricarpos albus	common snowberry	Sympalbu	6
Thalictrum occidentale	western meadowrue	Thalocci	12
Tiarella trifoliata	three-leaved foamflower	Tiartrif	4
Urtica dioica	stinging nettle	Urtidioi	2
Vaccinium membranaceum	black huckleberry	Vaccmemb	2
Vaccinium scoparium	grouseberry	Vaccscop	16
Valeriana sitchensis	Sitka valerian	Valesitc	3
Veratrum viride	Indian hellebore	Veraviri	7
Veronica sp.	speedwell	Verosp	1
Viola sp.	violet	Violsp	4
Xerophyllum tenax	bear-grass	Xerotena	9

Table C.4.2 Qualitative physical site conditions for sampled stands.

Plot	Position	Shape[1]	Topography	Texture[2]	Moisture	Nutrient	Coarse Fragment
1	crest	Convex	uneven	snd	dry	med.	High
2	lower	Unif	even	slt clay lm	moist	rich	High
3	lower	concave	uneven	lm	mesic	med.	high
4	upper	Unif	even	snd	dry	med.	High
5	lower	concave	even	slt	mesic	rich	Low
6	middle	Unif	hummocky	snd	moist	rich	High
7	middle	Unif	even	snd	mesic	med.	High
8	upper	Unif	even	lm	Mesic	rich	high
9	lower	concave	hummocky	snd lm	moist	rich	High
10	middle	Convex	uneven	snd	dry	poor	High
11	lower	concave	uneven	snd lm	mesic	rich	Med.
12	lower	Convex	even	slt clay lm	mesic	med.	Low
13	middle	Unif	hummocky	colluv.	mesic	med.	high
14	middle	Unif	even	snd	dry	poor	Med.
15	lower	Unif	even	slt clay lm	moist	rich	Low
16	middle	Unif	even	snd	Dry	poor	high
17	middle	Unif	even	snd	Mesic	med.	high
18	middle	Convex	uneven	colluv.	Dry	med.	high
19	lower	Convex	uneven	snd	moist	rich	High
20	middle	Unif	even	lm	mesic	med.	High
21	middle	Unif	even	snd	Mesic	med.	high
22	middle	Convex	even	snd	Mesic	med.	high
23	lower	Unif	even	snd lm	mesic	med.	Med.

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[1] Slope shape: convex, uniform (constant slope), concave

[2] Soil texture: snd=sandy, slt=silty, lm=loam, colluv=colluvium

Table C.4.3 Importance values for tree species (alive and dead) across all plots. Importance values are a sum of the proportions relative frequency, relative basal area, and relative density, and vary between 0 and 300.

Plot	Subalpine Fir	Spruce	Whitebark Pine	Lodgepole Pine	Cottonwood	Aspen	Douglas fir	Unknown
1	13.63	38.07	--	124.43	--	20.54	--	3.33
2	147.36	--	--	13.44	--	--	39.21	--
3	37.06	94.48	--	57.65	--	--	--	10.81
4	163.22	21.04	--	--	--	--	11.96	3.78
5	39.64	33.14	--	117.13	--	--	--	10.08
6	8.54	4.13	--	187.33	--	--	--	--
7	63.49	12.42	23.89	85.65	--	--	--	14.55
8	32.53	92.49	--	58.78	16.2	--	--	--
9	133.28	40.5	--	3.49	22.73	--	--	--
10	36.97	--	--	68.66	--	--	94.37	--
11	60.49	86.56	--	52.95	--	--	--	--
12	36.31	50.99	--	112.7	--	--	--	--
13	142.91	52.81	--	4.28	--	--	--	--
14	48.63	20.8	--	113.77	--	--	--	16.79
15	22.27	25.41	--	86.68	--	--	--	65.63
16	80.74	83.07	2.38	33	--	--	--	0.82
17	76.19	78.99	--	40.67	--	--	--	4.15
18	43.88	66.16	--	89.95	--	--	--	--
19	--	--	--	159.85	21.48	18.67	--	--
20	191.76	--	--	8.24	--	--	--	--
21	188.84	--	--	11.16	--	--	--	--
22	172.29	26.13	--	1.58	--	--	--	--
23	128.73	46.01	--	--	--	--	--	25.26

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