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Historic Influence of the Mountain Pine Beetle on Stand Dynamics in Canada's Rocky Mountain Parks

Pamela R. Dykstra and Tom F. Braumandl

Mountain Pine Beetle Initiative
Working Paper 2006-15

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Abstract

Forest disturbances such as the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) create ecological legacies that contribute to ecosystem recovery and help maintain biological processes. Ecological legacies include soil biota, live trees, standing and downed dead wood, and sources of seed. To help understand what habitat attributes we should seek in ecologically similar, recently disturbed managed forests to aid ecosystem recovery, we examined historic, unmanaged forests in two ecosystems in the Rocky Mountain national parks; one ecosystem in Kootenay, Banff and Yoho and one in Waterton Lakes. We measured structural attributes and species composition in circum-mesic forests disturbed by the mountain pine beetle 25 and 65 years before present. We found that the mountain pine beetle strongly influenced the structure and composition of the two studied ecosystems. The mountain pine beetle stimulated understory vegetation productivity, causing a sustained re-distribution of resources within stands. The mountain pine beetle increased the heterogeneity of stands and landscapes and created diverse pathways of stand development. This diversity created unique ecological legacies and post-disturbance assemblages of species across landscapes. Ecosystem recovery was apparent over the long term. However, because ecosystem recovery from mountain pine beetle disturbance appears to vary in different ecosystems, resilience to post beetle management actions such as salvage harvesting will likely also vary between ecosystems; the type and intensity of harvesting should reflect the sensitivity of ecosystems to additional disturbance.

Résumé

Les perturbations des forêts telles que le dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) entraînent des conséquences écologiques qui contribuent au rétablissement de l'écosystème et aident à maintenir les processus biologiques. Les conséquences écologiques comprennent la biote du sol, les arbres vivants, le bois mort debout et au sol et l'origine des graines. Afin d'aider à comprendre quels attributs de l'habitat on devrait rechercher dans des forêts aménagées écologiquement semblables et récemment perturbées pour contribuer au rétablissement de l'écosystème, on a examiné des forêts historiques non aménagées dans deux écosystèmes des parcs nationaux des Rocheuses, soit un à Kootenay, Banff et Yoho, et un autre dans les lacs Waterton. On a examiné les attributs structurels et la composition des espèces de forêts mésoïques perturbées par le dendroctone du pin il y a de 25 à 65 ans. On a découvert que le dendroctone de pin ponderosa influençait considérablement la structure et la composition des deux écosystèmes étudiés. Le dendroctone de pin ponderosa stimulait la productivité de la végétation du sous-étage, entraînant une redistribution soutenue des ressources au sein des peuplements. Le dendroctone de pin ponderosa a accru l'hétérogénéité des

peuplements et des paysages et a créé plusieurs voies de développement des peuplements. Cette diversité a donné lieu à des conséquences écologiques uniques et à des assemblages d’espèces dans tous les paysages après les perturbations. Le rétablissement de l’écosystème était évident à long terme. Cependant, étant donné que le rétablissement de l’écosystème après les perturbations attribuables au dendroctone du pin ponderosa semble varier dans différents écosystèmes, la résilience aux mesures de gestion prises après les ravages du dendroctone, telles que la coupe de récupération, est susceptible de varier entre les écosystèmes. Le type et l’intensité de l’exploitation doivent refléter la sensibilité des écosystèmes à une perturbation supplémentaire.

Executive Summary

The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic is exceptionally extensive and severe, with approximately 8.7 million hectares in the red-attack stage in fall 2005, and a cumulative impact affecting 400 million m3 of timber to date. The Canadian government announced the Mountain Pine Beetle Initiative (MPBI) in 2002 to address the socio-economic and ecological consequences of the current epidemic. The Epidemic Risk Reduction and Value Capture Research and Development Program of the MPBI is a strategically oriented, science-based component intended to reflect operational needs in its capture and transfer of knowledge. Among the operational knowledge gaps is a good understanding of the ecological impacts, risks, and opportunities associated with an epidemic of the scale that is ongoing in British Columbia and surrounding landscapes.

Increasingly, models of forest establishment and succession integrate the influence that disturbance has on the characteristics and development of forests. In particular, attention has begun to focus on the remnants—or "ecological legacies"—that survive from the pre-disturbance stand, including soil biota, live trees, standing and downed dead wood, and sources of propagules; and the role these legacies play in maintaining ecological function post-disturbance. Ecological legacies play a role in and persist through processes that occur on decadal time scales. This temporal scale suggests the need for a long term perspective to quantify ecosystem factors such as time lags in regeneration recruitment or persistence times of habitat elements.

Under a policy of minimal disruption to natural processes, the ecological conditions in the Rocky Mountain national parks (Banff, Yoho, Kootenay and Waterton Lakes; RMNP) allow study of the natural process of stand development that follows disturbance by the mountain pine beetle. Repeated infestations of mountain pine beetle have occurred in the RMNP. As a result, the landscape is now composed of stands in different states of recovery from temporally spaced disturbance events. For these events, the RMNP represent benchmark ecological conditions relevant to managed landscapes; similar forest types to those in the RMNP occur in montane regions of Alberta, British Columbia and the United States.

The objective of this study was to establish baseline information on the ecological characteristics that occur at different stages of succession, resulting from mountain pine beetle disturbance at different time intervals. Key questions posed by the MPBI and addressed by this study were:

- What is the post-beetle ecological character of stands?
- What ecological legacies should be sought post-beetle?
- Can or should ecological integrity be maintained in beetle-damaged landscapes?
- What are the beetle impacts on regeneration?

This paper presents a study of stand conditions following two historic mountain pine beetle outbreaks events in the 1940s and 1980s. We measured overstory and understory structural attributes, gathered cross-sectional tree discs and cores from the boles of

regeneration, and surveyed vegetation communities in 85 randomly located stands in two circum-mesic lodgepole pine ecosystem types. In Kootenay, Banff and Yoho national parks, we established plots in 17 stands in each of the 1940s and 1980s disturbance events, and in 17 control stands. In Waterton Lakes national park, we established plots in 17 stands from the 1980s disturbance event and in 17 control stands. We performed multivariate ordination on the overstory and understory structural attributes and the vegetation data to describe the relationships in the data set, and used analysis of variance (ANOVA) on all data to examine treatment effects.

In Waterton Lakes and Kootenay, Banff and Yoho, considerable agreement occurred between the ANOVA and the multivariate ordination results in the selection and significance of variables that separated the treatments; the multivariate ordination for the two ecosystems well differentiated the treatments in multivariate space, while the majority of the attributes selected by the ordination to describe the greatest variation in the data showed statistically significant differences in the ANOVA.

Overall in Waterton Lakes, the ordination attributed the greatest amount of variation to (in decreasing order of importance): three variables representing coarse woody debris (CWD) volume, comprising all decay classes of CWD; five variables representing vegetation volume; and total live basal area. Overall in Kootenay, Banff and Yoho, the ordination attributed the greatest amount of variation to (in decreasing order of importance): three variables representing live basal area, the number of stems of small regeneration (stems ≤ 30 cm in height), two variables representing vegetation volume and maximum stand age (age of the largest trees). For both ecosystems, the ANOVA revealed that differences between treatments were statistically significant; these differences were also biologically significant, with several variables showing doubling or even greater difference in values.

The rank order of all variables according to the amount of variation they represented differed between ecosystems, although two vegetation variables (graminoids and shrubs) and total live basal area (trees > 4 cm diameter-at-breast height [DBH]) were common to the Kootenay, Banff and Yoho and the Waterton Lakes ordinations. For these variables, vegetation represented greater variation in Waterton Lakes than it did in Kootenay, Banff and Yoho, and live basal area represented greater variation in Kootenay, Banff and Yoho than it did in Waterton Lakes.

In the ordination for Kootenay, Banff and Yoho, the 1940s stands were intermediate between the control and the 1980s disturbance, and more closely related to the control plots, revealing a gradual recovery of disturbed stands taking place over 65 years. However, the significant differences that existed between the control and 1940s disturbed stands suggest that the mountain pine beetle has altered the trajectory of these stands for both community and structural attributes. This altered trajectory suggests that the mountain pine beetle increases heterogeneity, and creates unique post-disturbance assemblages of species and habitat attributes, enhancing habitat values at stand and landscape levels.

We can summarize our study findings to date by returning to the study objectives. Regarding the ecological character of stands and ecological legacies following mountain pine beetle disturbance—first, we saw that coarse woody debris (CWD), vegetation and basal area represented the greatest variation between treatments, but that the rank order of their contribution to the variation in the data differed between the two ecosystems. Second, the mountain pine beetle stimulated understory vegetation productivity—a sustained re-distribution of resources between stands that persisted into the mid term. Third, the mountain pine beetle increased stand and landscape heterogeneity in three ways: via increased beta diversity of understory vegetation, by creating stands in the advanced recovery stage that have different habitat elements than control stands, and by initiating different trajectories of ecological legacies in different ecosystems. The latter finding shows that different habitat values occur over time across the landscape, originating from mountain pine beetle disturbance of similar timing.

Regarding the maintenance of ecological integrity in beetle-affected landscapes, the results clearly showed that ecological legacies existed and persisted following disturbance by the mountain pine beetle, and that recovery does gradually occur in disturbed stands, suggesting that an important 'life-boating' function exists for these legacies to help maintain ecological integrity in managed landscapes. However, we found a different recovery response between ecosystems, which may indicate that resilience to mountain pine beetle and to any additional disturbance differs between ecosystems. The success at maintaining ecosystem integrity will likely also differ, and be contingent upon the way in which additional disturbance (i.e., salvage) occurs. Finally, we found either no notable pulse of regeneration or a delay in regeneration following disturbance.

The similarities between findings in the two ecosystems suggest that some management interpretations about how to retain ecological functioning, for example, the need to manage for multiple habitat elements, may be ubiquitous across ecosystems. However, some of the differences between findings in the two ecosystems suggest that rates of recruitment and persistence of ecological legacies vary between ecosystems, with consequent differences in the types of habitat values that ecosystems would provide at different times following a widespread disturbance. Therefore, some management strategies should be adapted to suit local conditions. Because ecosystem recovery from mountain pine beetle disturbance appears to vary in different ecosystems, resilience to post beetle management actions such as salvage logging will likely also vary between ecosystems; the type and intensity of rehabilitation should reflect the sensitivity of ecosystems to additional disturbance.

We conclude the report with several recommendations for management of post-disturbance landscapes.

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Introduction

Background

Disturbances are discrete events that "…disrupt structure…and change resources…" in ecosystems (White and Pickett, 1985, p. 7). Increasingly, models of forest establishment and succession integrate the influence that disturbance has on the characteristics and development of forest stands (Oliver and Larson, 1996; Turner et al., 1997a; Turner et al., 1997b; Frelich and Reich, 1999; DeLong and Kessler, 2000; Franklin et al., 2002; Platt and Connell, 2003). In particular, attention has begun to focus on the remnants—or "biological legacies"—that survive from the pre-disturbance stand, including soil biota, chemistry and structure; live trees; standing and downed dead wood and sources of propagules ([herein referred to as ecological legacies] Harmon et al., 1986; Perry and Amaranthus, 1997; Turner et al., 1997b; DeLong and Kessler, 2000; Franklin et al., 2002; Platt and Connell, 2003). Remnants from the pre-disturbance stand that persist through the developing stand can mitigate the impacts of disturbance in two ways. First, ecological legacies create continuity of habitat structures and species, and second, they ameliorate some of the detrimental conditions caused by disturbance, for example, the ability of large woody debris to retain soil onsite that might otherwise erode (Perry and Amaranthus, 1997). Ecological legacies thus play an important role in ecosystem recovery following disturbance.

Disturbance by insects has an important role in changing stands and landscapes (Veblen et al., 1991; Schowalter, 2000; Veblen, 2000; Bebi et al., 2003; Taylor and Carroll, 2003). In landscapes of Canada and the western United States, the mountain pine beetle (mountain pine beetle; *Dendroctonus ponderosae* Hopkins) has a pervasive influence on montane, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats.) ecosystems (Wood and Unger, 1996; Ebata, 2003; Gibson, 2003; Ono, 2003; Taylor and Carroll, 2003). Management actions generally aim to limit the effects of the beetle on socio-economic systems such as employment reductions and the loss or degradation of timber supply. Consequently, the historic focus of most research has been to increase the ability to predict and limit beetle activity. Research has focused on increasing knowledge of the ecology, population biology, and behaviour of the mountain pine beetle at the level of trees and stands (e.g., Amman, 1973; Safranyik, 1978; Cole and Amman, 1980; Stark, 1982; Amman and Cole, 1983; Waring and Pitman, 1983; Amman, 1984; Bartos, 1988; Cole and McGregor, 1988; Shore and Safranyik, 1992; Shore et al., 1996; Bartos and Schmitz, 1998). More recently, the spatial components of mountain pine beetle ecology, behaviour, and population dynamics have become a focus for research (e.g., Polymenopoulos and Long, 1990; Mitchell and Preisler, 1991; Preisler, 1993; Binder and Bartos, 1995; Logan et al., 1998; Peltonen et al., 2002; Liebhold and Bjornstad, 2003).

The literature is less abundant and comprehensive about the ecological role of the beetle—the influence that the mountain pine beetle has on process and function in its environment. However, the literature suggests that the mountain pine beetle occupies three main ecological roles (Dykstra et al., *In prep.*). First, the beetle alters stand dynamics, generally accelerating succession (e.g., Roe and Amman, 1970; Amman, 1977; Peterman, 1978; Cole and Amman, 1980; Heath and Alfaro, 1990). Second, the mountain pine beetle creates ecological legacies primarily through contributions to the dead wood cycle, affecting many species (Harmon et al., 1986; Machmer and Steeger, 1995; Keisker, 2000; Schowalter, 2000; Steed and Wagner, 2002). Third, the mountain pine beetle interacts directly with other insect, bird and mammal species (Amman, 1970; Parker and Davis, 1971; Amman, 1972, 1973; Cole, 1975; Geiszler et al., 1980; Bull, 1983; Amman, 1984; Rasmussen, 1987; Gara, 1988; Rankin and Borden, 1991; Bergvinson and Borden, 1992; Hadley, 1994; Nebeker et al., 1995; Nevill and Safranyik, 1996; Wilson et al., 1998; Safranyik et al., 1999; Hayes and Daterman, 2001).

Mid– to long–term ecological effects following disturbance by the mountain pine beetle are rarely studied. For example, little is quantified about whether time lags occur between disturbance events and site regeneration, and what are the persistence times of ecological legacies such as dead and downed wood. Uncertainty about natural stand development following disturbance by the mountain pine beetle leaves an absence of empirically-based direction in ecosystem management, such as how to continue to maintain stand and landscape function in landscapes subject to salvage harvesting, and what is the successional progression and the expected time to recovery in landscapes disturbed by mountain pine beetle. Consequently, in managed forests following disturbance, ecological first principles may be the primary basis for the proposed maintenance of ecological integrity (e.g., Hughes and Drever, 2001; Eng, 2004). Site specific data in the context of forest disturbance are therefore increasingly necessary to build our understanding of forest development (Spies, 1997), and increase our understanding of the ecological role of the mountain pine beetle.

Regional Context

The current mountain pine beetle epidemic is exceptionally extensive and severe, with approximately 8.7 million hectares in the red-attack stage in fall 2005, and a cumulative impact affecting 400 million m3 of timber to date (Fall 2005) in British Columbia (British Columbia Ministry of Forests and Range, 2006). The mountain pine beetle is also active in surrounding landscapes in Alberta, Idaho, Montana and Washington (Gibson, 2003; Ono, 2003). The Canadian government announced the Mountain Pine Beetle Initiative (MPBI) in 2002 to address the socio-economic and ecological consequences of the current epidemic1. The Epidemic Risk Reduction and Value Capture Research and Development Program of the MPBI is a strategically oriented, science-based component intended to reflect operational needs in its capture and transfer of knowledge.

Among the operational knowledge gaps is a good understanding of the ecological impacts, risks, and opportunities associated with an epidemic of the scale that is ongoing in British Columbia and surrounding landscapes. Management actions such as salvage harvesting tend to have an additive effect on disturbed ecosystems, removing or damaging ecological legacies and delaying ecosystem recovery (Holling, 1973; Lindenmayer et al., 2004; Donato et al., 2006; Lindenmayer, 2006). A refined understanding of the impact of the mountain pine beetle on ecological processes is therefore necessary to contribute to ecological integrity in the managed landscapes

[1] http://mpb.cfs.nrcan.gc.ca/

recently disturbed by the mountain pine beetle and scheduled for harvest in the near future. Consequently, an Ecological Strategic Objective of the MPBI Epidemic Risk Reduction Program is to contribute to improved ecological integrity of post-beetle landscapes.

Ecological processes of interest include mountain pine beetle impacts on the ecological character and development of stands. The influence of the beetle on these processes can in part be understood through the successional development of forests that occurs following mountain pine beetle disturbance, and quantified by the ecological legacies that result and persist after mountain pine beetle disturbance. Many of the ecological processes of interest occur on decadal time scales. This temporal scale suggests the need for a long term perspective to quantify ecosystem factors such as time lags in recruitment or persistence times of habitat elements.

Under a policy of minimal influence with natural processes, the ecological conditions in the Rocky Mountain national parks (Banff, Yoho, Kootenay and Waterton Lakes; RMNP) allow study of the natural process of stand development that follows disturbance by the mountain pine beetle. The RMNP represent benchmark ecological conditions relevant to managed landscapes; similar forest types to those in RMNP occur in montane regions of Alberta, British Columbia and the United States, for example, the Montane Spruce biogeoclimatic zone of British Columbic (Meidinger and Pojar, 1991). Repeated infestations of mountain pine beetle have occurred in RMNP. As a result, the landscape is now composed of stands in different states of recovery from temporally spaced disturbance events.

This paper presents a retrospective study of stand conditions following historic mountain pine beetle events.

Study Objectives

The objective of this retrospective study was to establish baseline information on the ecological characteristics that occur at different stages of succession, resulting from mountain pine beetle disturbance at multiple time intervals.

The objective of this study fits in with the MBPI Program Ecological Objective to improve the ecology of forests impacted by infestation. 2 Key questions addressed by this study were:

- What is the post-beetle ecological character of stands?
- What ecological legacies should be sought post-beetle?
- Can / should ecological integrity be maintained in beetle-damaged landscapes?
- What are the beetle impacts on regeneration?

The study quantified structural and species composition of stands at different stages of succession (25 years and 65 years) following disturbance by the mountain pine beetle,

[2] http://mpb.cfs.nrcan.gc.ca/research/ecological_e.html

and quantified the differences that occur in forest development between stands with and without disturbance by the beetle.

Project Team and Responsibilities

The following organizations and individuals were involved in this study.

- Canadian Forest Service, Natural Resources Canada, Victoria, BC: Dave Harrison provided project administration and technical review of project deliverables.
- National Parks: Cyndi Smith (Waterton Lakes NP), Cliff White (Banff NP), Ken Schroeder (Yoho NP) and Dave Gilbride (Kootenay NP) acted as local liaison in their respective parks, and provided direction and advice throughout the project. Cyndi Smith also provided technical review of project deliverables.
- Biome Ecological Consultants Ltd., Nelson, BC: developed and implemented the research project, conducted all field and laboratory work, data entry, analysis, and reporting:
- Pamela Dykstra was the project leader, responsible for liaison with project team members, co-developing the sample plan, ensuring adherence to relevant standards and protocols, and performing statistical analysis and reporting.
- Tom Braumandl was the project ecologist, co-developing the sample plan, leading the field and laboratory work, and conducting statistical analyses.
- Art Stock Consulting Ltd., Nelson, BC: Dr. Art Stock was the project entomologist.
- Touchstone GIS Inc. Nelson, BC: Kathleen McGuinness was the project GIS analyst.
- Simon Fraser University, Burnaby, BC: Dr. Carl Schwarz and Ian Bercovitz, Department of Statistics and Actuarial Sciences, provided guidance and advice on the experimental design and statistical analyses.

Study Area

Waterton Lakes National Park is located on the east slope of the Rocky Mountains, in the extreme south western corner of Alberta. Over a relatively short distance, it encompasses the Continental Ranges of up to 2920 m in elevation to the Rocky Mountain foothills of relatively subdued terrain and Foothills Parkland vegetation. Waterton Lakes National Park exhibits the greatest floristic diversity in Alberta due to its relatively benign climate and habitat diversity. Study sites were distributed over much of the lower elevations of the park.

Kootenay National Park is located on the western slopes of the continental divide, lying east of the southern portion of Banff National Park. Kootenay National Park lies within the Main and Western Ranges of the Rocky Mountains between the Rocky Mountain Trench and the continental divide. The montane portions of the park, subject to mountain pine beetle activity, are dominated by the Kootenay River Valley.

The portions of Banff National Park in the study area lie directly to the east of Kootenay National Park and are in the Main Ranges of Rocky Mountains. Sites were located at low elevations in the Bow Valley from south of Lake Louise to near Castle Junction.

Yoho National Park lies east of the town of Golden and west of the continental divide within the Continental Ranges of the Rocky Mountains. The study area portion of the park lies along the Kicking Horse and Emerald Rivers.

We examined the Waterton Lakes and the Kootenay, Banff, Yoho ecosystems independently.

Historic outbreaks of mountain pine beetle have occurred in the parks—in the 1930s and 40s, covering approximately 70,000 ha in Kootenay, Yoho and Banff Parks; between 1978-1981 covering approximately 1,835 ha in Waterton Park; in the early 1980s through to the present, covering almost 20,000 ha in Kootenay Park; and a smaller infestation from 1991 onward covering approximately 1,500 ha in Yoho Park (Wood and Unger, 1996). An infestation began in 2000 in Banff Park and is ongoing. The disturbance interval in Kootenay roughly corresponds to the 42 year cycle found by Alfaro et al.*(2003)*.

Methods

Study Design

The analytical studies are control-impact surveys using a simple random sample. The studies are an analytical survey analogue to a single factor completely randomized design having a single factor (disturbance) with three levels of treatment in Kootenay, Banff and Yoho (1940s disturbance, 1980s disturbance and control), and two levels of treatment in Waterton Lakes (1980s disturbance and control). Prospective power analysis demonstrated that a sampling intensity of 17 stands per ecosystem type / treatment combination has sufficient power (0.8) to detect a difference of one standard deviation (SD) in any variable examined. For the proposed design, this level of sampling effort required a total of 85 stands.

Study Site Selection

The objectives for demarcating the populations of interest and selecting stands for measurement were two-fold: i) to create, where possible, homogeneity within the populations of interest; and ii) to represent in the disturbed populations the majority of the disturbance events (i.e., maximize in the treatment population the percentage of land base affected). Control populations had attributes mirroring those of the disturbed populations, with the exception that they were not included in the maps of mountain pine beetle activity. The following outlines the steps to build the spatial database, demarcate the population of interest at the landscape level, and select sample locations.

We collected, collated, and evaluated Ecological Land Classification (ELC) mapping; mountain pine beetle infestation mapping, fire mapping, stand origin mapping, water feature mapping, and road and trail mapping. All the data was geometrically intersected to create a resultant dataset for each park (or set of parks) against which database calculations were run to determine the location of control and sample plots. Comparison of mapping and aerial photography revealed that the mountain pine beetle mapping for Waterton Lakes had a systematic location error. We corrected this discrepancy by obtaining the original paper maps from which the polygons were digitized, and shifting portions of the polygons within the coverage, based on the neatlines of each paper map.

We created filters to stratify the data according to the following attributes: time since disturbance, road and trail access buffers, ecosystem type, stand age, number of infestations, subsequent fire disturbance, control and salvage harvesting, and polygon size.

Selection of Disturbance Events—Specification of Levels in the Factor Time–Since–Disturbance

The population dynamics of the beetle and the distribution of its preferred hosts result in a gradient of mortality severity between stands (Roe and Amman, 1970; Amman and Baker, 1972; McGregor, 1978; Safranyik, 1989; Schmidt, 1989; Stone and Wolfe, 1996), creating heterogeneity at the level of stands and consequently, landscapes (Roe and Amman, 1970; McGregor, 1978). Mortality of lodgepole pine ranges between 5% – 97%

during epidemics, leaving a range of stand conditions across disturbed landscapes; however, mortality most often occurs at intermediate levels (Roe and Amman, 1970; Amman and Baker, 1972; Amman, 1977; Cole and Amman, 1980; Stone and Wolfe, 1996). Peaks in the effects of mountain pine beetle on understory occur when heterogeneity is greatest, that is, in stands with intermediate levels of disturbance (Stone and Wolfe, 1996). Stands with intermediate levels of mortality (30% – 70%) formed the treatments, and stands not disturbed by mountain pine beetle (<10% disturbance) formed the controls. The average estimated mortality of sampled disturbed stands was 59% in Waterton Lakes; and 52% for the 1980s disturbance and 59% for the 1940s disturbance in Kootenay, Banff and Yoho.

The infestations in the 1930s–40s in Kootenay, Banff and Yoho; and in 1978–1981 in Waterton were the events with the most discrete time intervals. For the period 20-25 years before present for Kootenay and Yoho, we noted that there was no distinct spike in disturbed area from 1979 to 1994. In 1995 and 1996 there was a spike in disturbed area but these dates are too recent to capture the regeneration attributes (recruitment, survival) of interest, relative to the timing of distinct changes in the light environment (i.e., the timing of tree fall). We chose the 1981 to 1985 time period due to a slightly elevated area of disturbance within a sufficiently narrow time frame, and also to parallel the time of disturbance for the study in Waterton Lakes.

The times-since-disturbance and geographic locations reflected in the plot selection are:

1. approximately 60–65 years before present (infestation dates of 1941 to 1944 in Kootenay)
2. approximately 20–25 years before present (Waterton infestation dates 1979 to 1981; Kootenay and Yoho infestation dates 1981 to 1985).

We excluded areas within the populations of interest that were subject to fires subsequent to the infestation, to control for the effect that fire disturbance might have on succession.

Road and Trail Access Buffers

The 1 km road buffer accounted for 87% of the infestation in Waterton Lakes. The initial road buffer of 1 km accounted for 57% of all disturbances in Kootenay, Banff and Yoho Parks. Inspection of the mapping revealed that significant portions of the disturbances in Kootenay Park were beyond the 1 km road buffer. We increased the road buffer to 2 km in Kootenay Park for all periods of disturbance, increasing to 85% the total proportion of all disturbances included in the road buffers.

Selection of Ecosystem Types

The system of Ecological Land Classification for the parks integrates landforms, soils and vegetation in a hierarchical manner (Holland and Coen, 1982; Achuff et al., 1984; Achuff et al., 2002). The broadest level of the classification is the ecoregion which is based on vegetation structure and composition as it reflects regional climate. Four ecoregions are recognized in the Rocky Mountain National Parks: Foothills Parkland, Montane, Subalpine, and Alpine. These ecoregions are subdivided on the basis of landform and drainage class into ecosection. There is further subdivision of the ecosections into ecosites primarily on the basis of vegetation structure or composition, soil development or landform. Within Kootenay National Park, for example, 31 ecosections and 78 ecosites are recognized.

The vegetation classification for the Rocky Mountain National Parks was developed independently of the landform portion of the ELC and is generally integrated into the ELC at the level of the ecosite. Vegetation types can be found across ecosites, ecosections and even ecoregions. Vegetation types are based on dominant species in each physiognomic layer and characteristic combinations of species. Forested vegetation types are stratified by dominant tree species, and the classification recognizes both seral and late successional types. The mountain pine beetle responds to the successional status of stands and tree species. Vegetation type is therefore an appropriate scale at which to study the effects of mountain pine beetle.

The Rocky Mountain National Parks contain many vegetation types that the mountain pine beetle could potentially affect. Lodgepole pine occurs on a wide variety of sites from very dry sites on coarse soils and warm aspects through to wet fluvial and organic soil sites (Pfister and Daubenmire, 1973; Holland and Coen, 1982; Lotan and Perry, 1983; Achuff et al., 1984; Burns and Honkala, 1990). The mountain pine beetle appears to have the most significant effect on lodgepole pine where the latter occurs on mesic sites at intermediate elevations (e.g., Cole and Amman, 1980).

Our objective in selecting vegetation types was to capture a widespread community while restricting the amount of variation within the vegetation stratum. We therefore concentrated on widespread vegetation types found on mesic sites at intermediate elevation where lodgepole pine is dominant. For each of the two ecosystem types in the study, we examined the distribution of the mountain pine beetle disturbance across ecosites, and included the ecosites containing the vegetation types that are susceptible to mountain pine beetle disturbance, and in which the mapped disturbance was the greatest.

The ecological land classifications for Kootenay National Park (Achuff et al., 1984) and Banff and Jasper (Holland and Coen, 1982) note that vegetation types C3, C6, C9, C18, C19, C38, and C39 are closely related. Another related ecosystem type is C11 *Pinus contorta-Picea* spp./*Hylocomium.* These sites can occur on mesic sites and commonly contain *Sheperdia canadensis, Linnaea borealis, Spiraea betulifolia, Pleurozium schreberi* and *Hylocomnium splendens.* We excluded vegetation type C3 as it is drier than the above group and has dominant lodgepole pine regeneration rather than spruce regeneration as seen in the C6-C39 group. C11 is also found on mesic sites and contains the above species, but is dominated by moss rather than dwarf shrubs. Ecosites containing the C6-C39 vegetation group accounted for 41% the disturbance within the specified time periods and access buffer. A considerable area of the disturbance was mapped in ecosites that may contain mixed species stands (mixed wood vegetation type, C44). We added these ecosites to the population of interest as they may be dominated by lodgepole pine.

We compared Waterton Lakes National Park lodgepole pine vegetation types to the C6-C39 group and found that the Waterton types are well distinguished. Waterton vegetation types generally lack feathermosses and *Sheperdia* common to Kootenay and Banff, and have species such as *Thalictrum occidentale, Clintonia uniflora,* or *Xerophyllum tenax* that are uncommon or absent in Kootenay and Banff. We maintained Waterton lodgepole pine types as a separate stratum because of these distinctions. There are five lodgepole pine vegetation types in Waterton National Park: C65, C66, C67, C68, and C79. Vegetation type C66 appears to be relatively uncommon. Vegetation types C65 and C67 are closely related, having quite similar species composition, but differing in dominant species. Vegetation type C68 bears some similarities to C65 and C67 but is dominated by *Xerophyllum* and is generally found at higher elevations. Vegetation type C79 is restricted to relatively low elevations in the montane zone unlike the other types that occur both in the montane and subalpine zones. Vegetation type C79 is distinct with its high cover of *Calamagrotis rubescens* and widespread *Clintonia*. We therefore sampled sites belonging to vegetation types C65 and C67 in Waterton.

The two lodgepole pine vegetation communities we sampled were:

1. Kootenay, Banff, Yoho—C6, C11, C38, mesic on various aspects in montane and lower subalpine zones.
2. Waterton—C65, C67 and C79; mesic on various aspects in montane and lower subalpine zones.

We examined the Waterton Lakes and the Kootenay, Banff, and Yoho ecosystems independently.

Stand Origin

In Waterton Lakes, we did not screen for stand age (fire date) prior to sample polygon selection in the GIS processing because almost half of the infestation had no stand age data (Barrett, 1996). The bulk of the stands with stand age data fell within an approximately 50 year time span—with fire dates between 1833 and 1884. We consider this an acceptable range within which to sample, given degree of impact on stand structure expected and the precision of the stand age mapping. We rejected sites beyond this age range during air photo interpretation or on the ground.

In the disturbance event 60–65 years before present in Kootenay, we found that the time period of stand origin that was most abundant was between 1800 and 1842 (stands between 115 and 157 years old at the time of disturbance). The disturbed stands from this stand origin time period accounted for 47% of the area covered by that disturbance within our selected ecosites and road buffer.

In the disturbance event 20–25 years before present in Kootenay and Yoho, we found that 49% of the disturbance occurred in stands with origin dates of 1800-1830 (about 155 to 185 years at the time of disturbance). We limited our sample sites to these stand origin dates. Narrowing down the stand origin dates, in combination with the criteria for multiple disturbances meant that all potential stands that were disturbed several times in Yoho fall in a single, large polygon with stand origin dating from 1690. As a result, no disturbed polygons for the 1980s disturbance fall in Yoho, although control polygons for these disturbance periods do occur in Yoho.

Table 1 contains the areal results from applying ecosite, road buffer, and stand age criteria.

Table 1. Areal results from applying polygon selection criterion

<table>
<tr><th>Time-since-disturbance (years before present)</th><th>Total Area Disturbed</th><th>Road buffer (% of Disturbance within specified distance)</th><th>Ecosites (%of the Disturbance within the time periods of interest, road buffer, and indicated ecosites)</th><th>Stand origin (%of the Disturbance within time periods of interest, road buffer, ecosite of interest, and indicated stand origin dates)</th></tr>
<tr><td>60–65</td><td>Kootenay, Banff (21,977ha)</td><td>87% within 1 km in Banff and 2 km in Kootenay</td><td rowspan="2">Banff– 87% AL1, AT1, BK1, BK4, BV1, BZ2, CA4, CV1, FR1, GA1, GT2, HD1, HD3, IB1, ML2, NY1, NY3, PP1, PR1, PR2, PR4, PR6, PT1, PT3, PT5, RK1, SB2, SB3, SB4, SP1, VD2

Kootenay– 76% AT1, AT4, CV1, DG6, DR2, DR3, DR4, DR6, DR7, DR8, FR1, FR3, HD3, SB3, SB4

Waterton– 70% C67, C69

Yoho– 77% AT1, BK4, DG6, DR2, DR3, DR5, DR6, DR7, DR8, FR1, FR3, HD3, PR6, RK1, SB3, SB4</td><td>7,482ha (49%) in stands of origin dates 1800-1842</td></tr>
<tr><td>20–25</td><td>Waterton (1,398 ha); Kootenay, Yoho (3,133 ha)</td><td>Waterton: 87% within 1 km Kootenay and Yoho: 79% within 1 km in Yoho and 2 km in Kootenay</td><td>764ha (47%) in stands of origin dates 1800-1830 (Kootenay)</td></tr>
</table>

Multiple Disturbances

Only 38% (weighted average within road and ecosite buffers) of the disturbance area in Banff, Kootenay, and Yoho exhibited multiple infestations. However, we believe that the apparently low representation of multiple infestations is an artifact of the data—due largely to the lack of mountain pine beetle incidence data prior to the largest disturbance (the 1941-1944 events in Kootenay and Banff, which cover 70% of the disturbed area). This is corroborated by the fact that where records cover time periods of multiple disturbances, these are more common than single disturbances (e.g., 67% of the disturbed land base shows multiple disturbances for stands in the 1981-1985 events in Kootenay and Yoho).

Additionally, the insect and disturbance experts we consulted report that field data and anecdotal evidence indicate that multiple disturbances within a single stand are widespread in similar landscapes (R. Alfaro, unpublished data; A. Stock, B. Hawkes, pers. comm.), and other landscapes in British Columbia. We therefore chose to limit the sample site selection to those stands that exhibited multiple disturbances. One implication of selecting only stands that were disturbed many times is that no disturbed sites occur in Banff for the 1940s event, however, control stands do occur in Banff for this disturbance period.

Polygon Selection—Simple Random Sample with Replacement
In each combination of ecosystem/treatment, non-infested stands within the relevant access buffer, ecosite, and stand age parameters comprised the non-infested (control) populations. We set the minimum size for selected polygons at two hectares to avoid excess edge effects. From the disturbed and control areas remaining within all the filters, we selected potential sample polygons within each ecosystem/treatment using a simple random sample with replacement selection criteria.

Control and Salvage Operations
Control work and salvage logging took place in Banff and Kootenay during the 1940s infestation (Anonymous, 1941; Leech, 1943, 1944; Hopping and Mathers, 1945; Leech, 1945), and in Kootenay during the 1980s (Pick, 1985). Control work in Banff was pervasive, leaving no portion of the infestation in its natural state (Leech, 1943, 1944; Hopping and Mathers, 1945; Leech, 1945; Dordel, 2005). Salvage work in Kootenay in the 1940s focused on the area around the highway near McLeod Meadows (Anonymous, 1941). During the 1980s infestation, control work took place in areas that approached a control line established between Split Peak and Mount Wardle (Pick, 1985). In the latter case, specific to our study area, control work took place around Kootenay Crossing and Hector Gorge (D. Gilbride, pers. comm.). These areas were hand drawn on our sample polygon maps.

The need to sample stands in their natural (unsalvaged) state would have meant removing Banff from the study area for the 1940s infestation due to the control work there, had Banff not already been removed from the disturbed study area due to the multiple disturbance criteria. In Kootenay, we also discarded polygons occurring in the geographic locations of the salvage and control work in the 1940s and 1980s respectively (Anonymous, 1941; Pick, 1985).

Aerial Photograph Interpretation
We desired a minimum of 17 sites for each combination of ecosystem/treatment, for a total of 85 stands. We rejected numerous of the non-disturbed polygons in Waterton Lakes due to evidence of mountain pine beetle mortality, which was discernable on the 1:25,000 false colour infrared photos. However, due to the small scale of the aerial photography, we were unable to evaluate mortality or species composition on any other photos, with the exception of the 2004 1:30,000 scale true colour photos for portions of Banff and Yoho. We determined that in order to evaluate the level of disturbance, false colour infrared or true colour, 1:30,000 or larger scale photos are required. The other

assessments for which we used aerial photos (i.e., access issues, terrain and vegetation structure characteristics) could be done with smaller scale photos.

Although the scale of most photography was too small to directly discern tree species, we used topographic, terrain texture, and canopy structure cues, along with the presence of human development to develop an air photo signature (largely by process of elimination) to select stands within the vegetation types of interest. These cues consisted of:

- Sparse vegetation in controls (suggests young seral stands or deficit or excess of moisture relative to the desired circum-mesic conditions; reject)
- Adjacency to water combined with sparse vegetation in all areas (suggests excess moisture; reject)
- Sparse canopy on ridge tops (suggests shallow or coarse soil, topographic shedding position [deficit of moisture]; reject)
- Open canopy adjacent to grasslands and shrub lands (occurred primarily in Waterton Lakes where sites occurred near parkland; reject)
- Excessive disturbance (small polygons adjacent to roads where road disturbance would be pervasive, roads through very narrow polygons; adjacency to picnic or campground sites; reject)
- Excessive deciduous (polygons with greater than 25%; reject)
- Dense, short canopy (indicative of immature stands; reject).

The total number of polygons air photo interpreted for each cell ranged from 19 to 87, with a total of 294 polygons evaluated prior to the commencement of field work. We generated a list and map of suitable polygons consistent with the sampling level targeted by the study plan (85 polygons in total, 17 in each ecosystem/treatment combination). Maintaining the order from the random selection procedure, we also mapped and listed additional polygons for each ecosystem/treatment combination, and drew from this list when we rejected polygons in the field. Field rejection of polygons occurred when within–stand evidence demonstrated that the polygon did not conform to the mapped attributes for lodgepole pine dominance, disturbance level, disturbance date, stand age, or environmental factors.

Data Collection

We located sample locations on the ground by walking to the selected sample polygon from the nearest trail or road guided by a backpack GPS receiver. We placed the sample plots in the first suitable location encountered on the approach. Selection criteria included vegetation type, desired level (estimated percent of basal area) and origin of mountain pine beetle mortality (assessed by observation of insect galleries and condition of dead stems—degree of decay, amount of bark and foliage present), stand age, absence of salvage logging and suitable size to avoid edge effects. Due to on-the-ground rejection of plots and random sample selection with replacement, we established plots in 11 stands in the 1980s mountain pine beetle disturbance in Kootenay, Banff and Yoho.

We collected overstory and understory stand structure data using a nested fixed-radius plot design (see caption in Figure 1 for details). We collected coarse woody debris (> 7 cm in diameter) along a randomly oriented 30 meter transect in five decay classes

(Harmon et al., 1986). We collected vegetation data using two methods: shrub intersect sampling for tall (>50 cm in height) shrubs, and four, 1 m^2 vegetation quadrants for cover and modal height of all species of low shrubs, forbs, graminoids and bryophytes, as well as strata covers and modal heights for these categories. We collected tree increment cores from the largest diameter trees for each species present in the plot, in order to determine the maximum age of the plot. We also collected tree increment cores and cross-sectional tree discs from the regeneration layer, to estimate regeneration ages. Wherever possible, we took increment cores at 30 cm from the soil surface. We also excavated and described a (minimum) 50 cm deep soil pit within 20 meters of the plot centre, to assess soil moisture regime and identify anomalous soil conditions.

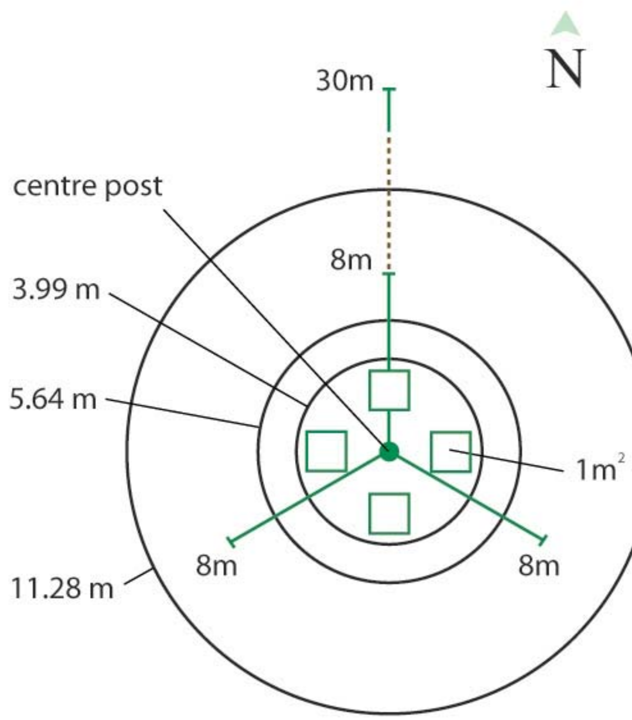

Figure 1. Plot layout.

For the overstory, species and diameter at breast height (dbh) were taken in the 11.28 m radius plot (trees greater than 30 cm dbh in KBY and 25 cm dbh in Waterton Lakes) and in the 5.64 m plot (trees greater than 4.0 cm dbh). For the understory, counts by species were taken in three size classes: 0–30 cm in height (3.99 m plot), >30 cm–1.3 m in height (5.64 m plot) and >1.3 m in height and <4.0 cm dbh (5.64 m plot). Coarse woody debris > 7 cm in diameter was tallied by species, decay class and diameter along a randomly oriented, 30 m transect. Tall shrub intersect data were collected along three eight m transects, the first of which was randomly located and corresponded to the bearing of the coarse woody debris transect, and the second and third of which were located 120º and 240º respectively, from the first transect. Low shrub, forb, graminoid and bryophyte cover and modal height data were collected in four, 1 m^2- quadrants located in cardinal directions with respect to the plot centre. We marked the center of the plot with 1 m of rebar and a tag bearing the plot number and the distance and bearing to the three 'landmark' trees closest to plot centre.

Tree Ageing

We mounted overstory and understory layer tree increment cores and understory cross-sectional tree discs on corrugated cardboard labelled with the plot and tree number. Cores and discs were air dried. We sanded cores and discs using 400 grit paper. We aged tree cores and discs using a 7–30x binocular microscope. We made an age correction for trees drilled at breast height (British Columbia Ministry of Forests and Range, 2005). Because we drilled live overstory trees only to obtain a reference age for the stands, we did not cross date these trees. We examined a subset (15) of understory tree discs applying cross-dating methods from Yamaguchi (1991), looking for repeated patterns of narrow rings. However, we found no consistent pattern of narrow rings in the subset examined. This absence of a pattern is likely due to the influence of low light conditions in the understory overwhelming macro-climatic conditions. Consequently, we did not cross-date understory trees.

Data Analysis

The analysis had two components; multivariate ordination and analysis of variance (ANOVA). Ordination techniques seek to extract a small number of important relationships that best describe patterns in the data, from a large number of possible relationships (McCune and Mefford, 1999). We used PC-ORD v. 4.34 (McCune and Mefford, 1999) to perform nonmetric multidimensional scaling (NMS) (Mather, 1976). Nonmetric multidimensional scaling is an ordination technique that searches for the best position of entities (in this case, plots) on axes that represent the variables which explain the greatest variation in the data (Clark, 1993; McCune and Grace, 2002). One of the advantages of NMS over other multivariate techniques is that it 'sees' a wider range of structures in the data (McCune and Grace, 2002), thereby exploring a greater number of possible relationships. However, because the analyst does not submit levels of treatment to the ordination, NMS is 'blind' to treatment effects; any patterns revealed by NMS result solely from the relationships between entities.

We used NMS in two ways: to generate hypotheses about the structural data, and to explore relationships between the treatments and the vegetation data. We therefore performed two ordinations in each of the ecosystem types (i.e., Waterton Lakes and Kootenay, Banff and Yoho). Our objectives with the structural data were to observe i) whether the ordination would differentiate disturbed and control stands based on structural attributes, and ii) if patterns in the data were apparent from i), what variables best differentiated the disturbed from the control stands. Our objectives with the vegetation data were to see if species composition differed between the disturbance treatments and see how vegetation composition was related to the structural attributes. These analytical objectives relate back to the study objectives to identify the post-beetle ecological character of stands, to identify ecological legacies that persist post-beetle, and to assess beetle impacts on regeneration.

The NMS utilized a random starting configuration for the preliminary runs. We performed 40 runs with real data and 50 runs with random data for the preliminary runs. The probability of obtaining the observed results by chance alone was 0.0196. In NMS, like other ordination techniques, a tradeoff must be made between the dimensionality of the solution, and hence the amount of variation represented, and the interpretability of the results. Solutions above three dimensions are difficult to interpret. Ideally, solutions of three or fewer dimensions represent a significant amount of the total variation. We assessed the appropriate number of dimensions by the marginal change in stress gained with added dimensionality. We then submitted the best starting configuration and desired number of dimensions for the final runs. We ran up to 400 iterations to obtain a stable solution. We assessed the stability of the final solution by graphing stress against the number of iterations run. For Waterton Lakes and Kootenay, Banff and Yoho species data, the NMS ordinations utilized a Euclidean distance measure owing to the nature of the data transformation (presence of negative values). We utilized the Jaccard distance measure for the Kootenay, Banff and Yoho structural variable ordination, as the data were suitable for this distance measure (non-negative values) and it resulted in the most easily interpreted result.

Second, we used ANOVA to test the hypotheses generated by the multivariate analysis. In JMP (SAS Institute Inc, 2004), our objective was to use ANOVA and contrasts (Tukey HSD tests in the Kootenay, Banff and Yoho ecosystem) between levels of treatment to determine whether there was statistical significance for the differences in the values of the structural attributes that were selected by the multivariate analysis. This analytical objective relates back to the study objectives by highlighting unique post-beetle ecological legacies (i.e., whether legacies differed from undisturbed stands), to examine evidence for long term ecological integrity in disturbed stands (i.e., whether disturbed stands maintained habitat elements over the long term, compared to undisturbed stands), and to determine the degree to which impacts on regeneration in beetle stands differed from undisturbed stands.

We calculated vegetation species diversity indices on a plot basis and assessed treatment effects using ANOVA and Tukey HSD tests (the latter in the Kootenay, Banff and Yoho ecosystem) for the following: species richness (number of species present in each plot), species evenness, Shannon-Weiner and Simpson's indices.

We manipulated the dataset to address assumptions of the analyses. We averaged values for the vegetation sub-plots at the plot level, and summed values from the vegetation transects to avoid pseudo-replication (Hurlbert, 1984). We assessed plots of the residuals for normality and homogeneity of variance (Sokal and Rohlf, 1995). Where data were non-normally distributed we used square root or log10 transformations to normalize the data. We added a constant in order to log transform variables with zero values. Because our data contained some very small values (minimum .001), we employed the following formula to retain the magnitude of the variation in the data and the zero values, and to produce non-negative results (McCune and Grace, 2002):

$b = \log(x + d) - c$

Where:

b is the transformed value,

x is original value,

Min (x) is the smallest nonzero value,

Int (x) is the integer of x,

c = order of magnitude constant = Int (log(min(x))) and

d = decimal constant, log-1 (c)

We also manipulated the dataset to generate variables for analysis. We created three CWD variables by combining the less decayed CWD classes one and two (CWD12); and the more advanced decay CWD classes three, four and five (CWD345); and all CWD (CWD). We created four live tree diameter classes by combining basal area for trees > 4 cm–10 cm DBH (liveBA1); > 10 cm–20 cm DBH (liveBA2); > 20 cm–30 cm (liveBA3); and > 30 cm DBH (liveBA4). We then created three basal area variables by combining live BA1 and live BA2 (liveBA12); live BA3 and live BA4 (liveBA34); and all live trees (liveBA). For the Kootenay, Banff and Yoho ecosystem, we also examined live BA4. Variables for dead tree basal areas mirrored the live tree variables (dead BA12, dead BA34, deadBA). We created indices of vegetation volume by multiplying vegetation strata covers by their modal heights (in the categories tall shrub [Shrub], dwarf shrub [Dwshrub], graminoids [Gram], forbs [forb] and bryophytes and lichens [Moss]). We then created a summary vegetation variable by summing the volume index values for graminoids, forbs, bryophytes, and dwarf and tall shrubs (Veg).

We weighted the age of the regeneration by first averaging ages by regeneration size class at the plot level. The average age of each size class was then weighted by the count of the respective regeneration size class divided by the count of all size classes of regeneration within each plot. The weighted age for the plot was the sum of the weighted ages by diameter class.

We deleted ‘rare’ vegetation species (present in 5% or fewer plots) from the species ordinations to reduce the noise associated with uncommonly occurring species (McCune and Grace, 2002). For the Waterton Lakes species ordination we removed from the dataset 47 species with fewer than three occurrences. We included 54 species in the ordination. We log transformed the species values which resulted in much reduced skew and kurtosis. For the Kootenay, Banff and Yoho species ordination, we removed from the dataset 44 species with fewer than four occurrences. We included 49 species in the ordination. We log transformed the species values which resulted in much reduced skew and kurtosis.

We relativized the structural data for the multivariate analysis to overcome problems with high coefficients of variation and with the differences in units of measurements among the variables. Relativization standardizes the values of the variables, facilitating comparisons among them. We employed a general relativization by variable, dividing each value by the sum of squares for that variable. (McCune and Grace, 2002).

We performed both univariate and multivariate outlier analyses and examined outliers. We corrected outliers caused by errors in data entry, but most outliers were legitimate values.

Results

Waterton Lakes

Structural Variable Ordination

We selected a 3–dimensional solution with stress stabilizing after about 50 iterations. The ordination represented a high degree of the total variation in the data (91%) with axis one accounting for 18%, axis two accounting for 16%, and axis three accounting for the bulk of the variation at 57%.

The ordination attributed the greatest amount of variation in the data to several categories of coarse woody debris and vegetation biomass;
Table 2 lists the variables most highly correlated with the ordination axes. Values presented are only those that exceed an r^2 of .320—a threshold commonly used to demarcate meaningful correlation (Tabachnick and Fidell, 1996).

Table 2. Waterton structural variable correlations with ordination axes.
The values following the column headings indicate the amount of variaiton represented by each axis. The positive and negative signs following the r^2 values indicate whether the variable is positively or negatively correlated with the given axis (i.e., plots found at high values—upper or right oriented locations—on the axes will have high values for the variables represented by the axes if positively correlated; and vice versa for plots with low values on the axes).

VARIABLE[i]	Axis 1 (18%)	Axis 2 (16%)	Axis 3 (57%)
	r^2	r^2	r^2
sqCWD12	.419 -		.553 -
sqCWD345		.330 -	.356 -
sqCWD	.427 -		.603 -
logGram		.565 +	
logMoss			.466 +
forb			.440 -
sqShrub			.337 -
logVeg			.416 -
liveBA	.382 +		

[i] sqCWD12—square root of coarse woody debris volume (m^3/ha)(decay classes 1 and 2)
sqCWD345—square root of coarse woody debris volume (decay classes 3, 4, and 5)
sqCWD—square root coarse woody debris volume (all decay classes)
logGram—log graminoid volume (cover X height)
logMoss—log bryophyte and lichen volume
forb—forb volume
logVeg—log of the sum of all vegetation strata volumes
sqShrub—square root of tall shrub volume
liveBA—basal area (m^2/ha) of all diameter classes (> 4.0 cm DBH) of live trees.

Treatments showed distinct patterns on the ordination axes; control plots occurred in mid to upper portions of axis 3, while beetle plots occurred on the lower portion of axis 3 (Figure 23). The exception to this pattern was the disturbed plot with the lowest level of mortality (initially identified as a control plot until field sampled) and the driest plot sampled. While patterns of treatment occurrence with respect to the ordination were apparent, the treatments did not form clear, well-separated groups. The majority of the control plots occurred in the centre right area on the plot of axes 2 and 3 (Figure 2). On the plot of axes 1 and 3 (Figure 3), the majority of beetle plots occurred in the lower left and the majority of control plots are in the centre. Refer to
Table **2** for the variables and variable weights associated with each axes. The relationships between the variables in
Table 2 and axes 2 and 3 and axes 1 and 3 are shown in Figure 4 and Figure 5. The vectors representing variables sqCWD12, sqCWD345, sqCWD, forb, sqShrub and logVeg occurred in the cloud of disturbed plots (disturb=2) on the two figures. The logMoss vector occurred in the upper left area of the two figures, a region not strongly dominated by one treatment. Larger values of LiveBA, and lgBA34 were associated with control plots in the right centre of Figure 5. LogGram was strongly correlated with axis 2 but not with axis 3 and is seen in the right centre of Figure 4.

Species correlations with the structural ordinations revealed a few strong relationships. The species with the strongest correlation was *Abies lasiocarpa* (r^2=.272 with axis 1). However, *Abies* was not associated with one treatment more strongly than another. Species that explain portions of the correlations with vegetation strata variables cited above included:

- *Calamagrostis rubescens,* accounting for the bulk of the logGram correlation,
- *Thalictrum occidentale,* accounting for some of the forb correlation,
- *Sorbus scopulina,* accounting for some of the sqShrub correlation, and
- *Dicranum* spp. and unknown moss species, accounting for the bulk of the logMoss correlation.

The similarity of the directions of the species vectors in Figure 6 and the structural attribute vectors in Figure 4 show the above relationships.

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[3] For all ordination figures, the points represent plots. The distance between points is related to plot similarity. Disturb 0=control, 2=1980s disturbance, 6=1940s disturbance.

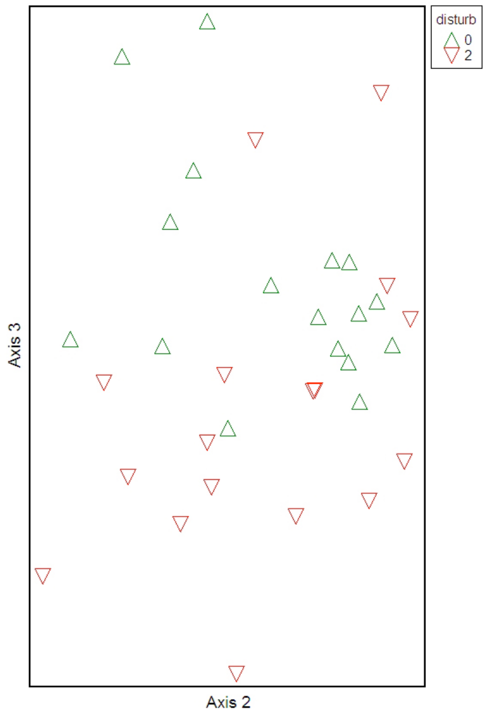


Figure 2. Waterton Lakes structural NMS plot of axes 2 and 3.

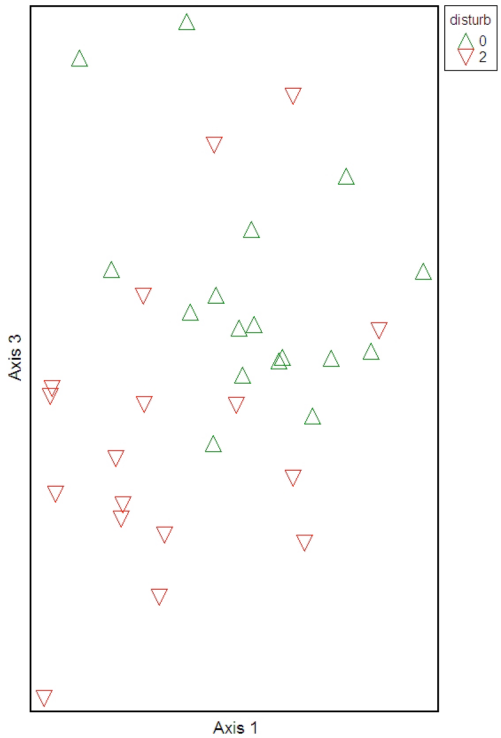


Figure 3. plot of Waterton Lakes structural NMS axes 1 and 3.

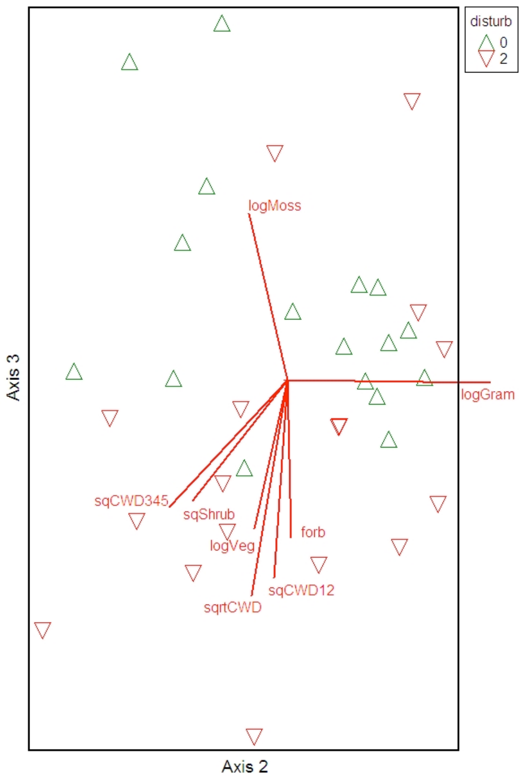


Figure 4. Joint plot of Waterton Lakes structural NMS—plot of axes 2 and 3 with correlated structural variables. The angle and length of line in a joint plot indicates the direction and strength of the relationship between the variable and the ordination axes.

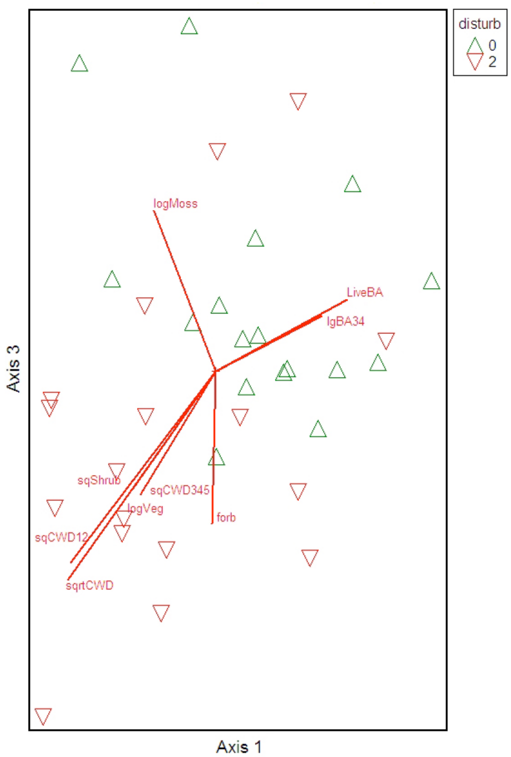


Figure 5. Joint plot of Waterton Lakes structural NMS—plot of axes 1 and 3 with correlated structural variables.

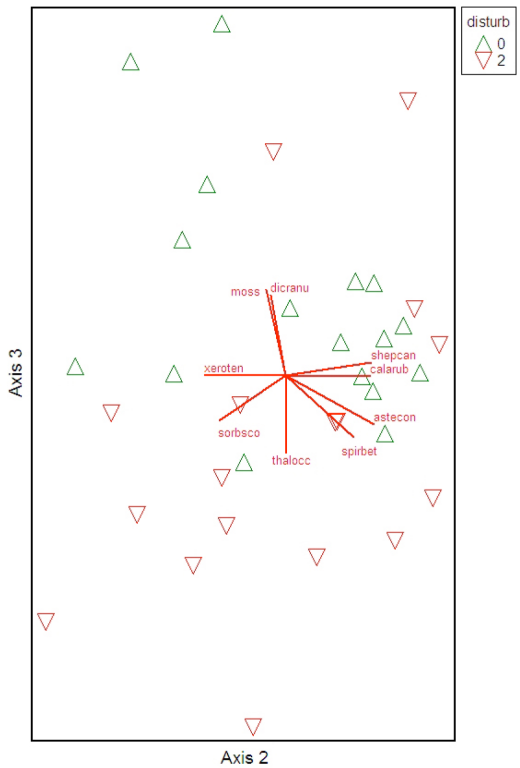


Figure 6. Joint plot of Waterton Lakes structural NMS—plot of axes 2 and 3 with correlated species.

Analysis of Variance

The explanatory variables with r^2 values above the 0.320 threshold selected by the ordination were also significant (P<0.05) according to the analysis of variance, with the exception of the amount of graminoids, which was not significant for the ANOVA (Table 2, Table 3, Figure 7). The disturbed stands had significantly more coarse woody debris than the controls in all decay classes; and greater amounts of forbs and tall shrubs, and all vegetation combined, than the controls (Table 3, Figure 7). The control stands had higher total basal areas than the disturbed stands.

The analysis of variance additionally indicated significance for variables with r^2 values below the 0.320 threshold. Similar to the pattern seen with associated variables with r^2 values above the 0.320 threshold selected by the ordination, the disturbed stands had greater amounts of dwarf shrubs than the controls, whereas the basal areas in both the smaller and larger diameter classes were greater in the control than in the disturbed stands (Table 3, Figure 7).

There were no significant difference in counts for any regeneration count category between the controls and the 1980s in Waterton Lakes. Regeneration in all classes totaled 3,550 stems / ha for the disturbed plots and 4,105 stems/ha for the controls. The average count-weighted regeneration age was 19 years for the disturbed plots and 24 years for the control.

The effect test for species richness was marginally significant (P=0.0882), with disturbed stands having a greater number of species than the control stands (Table 3).

Table 3. Analysis of Variance results for Waterton Lakes.

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Estimates— Sd = standard deviation CI = confidence interval	Control	Disturbance
sqCWD12						**CWD decay class 1 and 2 (m3/ha)**		
Model	1	279.04	279.04	12.45	0.0013	Mean (sd)	47.43 (46.17)	163.54 (113.04)
Error	32	717.00	22.41			Lower 95% CI	23.69	105.42
C. Total	33	996.04				Upper 95% CI	71.17	221.66
sqCWD345						**CWD decay class 3, 4 and 5 (m3/ha)**		
Model	1	41.62	41.62	3.80	0.0600	Mean (sd)	10.35 (17.34)	35.74 (42.17)
Error	32	350.29	10.95			Lower 95% CI	1.43	14.06
C. Total	33	391.91				Upper 95% CI	19.26	57.43
sqCWD						**CWD all decay classes (m3/ha)**		
Model	1	311.08	311.08	12.19	0.0014	Mean (sd)	57.78 (49.36)	199.28 (132.52)
Error	32	816.84	25.53			Lower 95% CI	32.4	131.15
C. Total	33	1127.92				Upper 95% CI	83.15	267.42
lgliveBA12						**Live basal area tree class 1 and 2 (m2/ha)**		
Model	1	2.87	2.87	7.26	0.0111	Mean (sd)	15.59 (11.15)	7.34 (7.22)
Error	32	12.63	0.39			Lower 95% CI	9.85	3.62
C. Total	33	15.50				Upper 95% CI	21.32	11.06
lgliveBA34						**Live basal area tree class 3 and 4 (m2/ha)**		
Model	1	1.13	1.13	24.12	<.0001	Mean (sd)	31.45 (11.81)	14.47 (6.25)
Error	32	1.50	0.05			Lower 95% CI	25.37	11.26
C. Total	33	2.63				Upper 95% CI	37.52	17.69
liveBA						**Live basal area all tree classes (m2/ha)**		
Model	1	5406.27	5406.27	43.63	<.0001	Mean (sd)	47.03 (13.14)	21.81 (8.67)
Error	32	3965.51	123.92			Lower 95% CI	40.28	17.36
C. Total	33	9371.78				Upper 95% CI	53.79	26.27
forb						**Forb volume (index)**		
Model	1	8.49	8.49	3.53	0.0694	Mean (sd)	2.03 (1.40)	3.03 (1.69)
Error	32	77.00	2.41			Lower 95% CI	1.31	2.1642
C. Total	33	85.49				Upper 95% CI	2.75	3.90
lgDwshrub						**Dwarf shrub volume (index)**		
Model	1	4.12	4.12	18.88	0.0001	Mean (sd)	2.63 (2.87)	8.30 (5.72)
Error	32	6.99	0.22			Lower 95% CI	1.1591	5.36
C. Total	33	11.11				Upper 95% CI	4.11	11.24
sqShrub						**Tall shrub volume (index)**		
Model	1	73.25	73.25	8.09	0.0077	Mean (sd)	7.29 (12.44)	33.60 (41.07)
Error	32	289.56	9.05			Lower 95% CI	0.893	12.486
C. Total	33	362.81				Upper 95%	13.69	54.72

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Estimates— Sd = standard deviation CI = confidence interval	Control	Disturbance
						CI		
logVeg						**Vegetation volume—all vegetation strata (index))**		
Model	1	2.64	2.64	14.11	0.0007	Mean (sd)	12.66 (11.91)	45.75 (44.12)
Error	32	6.00	0.19			Lower 95% CI	6.541	23.07
C. Total	33	8.64				Upper 95% CI	18.79	68.44
SPPRICH						**Species Richness (number of species)**		
Model	1	76.50	76.50	3.09	0.0882	Mean (sd)	16.12 (5.53)	19.11 (4.34)
Error	32	791.53	24.74			Lower 95% CI	13.27	16.89
C. Total	33	868.03				Upper 95% CI	18.96	21.35

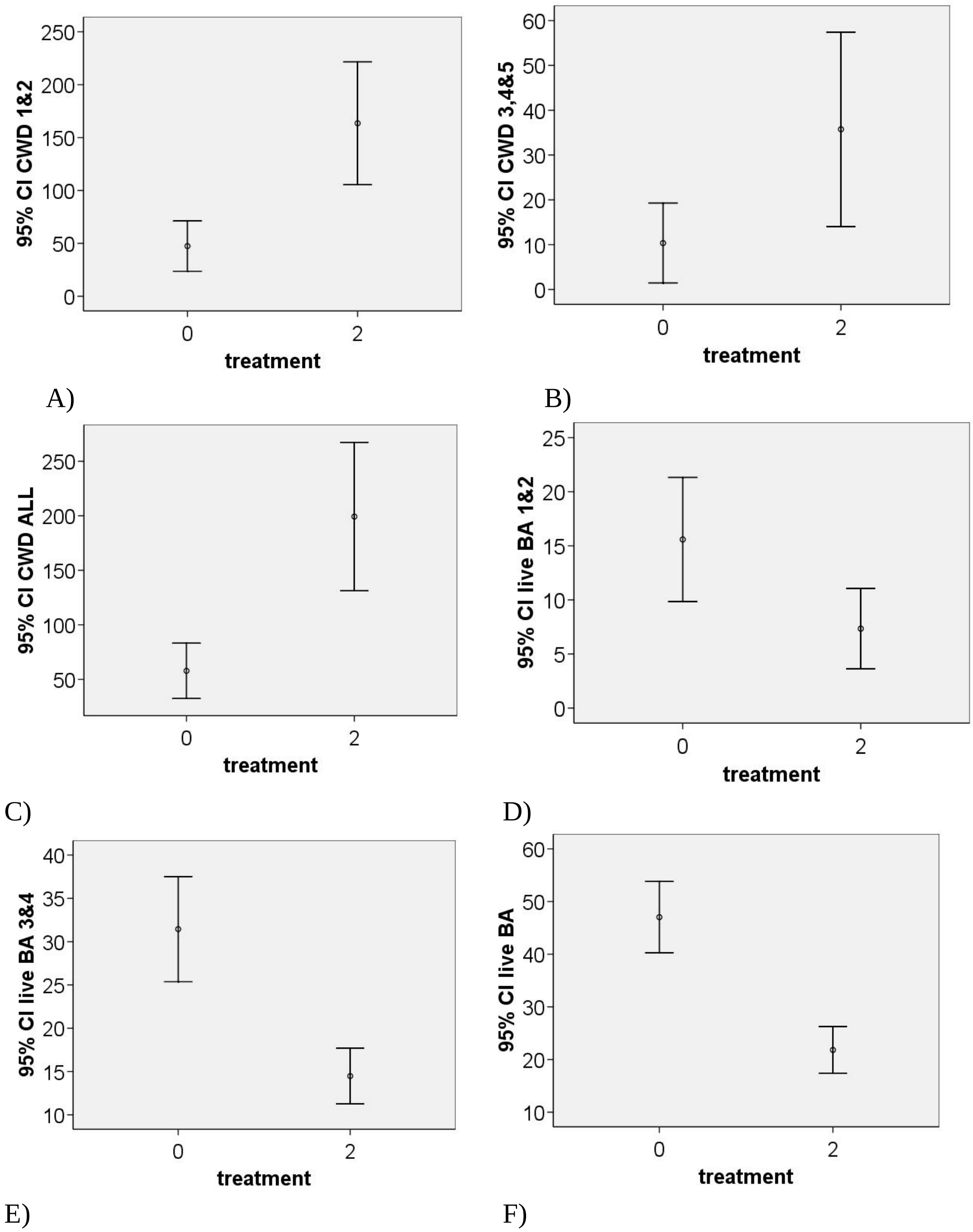
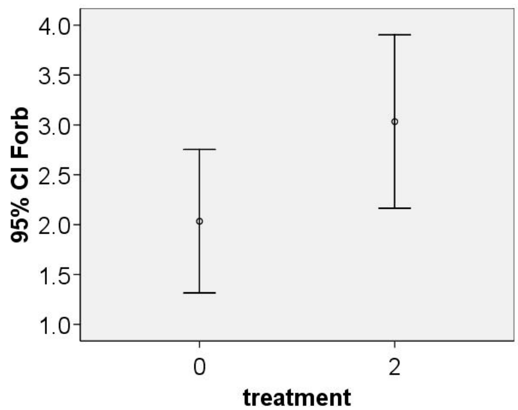
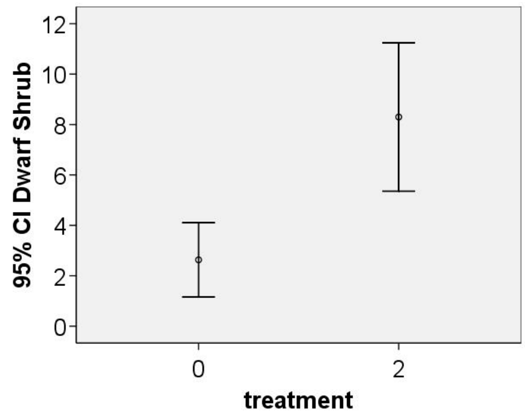


Figure 7. *Caption on next page***.**





G)

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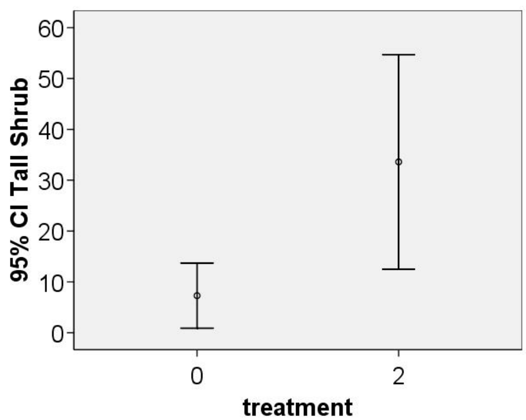
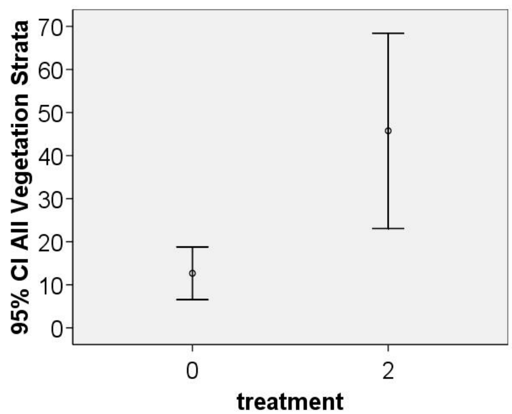




I)

J)

Figure 7. *Figure continued from previous page.*
Comparison of parameter estimates for select variables—Waterton Lakes.
Circles indicate means, error bars indicate 95% confidence intervals (95% CI) for A) CWD decay classes 1 and 2; B) CWD decay classes 3, 4, and 5; C) All decay classes CWD (CWD scale in M3/ha); D) live basal area DBH classes 1 and 2 (4–20 cm DBH); E) live basal area DBH classes 3 and 4 (>20 cm DBH); F) all live basal area (> 4 cm DBH) (live basal area scale in m2/ha); G) forb volume index; H) dwarf shrub volume index; I) tall shrub volume index; J) all vegetation strata volume index (volume scale derived from % cover multiplied by modal height). For treatments, 0 = control, 2=disturbance.

Species Ordination

For Waterton Lakes, the Ecological Land Classification describes a limited number of vegetation types to which the plots belong. The majority of plots (27) were classified as vegetation type C65 *Pinus contorta/Arnica cordifolia-Spiraea betulifolia.* Six plots were classified as C67 *Pinus contorta/Vaccinium myrtillus* and one control plot was classified as C79 *Pinus contorta/Calamagrostis rubescens-Aster conspicuus.* Because of the altered environmental conditions and consequent differences in the disturbed plot plant communities, we reviewed the ELC to determine if these plots were best classified as open or shrub vegetation types. Although the disturbed sites don’t fit the C65 and C67 group as well as do the control plots, they are more suited to these vegetation types than they are to the open or shrub vegetation types; we would describe a number of the disturbed plots as successional variants of C65 and C67.

We selected a 3–dimensional solution with stress stabilizing after about 75 iterations. The ordination represented a high degree of the total variation in the data (81%) with axis one accounting for 18%, axis two accounting for 28%, and axis three accounting for 35%. Table 4 lists the species most highly correlated with the ordination axes. Values presented are only those that exceed an r^2 of .250.

We did not see clear distinctions between control and disturbed plots with the species ordination. Although we saw some affinities between species, strong groupings of plots within the vegetation ordination space were not obvious. The ordination indicated four species groupings (Figure 8, Figure 9, Figure 10):

- *Symphoricarpos albus, Amelanchier alnifolia, Rubus parviflorus*
- Seen in middle left of Figure 8 and Figure 9, this group was associated with a fairly isolated group of disturbed plots
- *Vaccinium membranaceum, Veratrum viride*
- Seen in the lower centre of Figure 8 and Figure 9
- *Angelica dawsonii, Epilobium angustifoliium, Bromus ciliatus, Thalictrum occidentale, Picea*
- Seen in the centre of Figure 8 and the left centre of Figure 10
- *Calamagrostis rubescens, Sheperdia canadensis, Hedysarum sulphurescens, Aster ciliolatus, Aster conspicuous, Campanula rotundifolia*
- Seen in the upper portion of Figure 8 and Figure 10.

When structural variables were correlated with the species ordination, we observed only three variables with reasonable correlations with the vegetation ordination axes.

- Log dwarf shrub, r^2=.515 (negative correlation on axis 1), the direction of this correlation coincided with that for the *Symphoricarpos* group above
- Log live basal area diameter classes 1 and 2 (4-20cm), r^2= .360 (positive correlation on axis 1), no species correlation corresponded with this variable
- square root coarse woody debris, r^2= .253 (negative correlation on axis 3), the direction of this correlation coincided with the *Vaccinium membranaceum group above.*

In Waterton Lakes, the control plots contained 69 species; the disturbed plots contained 87 species (see Appendix 1 for species list). Twenty-four species were unique to disturbed plots, a number of which are light-loving species, for example, *Allium ceruum, Apocynum androsamaefolia, Castilleja* sp., *Geranium viscosisimum, Pteridium aquifolium.* Seven species were unique to control sites (five of which are closed canopy species— three mosses and two forbs, *Pyrola chlorantha, Corallorhiza* sp.).

Table 4. Waterton Species correlations with ordination axes.
The values following the column headings indicate the amount of variation by each axis. The positive and negative signs following the r^2 values indicate whether the variable is positively or negatively correlated with the given axis.

VARIABLE	Axis 1 (18%)	Axis 2 (28%)	Axis 3 (35%)
	r^2	r^2	r^2
Amelanchier alnifolia	.475 -		
Acer glabrum	.474 -		.406 -
Rubus parviflorus	.444 -		
Symphoricarpos albus	.430 -		
Vaccinium membranaceum			.425 -
Veratrum viride			.418 -
Calamagrostis rubescens			.416 +
Angelica dawsonii		.340 -	
Mahonia repens		.322 +	
Abies lasiocarpa		.314 -	
Epilobium angustifoliium		.286 -	
Sheperdia canadensis			.273 +

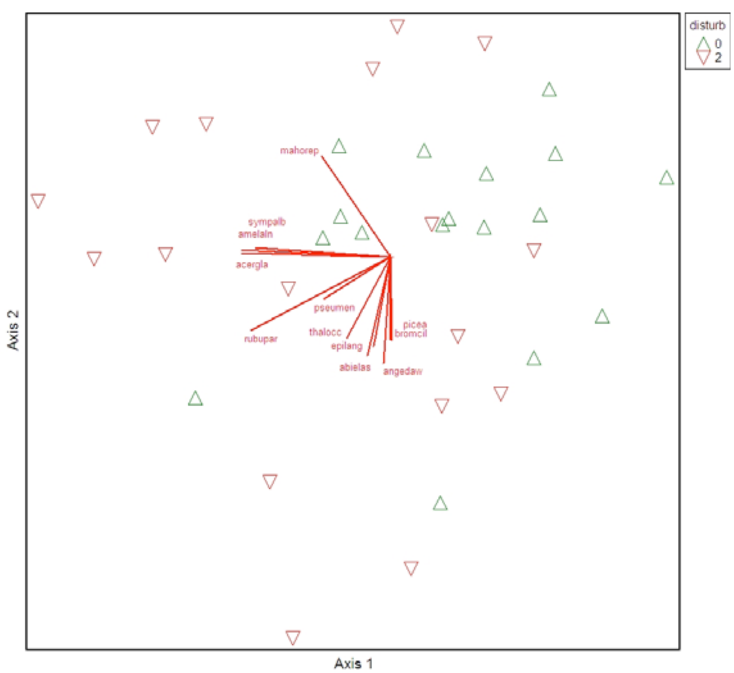


Figure 8. Joint plot of WATERTON species NMS—plot of axes 1 and 2 with correlated species.

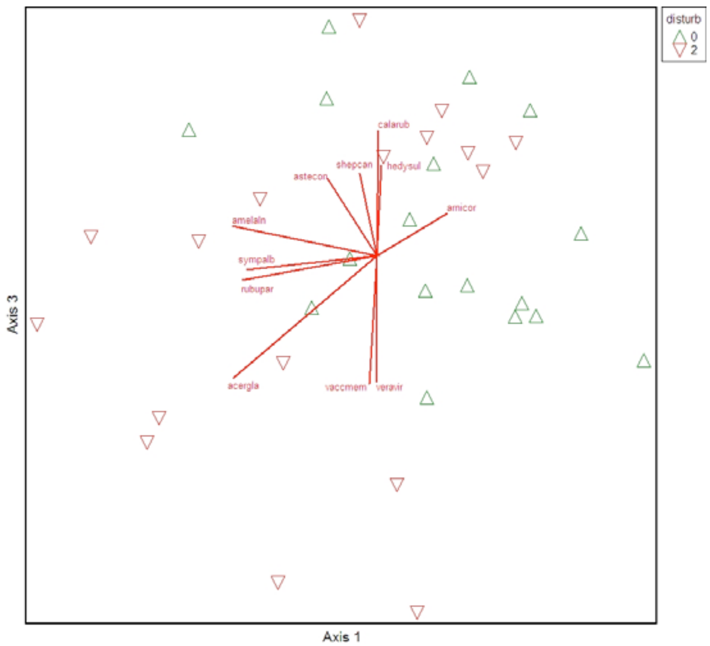


Figure 9. Joint plot of WATERTON species NMS—plot of axes 1 and 3 with correlated species.

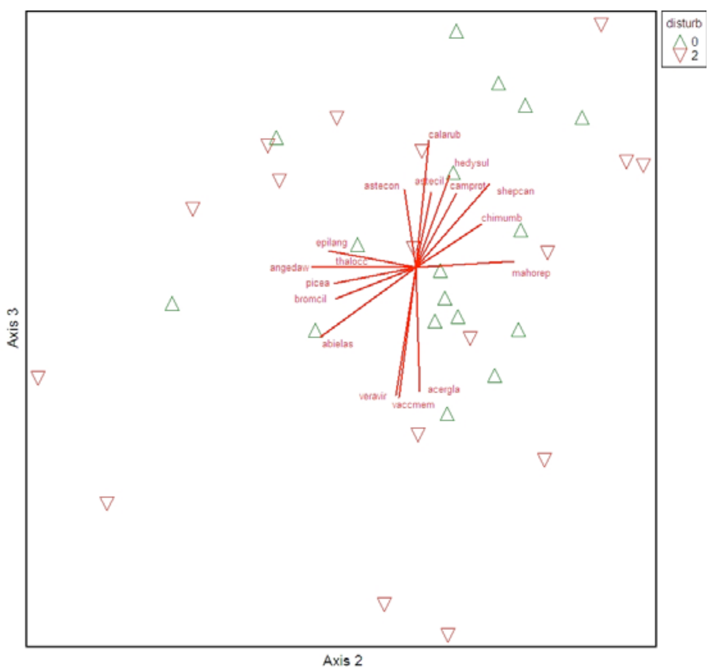


Figure 10. Joint plot of WATERTON species NMS—plot of axes 2 and 3 with correlated species.

Kootenay, Banff and Yoho

Structural Variable Ordination

We selected a 3–dimensional solution with stress stabilizing after about 70 iterations. The ordination represented a high degree of the total variation in the data (82%) with axis one accounting for 33%, axis two accounting for 23%, and axis three accounting for 26%.

The ordination attributed the greatest amount of variation in the data to three variables of live basal area, two of vegetation biomass and one of small regeneration; Table 5 lists the variables most highly correlated with the ordination axes.

We observed clear patterns between the treatments and the ordination axes. We can see on Figure 11, Figure 12, and Figure 13 that the control (disturb 0) was well separated from the 1980s infestation (disturb 2) with the 1940s infestation (disturb 6) intermediate between the control and the 1980s plots. The three treatments formed three distinct clouds on the plot of axes 1 and 2 (Figure 11); control on the lower left, 1940s disturbance in the lower centre and the 1980s disturbance in the upper portions. The control plots occurred in the lower left and the 1980s disturbance plots in the upper right portion, while the 1940s disturbance plots were intermediate between the control and 1980s on the plot of axes 1 and 3 (Figure 12). Figure 13 shows a somewhat similar pattern to Figure 12, however here the 1940s plots were more closely related to the control plots.

Greater total live basal area (liveBA) and live basal area of the larger diameter classes (liveBA34, live4BA) was correlated with control plots (Figure 14, Figure 15); greater graminoid volume (logGram) was associated with the more recent disturbance (Figure 14 and Figure 16); while greater large shrub volume (logShrub) and total vegetation volume (logVeg) and greater maximum age (MaxAge) were associated with the 1940s disturbance and control plots (Figure 14 and Figure 16). Greater amounts of small regeneration (lgReg3) were not associated with any particular treatment but were strongly correlated with axis 3 (Figure 15 and Figure 16).

When we correlated species distributions with the structural attribute ordination, we observed relationships between some species and treatments. *Calamagrostic rubescens, Amelanchier alnifolia* and *Fragaria virginiana* were associated mostly closely with 1980s disturbance plots. *Arnica cordifolia* was associated with both 1940s disturbance and control plots. *Juniperus communis* was also associated with both 1940s disturbance and control plots, but with different plots than *Arnica* (Figure 17 and Figure 18).

Table 5. Kootenay, Banff, Yoho structural variable correlations with ordination axes.

VARIABLE[ii]	Axis 1 (33%)	Axis 2 (23%)	Axis 3 (26%)
	r^2	r^2	r^2
liveBA	.716 -		
liveBA34	.701 -		
lgReg3			.612 +
logGram		.424 +	
logShrub		.384 -	
live4BA	.353 -		
MaxAge		.339 -	

[ii] liveBA34—basal area (m^2/ha) of diameter classes 3 and 4 (> 20 cm DBH) of live trees
lgReg3—log of count of class 3 regeneration (<30cm in height)
logShrub—log of tall shrub volume
live4BA—basal area (m^2/ha) of diameter class 4 (> 30 cm DBH) of live trees
MaxAge—maximum age of sampled live trees
See
Table **2** for definitions of other variables

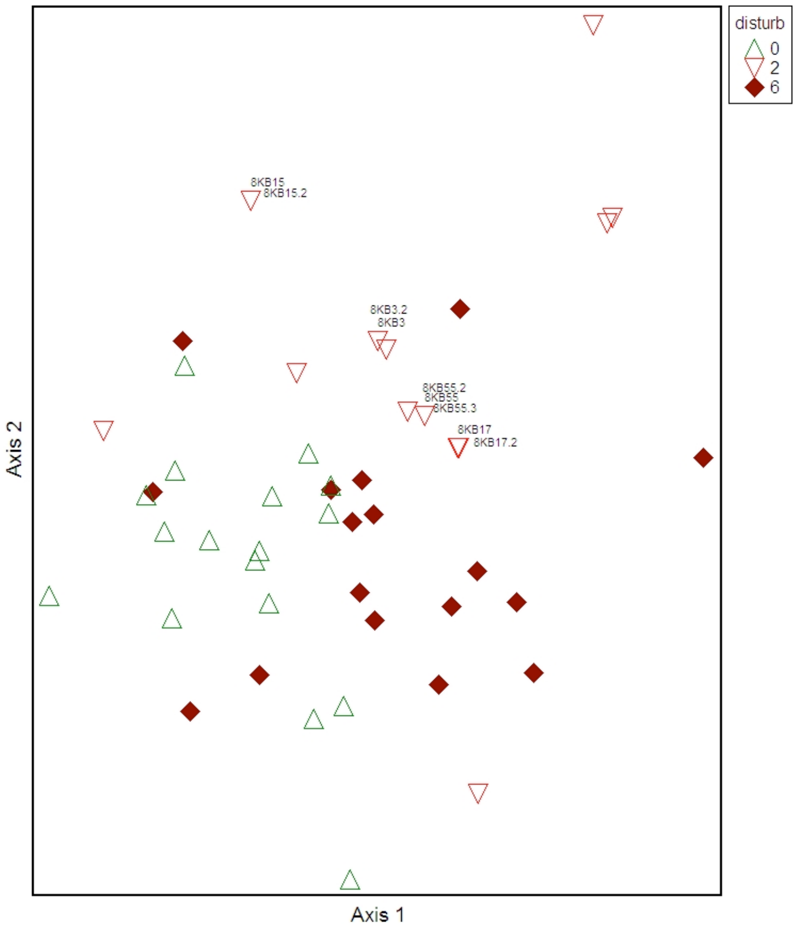


Figure 11. Kootenay, Banff, Yoho structural NMS—plot of axes 1 and 2 by disturbance (replicated plots in disturb=2 are shown with replicated plot numbers).

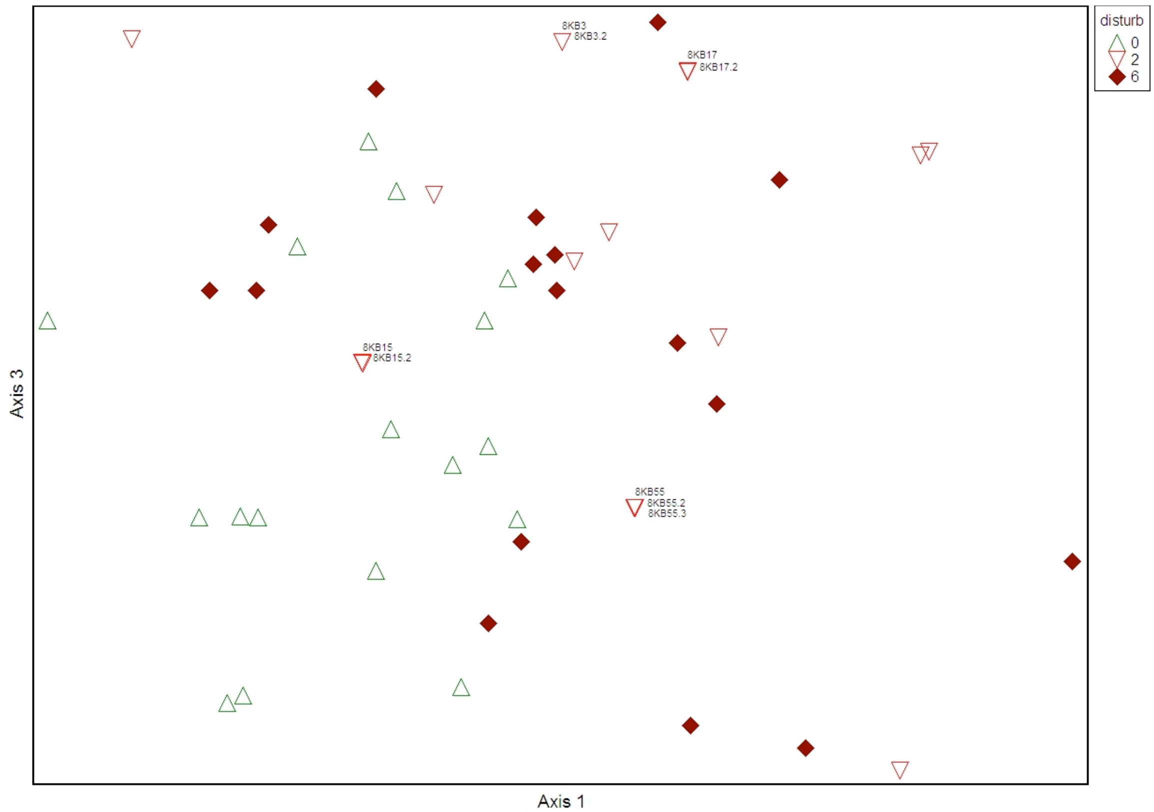


Figure 12. Kootenay, Banff, Yoho structural NMS—plot of axes 1 and 3 by disturbance (replicated plots in disturb=2 are shown with replicated plot numbers).

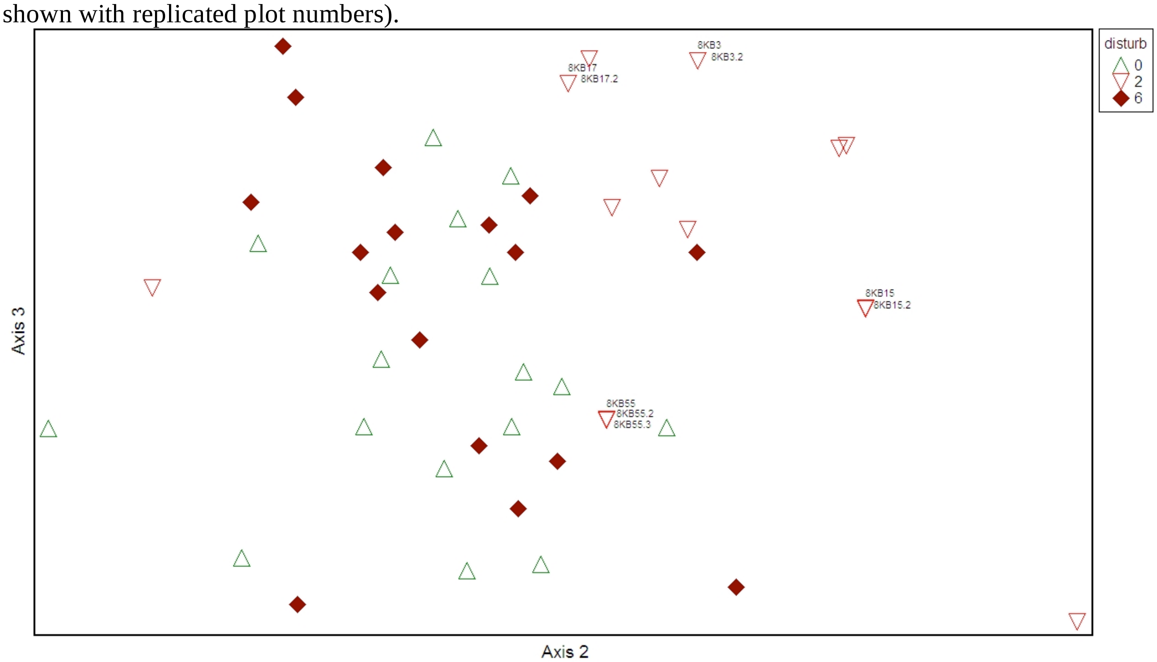


Figure 13. Kootenay, Banff, Yoho NMS—plot of axes 2 and 3 by disturbance (replicated plots in disturb=2 are shown with replicated plot numbers).

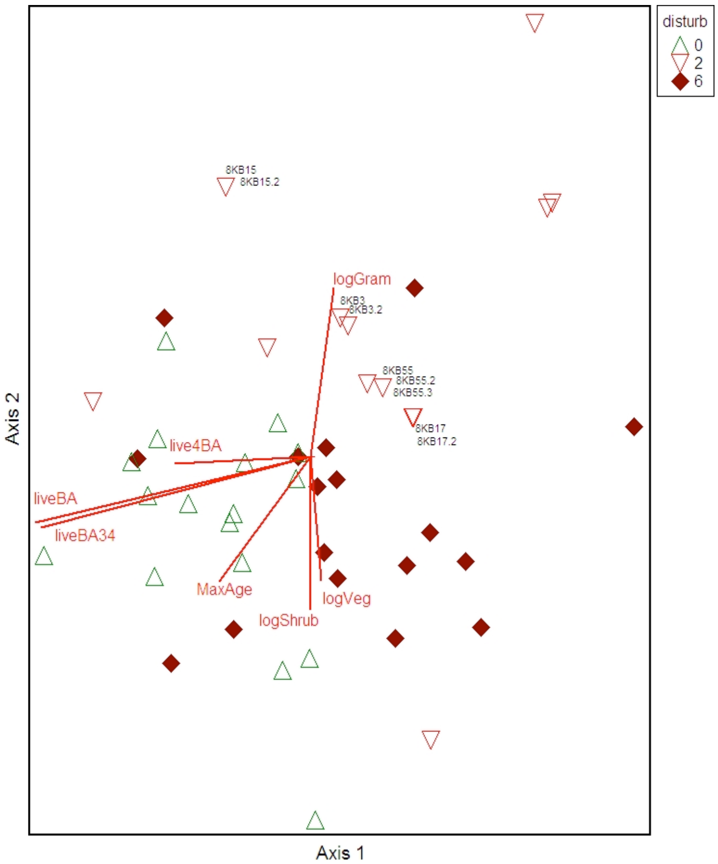


Figure 14. Joint plot of Kootenay, Banff, Yoho structural NMS—plot of axes 1 and 2 with correlated structural variables (replicated plots in disturb=2 are shown with replicated plot numbers).

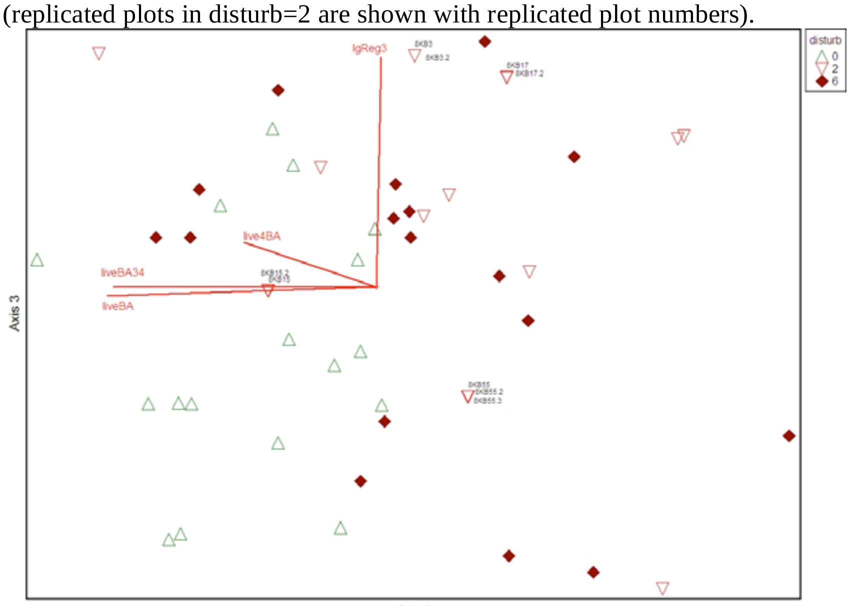


Figure 15. Joint plot of Kootenay, Banff, Yoho structural NMS—plot of axes 1 and 3 with correlated structural variables (replicated plots in disturb=2 are shown with replicated plot numbers).

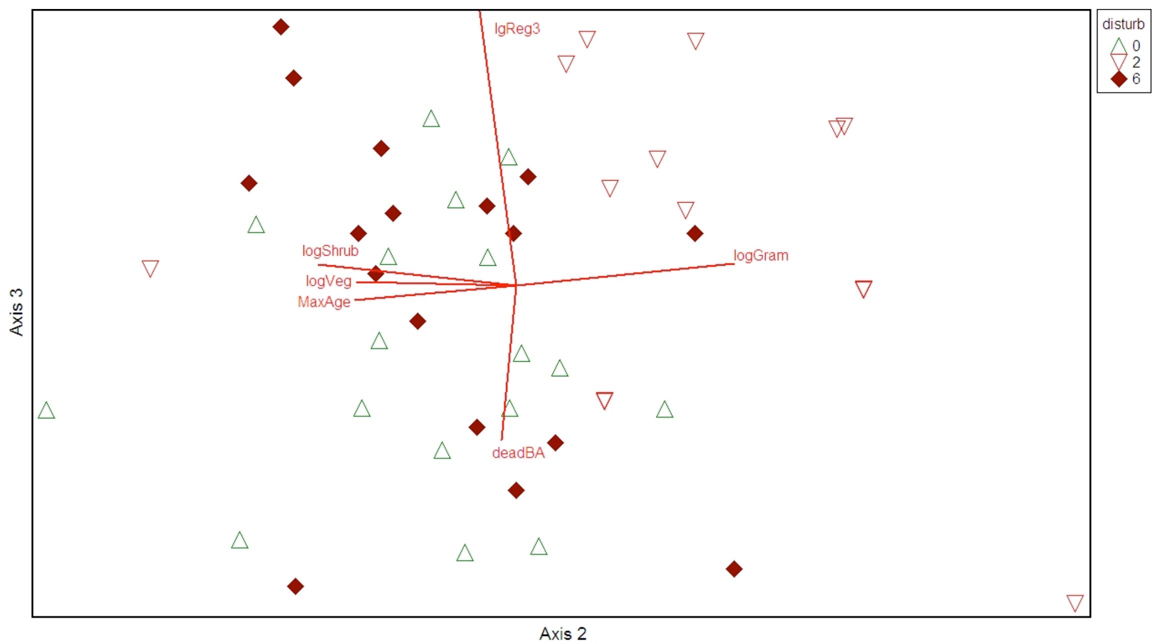


Figure 16. Joint plot of Kootenay, Banff, Yoho structural NMS—plot of axes 2 and 3 with correlated structural variables (replicated plots in disturb=2 are shown with replicated plot numbers).

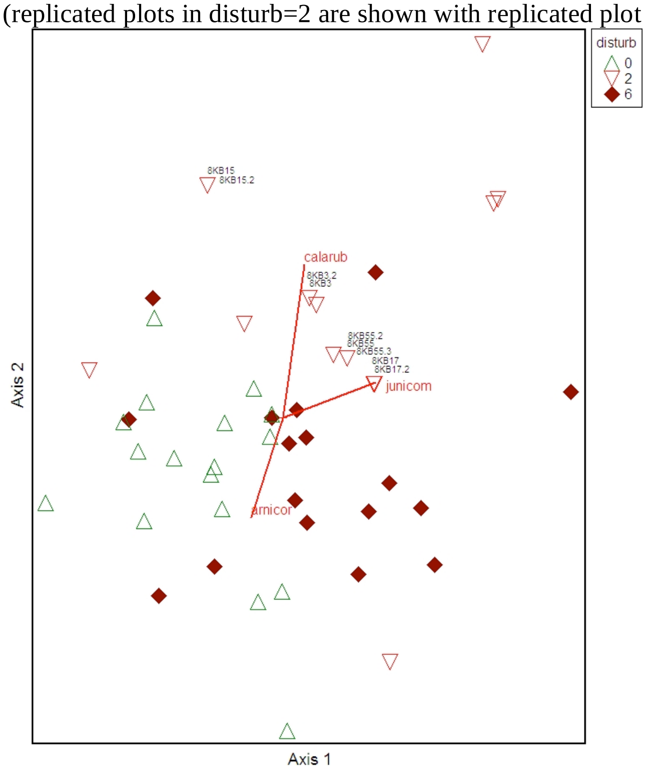


Figure 17. Joint plot of Kootenay, Banff, Yoho structural NMS—plot of axes 1 and 2 with correlated species (replicated plots in disturb=2 are shown with replicated plot numbers).

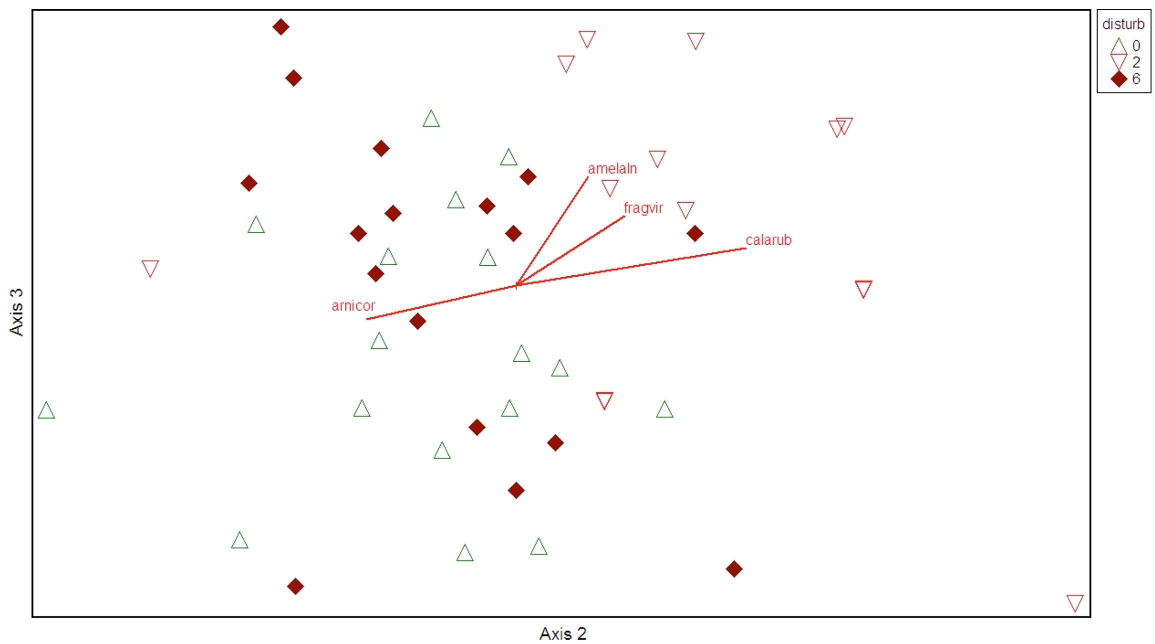


Figure 18. Joint plot of Kootenay, Banff, Yoho structural NMS—plot of axes 2 and 3 with correlated SPECIES.

Analysis of Variance

The explanatory variables selected by the ordination with r^2 values above the 0.320 threshold were also significant (P<0.05) according to the analysis of variance, with the exception of the amount of tall shrubs, which was not significant for the ANOVA (Figure 19, Figure 20, Table 5, Table 6). The treatments were all significantly different from each other for live basal area in all diameter classes combined, and diameter class three and four (trees > 20 cm DBH) combined. The controls had the largest basal area, followed by the 1940s disturbance, and the 1980s disturbance had the least basal area. The effect test for diameter class four alone had a P-value of 0.0776, and a contrast of the treatments showed that the control had a greater (P=0.0256) amount of large tree basal area than the 1980s disturbance. The count of small regeneration (≤ 30 cm in height; lgReg3) was significantly greater in the 1940s disturbance than in the controls. The volume of graminoids was significantly greater in the 1980s disturbance than in either the 1940s disturbance or the controls. The treatments were all significantly different from each other for the maximum stand age (defined by the age of largest DBH trees); the controls were the oldest stands, followed by the 1940s disturbance and the 1980s disturbance.

The analysis of variance additionally indicated significance for variables with r^2 values below the 0.320 threshold (Table 6). Similar to the pattern seen with associated variables with r^2 values above the 0.320 threshold selected by the ordination, the basal area of small diameter live trees (DBH >4 cm–20 cm) was higher in the control than in the 1980s disturbed stands; and the volume of dwarf shrubs was significantly greater in the 1980s disturbance than in either the 1940s disturbance or the control stands. Conversely, the volume of moss was greater in the 1940s disturbance than in the 1980s disturbance. The volume of coarse woody debris in all decay classes and in the more advanced decay classes was greater in the 1940s disturbance than in the controls; and for the advanced decay classes, the volume was also greater in the 1940s disturbance than in the 1980s disturbance. The count-weighted age of regeneration (all stems ≤ 4 cm DBH) was greater in the control than in either the 1980s or 1940s disturbance. The effect test for the basal area of all diameter classes of dead, standing trees had a P-value of 0.0652, and a contrast of the treatments showed that the control had greater (P=0.0271) basal area than the 1980s disturbance and marginally significantly greater (P=0.0778) basal area than the 1940s disturbance.

The effect test for species richness was marginally significant (P=0.0608), and a contrast of the treatments showed that the 1940s disturbance had a greater (P=0.0190) number of species than the 1980s disturbance. The effect test for species evenness was marginally significant (P=0.0987), and a contrast of the treatments showed that the species occurred in the 1980s disturbance with greater evenness than they occurred in the 1940s disturbance. Shannon-Weiner and Simpson’s diversity indices did not differ between the treatments.

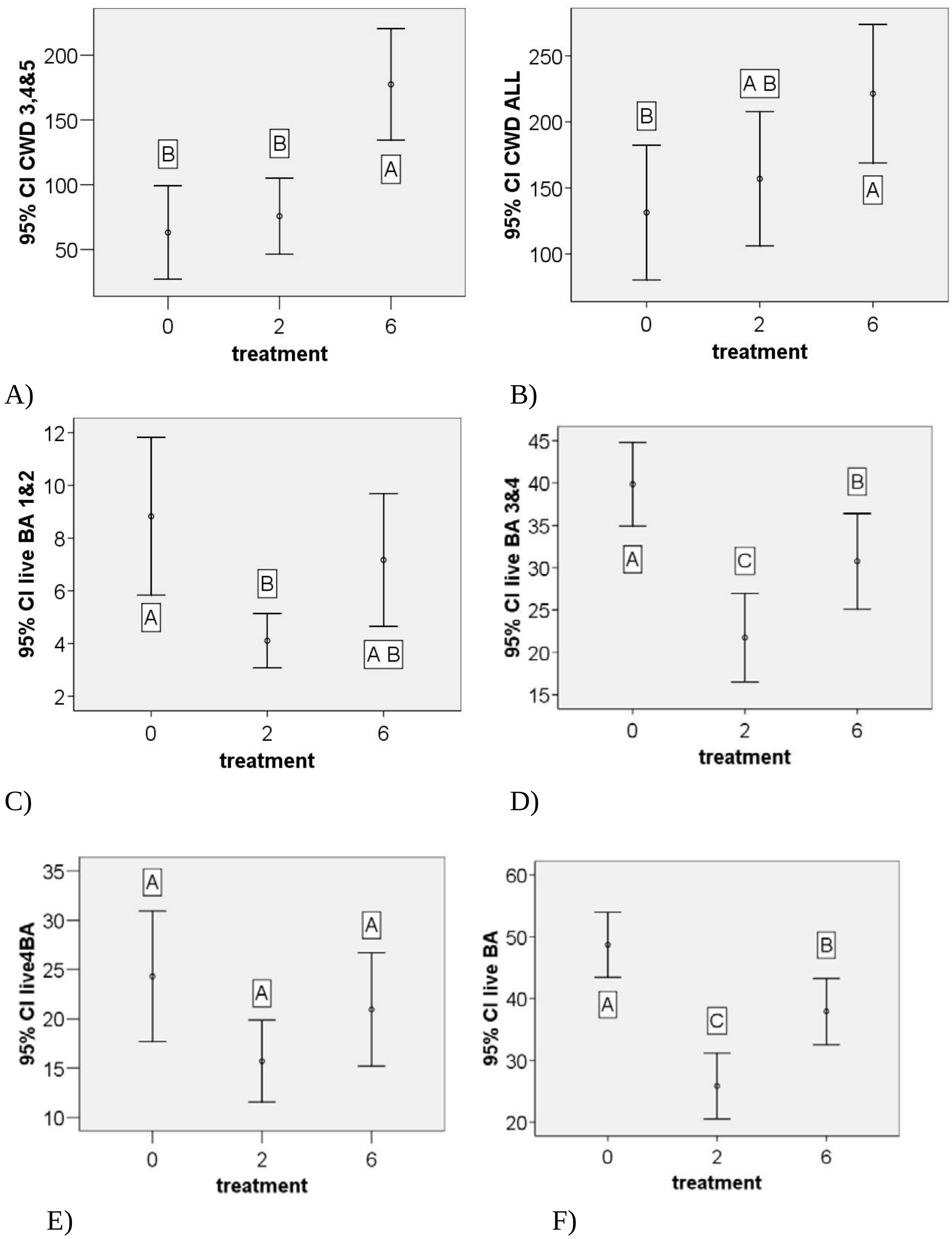
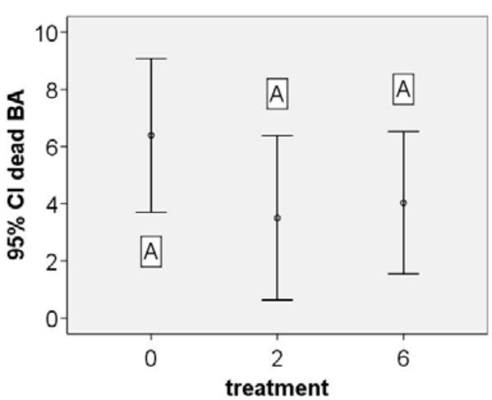
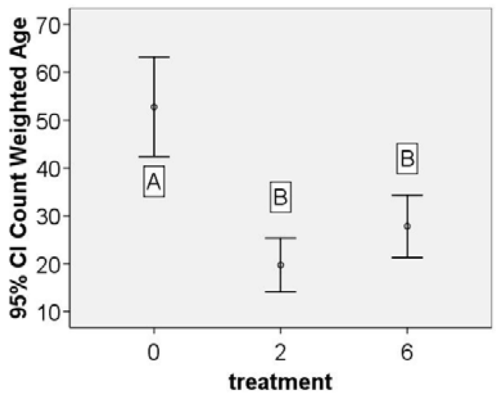
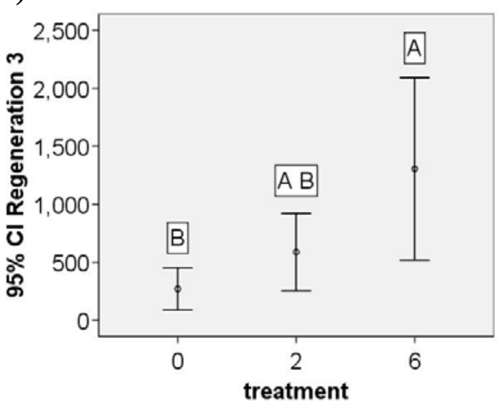


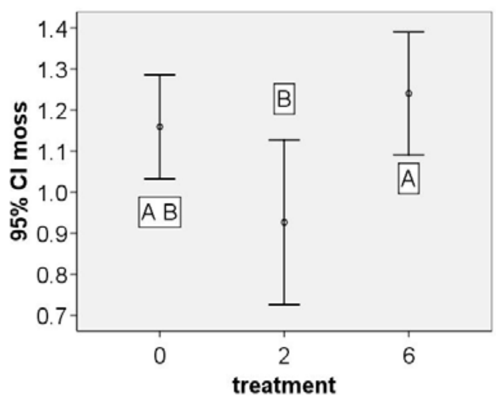
Figure 19. *Caption on next page*.





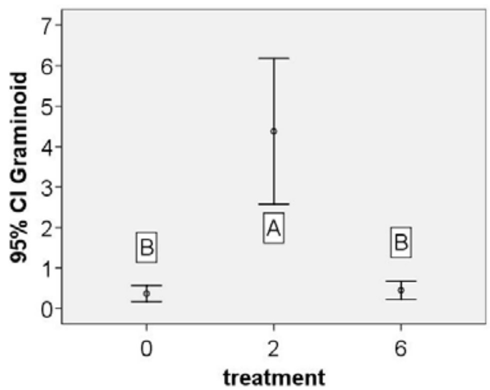
G) H)





I) J)

Figure 19. Comparison of parameter estimates for select variables—Kootenay, Banff, Yoho.
Circles indicate means, error bars indicate 95% confidence intervals (95% CI) for A) CWD decay classes 3, 4 and 5; B) All decay classes CWD (CWD scale in M3/ha); C) live basal area DBH classes 1 and 2 (4–20 cm DBH); D) live basal area DBH classes 3 and 4 (>20 cm DBH); E) live basal area DBH class 4 (>30 cm DBH); F) all live basal area (> 4 cm DBH) (live basal area scale in m2/ha); G) all dead basal area (> 4 cm DBH) (dead basal area scale in m2/ha); H) regeneration classes 1, 2, and 3 (trees < 4.0 cm DBH) count-weighted age (weightedage; scale in years); I) regeneration class 3 (scale in # stems/ha); J) moss volume index; K) graminoid volume index; L) dwarf shrub volume index (volume scale derived from % cover multiplied by modal height). Levels not connected by the same letter are significantly ($P<0.05$) different. For treatments, 0 = control, 2 = 1980s disturbance, 6 = 1940s disturbance. BA = basal area; CI = confidence interval. *Figure continued on next page.*



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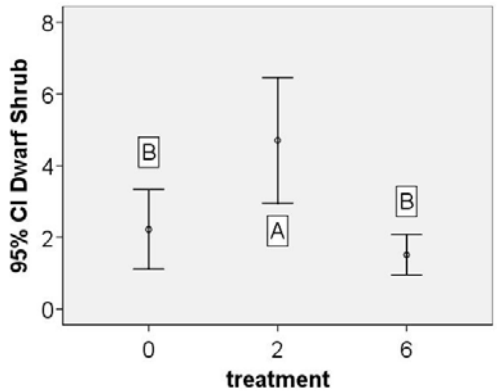

L)

Figure 19. *Figure continued from previous pages.* Comparison of parameter estimates for select variables—Kootenay, Banff, Yoho.

Circles indicate means, error bars indicate 95% confidence intervals (95% CI) for A) CWD decay classes 3, 4 and 5; B) All decay classes CWD (CWD scale in M3/ha); C) live basal area DBH classes 1 and 2 (4–20 cm DBH); D) live basal area DBH classes 3 and 4 (>20 cm DBH); E) live basal area DBH class 4 (>30 cm DBH); F) all live basal area (> 4 cm DBH) (live basal area scale in m2/ha); G) all dead basal area (> 4 cm DBH) (dead basal area scale in m2/ha); H) regeneration classes 1, 2, and 3 (trees < 4.0 cm DBH) count-weighted age (weightedage; scale in years); I) regeneration class 3 (scale in # stems/ha); J) moss volume index; K) graminoid volume index; L) dwarf shrub volume index (volume scale derived from % cover multiplied by modal height). Levels not connected by the same letter are significantly (P<0.05) different. For treatments, 0 = control, 2 = 1980s disturbance, 6 = 1940s disturbance. BA = basal area; CI = confidence interval

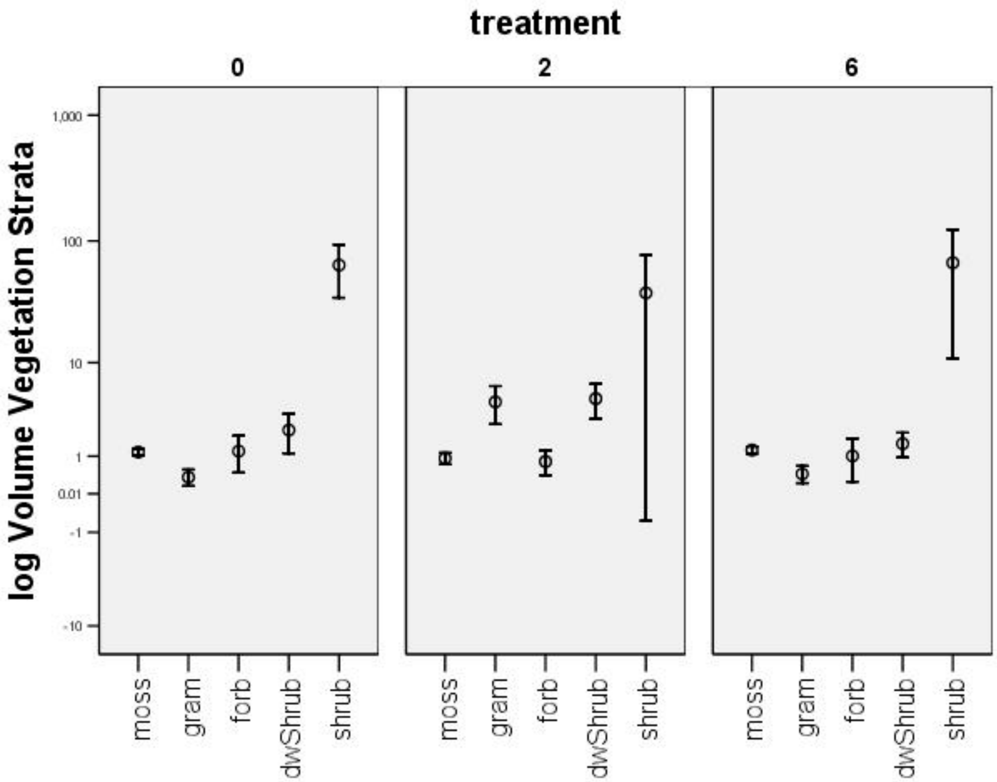

Figure 20. Volume for all vegetation strata in Kootenay, Banff, Yoho. Note log axis.

Table 6. Analysis of Variance and Tukey HSD test results, and parameter estimates for Kootenay, Banff, Yoho.

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Tukey Multiple HSD— Levels not connected by the same letter are significantly (P<0.05) different		Estimates — Sd = standard deviation CI = confidence interval	Control	1980s Disturb.	1940s Disturb.
sqCWD345								**CWD decay class 3, 4 and 5 (m3/ha)**			
Model	2	406.37	203.18	12.08	<.0001	6	A	Mean (sd)	63.12 (70.30)	75.76 (57.32)	177.50 (83.51)
Error	48	807.20	16.817			2	B	Lower 95% CI	26.98	46.29	134.57
C. Total	50	1213.56				0	B	Upper 95% CI	99.27	105.23	220.44
CWD ALL								**CWD all decay classes (m3/ha)**			
Model	2	73168.59	36584.3	3.65	0.0334	6	A	Mean (sd)	131.37 (99.30)	156.91 (98.92)	221.39 (102.08)
Error	48	481016.03	10021.2			2	A B	Lower 95% CI	80.32	106.05	168.91
C. Total	50	554184.62				0	B	Upper 95% CI	182.43	207.77	273.87
lgLIVEBA12								**Live basal area tree class 1 and 2 (m2/ha)**			
Model	2	0.76	0.388	3.43	0.0405	0	A	Mean (sd)	8.82 (5.82)	4.10 (2.01)	7.17 (4.90)
Error	48	5.33	0.11			6	A B	Lower 95% CI	5.84	3.07	4.65
C. Total	50	6.10				2	B	Upper 95% CI	11.82	5.14	9.69
LIVEBA34								**Live basal area diameter class 3 and 4 (m2/ha)**			
Model	2	2796.86	1398.43	13.25	<.0001	0	A	Mean (sd)	39.88 (9.65)	21.74 (10.16)	30.76 (10.97)
Error	48	5066.13	105.54			6	B	Lower 95% CI	34.92	16.51	25.12
C. Total	50	7862.99				2	C	Upper 95% CI	44.84	26.96	36.40
LIVEBA4								**Live basal area diameter class 4 (m2/ha)**			
Model	2	639.47	319.74	2.70	0.0776	0	A	Mean (sd)	24.30 (12.85)	15.69 (8.09)	20.93 (11.19)
Error	48	5689.62	118.53			6	A	Lower 95% CI	17.69	11.53	15.18
C. Total	50	6329.10		0.08		2	A	Upper 95% CI	30.90	19.85	26.68

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Tukey Multiple HSD— Levels not connected by the same letter are significantly (P<0.05) different				Estimates — Sd = standard deviation CI = confidence interval	Control	1980s Disturb.	1940s Disturb.
LIVEBA										**Live basal area all diameter classes (m2/ha)**			
Model	2	4448.36	2224.18	20.91	<.0001	0	A			Mean (sd)	48.71 (10.26)	25.84 (10.29)	37.93 (10.39)
Error	48	5104.84	106.35			6		B		Lower 95% CI	43.43	20.55	32.59
C. Total	50	9553.21				2			C	Upper 95% CI	53.98	31.13	43.28
qDEADBA										**Dead basal area all diameter classes (m2/ha)**			
Model	2	10.27	5.14	2.89	0.0652	0	A			Mean (sd)	6.40 (5.25)	3.50 (5.60)	4.03 (4.85)
Error	48	85.27	1.78			6	A			Lower 95% CI	3.70	0.62	1.54
C. Total	50	95.54				2	A			Upper 95% CI	9.09	6.38	6.53
lgREG3										**Regeneration class 3 (< 30 cm height— count)**			
Model	2	1.185	0.59	3.8171	0.0289	6	A			Mean (sd)	271 (353)	588 (642)	1305 (1532)
Error	48	7.45	0.16			2	A	B		Lower 95% CI	89	258	517
C. Total	50	8.64				0		B		Upper 95% CI	452	918	2094
REGEN AGE										**Weighted age all regeneration (index)**			
Model	2	11067.9	5049.1	21.89	<.0001	0	A			Mean (sd)	52.77	19.70	27.81
Error	48	21166.1	230.5			6		B		Lower 95% CI	45.36	60.176	45.366
C. Total	50	11067.9				2		B		Upper 95% CI	12.29	27.109	12.299

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Tukey Multiple HSD— Levels not connected by the same letter are significantly (P<0.05) different		Estimates — Sd = standard deviation CI = confidence interval	Control	1980s Disturb.	1940s Disturb.
MOSS								**Moss volume (index)**			
Model	2	0.90	0.45	4.54	0.0156	6	A	Mean (sd)	1.16 (0.25)	0.93 (0.39)	1.24 (0.29)
Error	48	4.77	0.10			0	A B	Lower 95% CI	1.03	0.73	1.0905
C. Total	50	5.68				2	B	Upper 95% CI	1.29	1.13	1.39
logGRAM								**Gram volume (index)**			
Model	2	13.26	6.63	12.25	<.0001	2	A	Mean (sd)	0.36 (0.39)	4.38 (3.49)	0.45 (0.44)
Error	48	25.97	0.54			6	B	Lower 95% CI	0.16	2.5824	0.22
C. Total	50	39.23				0	B	Upper 95% CI	0.57	6.17	0.68
logDWSHRUB								**Dwarf shrub volume (index)**			
Model	2	2.44	1.22	6.24	0.0039	2	A	Mean (sd)	2.22 (2.17)	4.71 (3.42)	1.51 (1.08)
Error	48	9.40	0.20			0	B	Lower 95% CI	1.11	2.95	0.96
C. Total	50	11.842016				6	B	Upper 95% CI	3.33	6.47	2.07
MAXAGE								**Maximum Stand Age (age of largest DBH tree)**			
Model	2	29129.06	14564.5	14.15	<.0001	0	A	Mean (sd)	178 (21)	120 (38)	151 (35)
Error	48	49407.77	1029.3			6	B	Lower 95% CI	167	101	134
C. Total	50	78536.82				2	C	Upper 95% CI	189.	139	170
SPP RICHNESS								**Species Richness (number of species)**			

VARIABLE Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	Tukey Multiple HSD— Levels not connected by the same letter are significantly (P<0.05) different		Estimates — Sd = standard deviation CI = confidence interval	Control	1980s Disturb.	1940s Disturb.
Model	2	96.82	48.41	2.97	0.0608	6	A	Mean (sd)	17.29 (4.06)	17.00 (3.79)	20.06 (4.25)
Error	48	782.47	16.30			0	A	Lower 95% CI	15.207	15.051	17.874
C. Total	50	879.29				2	A	Upper 95% CI	19.38	18.95	22.24
SPP EVENNESS								**Species Evenness (index)**			
Model	2	0.11	0.05	2.4312	0.0987	2	A	Mean (sd)	0.54 (0.13)	0.56 (0.13)	0.45 (0.19)
Error	48	1.08	0.02			0	A	Lower 95% CI	0.47	0.49	0.35
C. Total	50	1.19				6	A	Upper 95% CI	0.60	0.62	0.55

Species Ordination

The plots in Kootenay, Banff and Yoho were classified according to the Ecological Land Classifications in a limited number of vegetation types. The bulk of the control and 1940s disturbance plots were classified as C11, *Pinus contorta-Picea* spp./*Hylocomium splendens* with one plot classified as C6, *Pinus contorta/Shepherdia canadensis/Aster conspicuous* and two plots as transitional C11/C6. Four of the 1940s disturbance plots were classified as C5 *Picea glauca-Pseudotsuga menziesii/Hylocomium splendens,* one as C1 *Pseudotsuga menziesii/Elymus innovatus*, and one as C13 *Picea engelmannii-Abies lasiocarpa/Hylocomium splendens.* The C5 and C13 plots have presumably developed from C11 following the mortality caused by the mountain pine beetle.

We selected a 2–dimensional solution with stress stabilizing after about 30 iterations. The ordination represented a high degree of the total variation in the data (79%) with axis one accounting for 35%, and axis two accounting for 44%.

Table 7 lists the species most highly correlated with the ordination axes. Values presented are only those that exceed an r^2 of .260.

We observed patterns of treatments on the ordination axes: control plots were low on axis one and central to high on axis two; the 1980s disturbance plots occurred centrally on axis one and low on axis two; and the 1940s disturbance occurred high on both axes (Figure 21). The 1980s disturbance plots had the most within-group similarity given their relatively tight cloud. The control plots formed two groups: five plots from Yoho in an isolated group and a tight cluster of plots near the centre of the ordination space from Banff. The 1940s disturbance plots had the most within treatment variability.

Elymus innovatus, Fragaria virginiana, Calamagrostis rubescens, Populus tremuloides, and Rosa acicularis were associated with 1980s disturbance plots (Figure 22). *Vaccinium myrtillus, Vaccinium membranaceum,* and *Ptilium crista-castrensis* were associated with the isolated group of control plots. *Acer glabrum, Betula papyrifera, Rubus parviflorus,* and *Viburnum edule* were associated with the 1940s disturbance plots.

When we correlated structural variables with the species ordination, only two variables were strongly correlated with the vegetation axes: maximum live tree age was positively correlated with axis 2 (r^2 = .419), and volume of graminoid species was negatively correlated with axis 2 (r^2 = .676) (Figure 23).

Table 7. KOOTENAY, BANFF, YOHO species correlations with ordination axes.

VARIABLE	Axis 1 (35%)	Axis 2 (44%)
	r^2	r^2
Elymus innovatus		.531 -
Betula papyrifera	.516 +	
Vaccinium membranaceum		.414 +
Fragaria virginiana		.409 -
Acer glabrum	.396 +	.300 +
Cornus canadensis		.377 +
Vaccinium myrtillus		.346 -
Populus tremuloides		.328 -
Calamagrostis rubescens		.322 -
Ptilium crista-castrensis		.305 +
Rosa acicularis		.292 -
Rubus parviflorus		.279 +
Viburnum edule	.269 +	

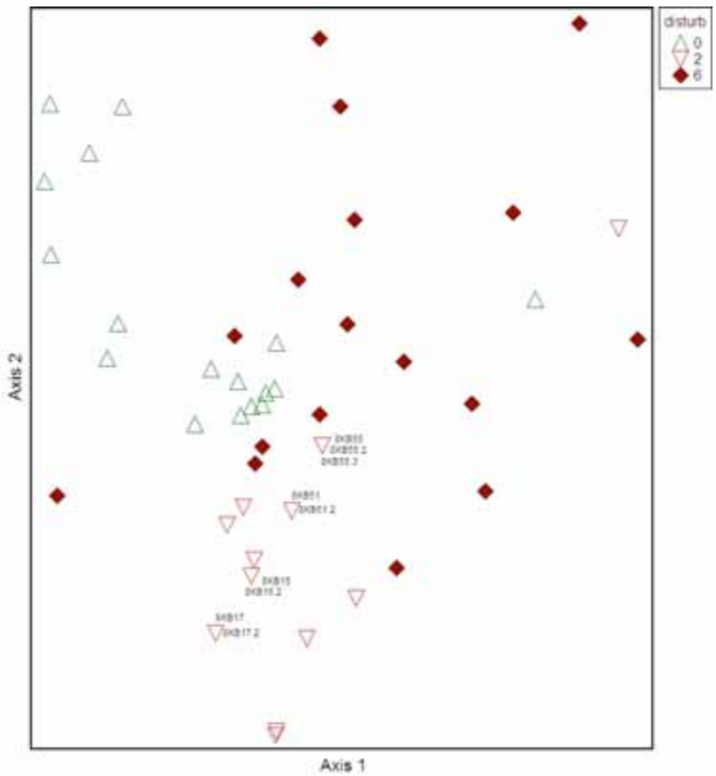

Figure 21. KOOTENAY, BANFF, YOHO SPECIES NMS—plot of axes 1 and 2 by disturbance.

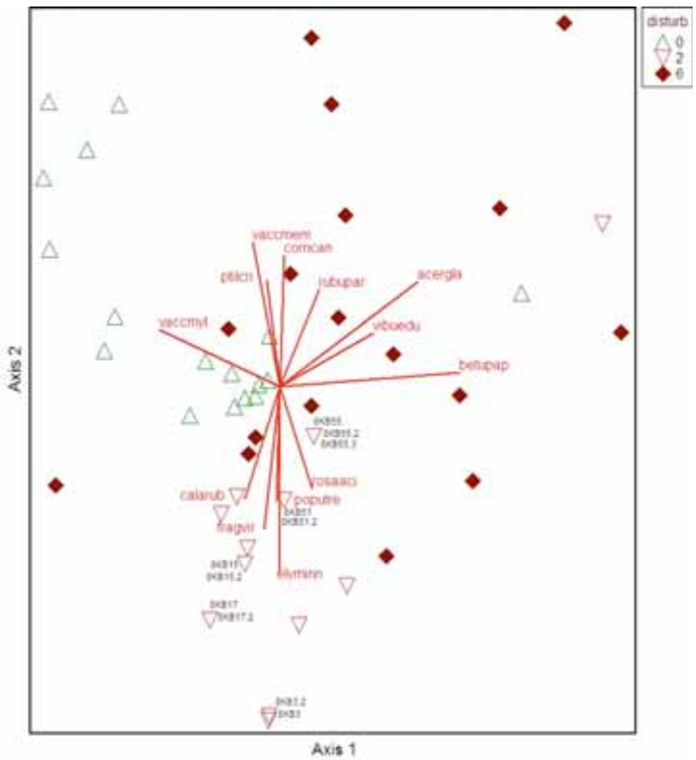

Figure 22. KOOTENAY, BANFF, YOHO SPECIES NMS— Joint plot of species correlations with axes 1 and 2.

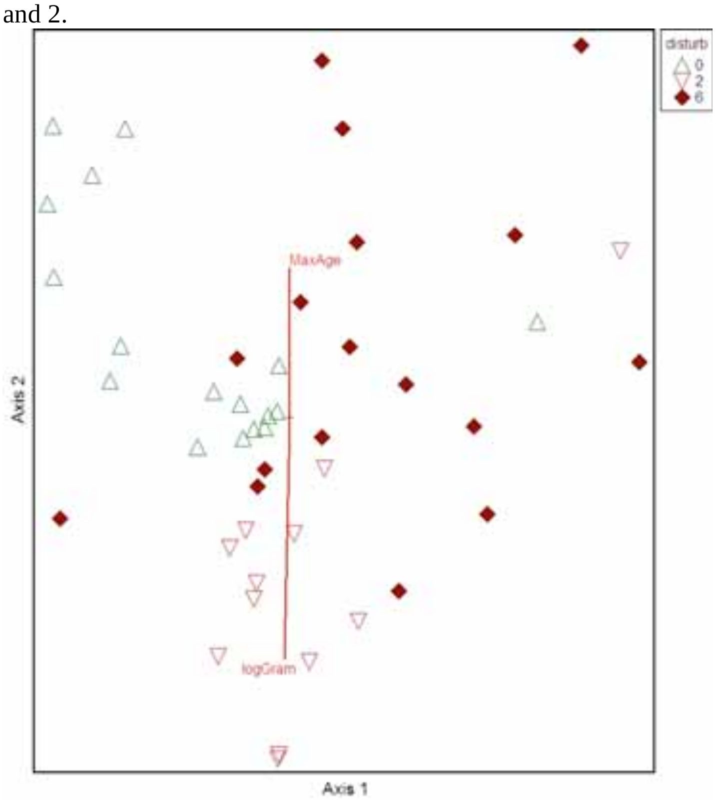

Figure 23. KOOTENAY, BANFF, YOHO SPECIES NMS—Joint plot of structural variable correlations with axes 1 and 2.

Discussion

Structural Attributes

Relationship between the Multivariate Ordination and the ANOVA

In Waterton Lakes, considerable agreement occurred between the ANOVA and the multivariate results in the selection and significance of variables that differentiate the treatments. However, while the two types of analyses complement one another, they also offer independent interpretations of the data; there were several variables for which the ANOVA showed significant differences that were below the threshold r^2 value of 0.320 in the multivariate analysis. For example, for the ANOVA, dwarf shrub had one of the lowest P-values (0.0001) of all the variables, with three times the amount of dwarf shrub occurring in the disturbance than occurred in the control. Yet dwarf shrub had a relatively weak correlation with the ordination axes (maximum $r^2 = 0.224$ on axis three). Similarly, variables for live basal area of small (≤ 20 cm DBH; liveBA12) and large (> 20 cm DBH; liveBA34) trees showed weak correlations with the ordination axes (maximum $r^2 = 0.029$ on axis two for liveBA12 and 0.224 on axis three for liveBA34). The correlation structure of the data did not distinguish dwarf shrub and the live basal area variables likely because plots with higher index values for these variables were widely distributed in multivariate space according to the values of other variables.

Conversely, the ordination selected graminoid and moss from among the vegetation variables as representative of the greatest amount of variation in the Waterton Lakes data set, while these two variables did not differ significantly between treatments according to the ANOVA. From Figure 4 and Figure 5, it appears that graminoid and moss volume were associated with a treatment effect. However, Figure 24 shows that high graminoid volume was associated with all plots, irrespective of treatment, at higher values of axis two. Two control plots with very high values affected the strength of the correlation described by moss volume. These control plots had 10% and 8% cover; whereas the majority of the control plots had either no bryophytes and lichens or this vegetation was present with very low cover (i.e., 1%). The apparent discrepancy between the multivariate and ANOVA results for dwarf shrub, live basal area variables and mosses and graminoids can therefore be interpreted in two ways. First, because the multivariate analysis is ‘blind’ to treatment, the ordination may select variables that exhibit considerable variability, but show no pattern with respect to treatment. Second, the multivariate analysis can fail to select variables that have univariate significance because of a higher order interaction between other variables.

Kootenay, Banff and Yoho also saw considerable agreement between the ANOVA and the multivariate results in the selection and significance of variables that differentiate the treatments. However, as in Waterton Lakes, there were several variables for which the ANOVA showed significant differences that were below the threshold r^2 value of 0.320 in the multivariate analysis, including coarse woody debris (maximum $r^2 = 0.212$ for all CWD (CWD) on axis one); live basal area of smaller trees (≤ 20 cm DBH; live BA12; maximum $r^2 = 0.276$ on axis three); moss (maximum $r^2 = 0.114$ on axis three); and dwarf shrub (lgDwShrub; maximum $r^2 = 0.113$ on axis one). As suggested for the Waterton Lakes data, the absence of these variables above the 0.320 threshold was likely an artifact of the multivariate data structure; the multivariate analysis can assign lower explanatory power to variables that have univariate significance because of a higher order interaction between other variables.

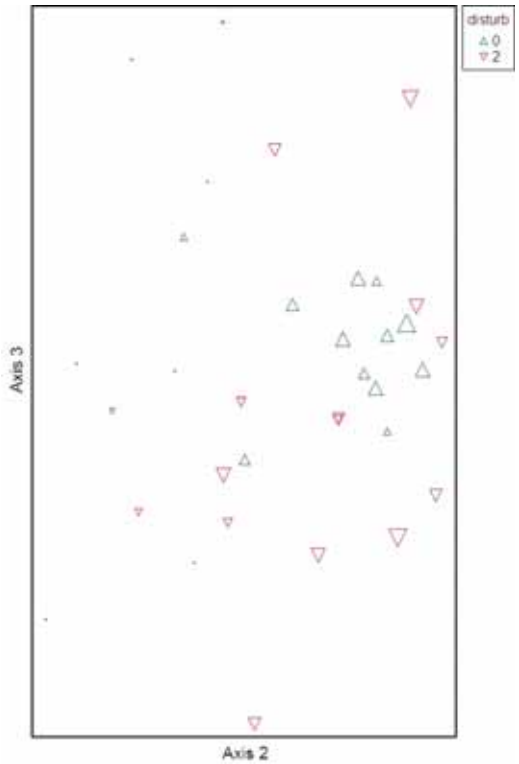

Figure 24. Waterton structural ordination plot of logGram on Axes 2 and 3 (symbol size indicates magnitude of value).

Treatments in Waterton Lakes were quite clearly distinguished in multivariate space. The ordination attributed the greatest amount of variation to (in decreasing order of importance): three CWD variables comprising all decay classes of CWD; five vegetation variables and total live basal area (stems > 4 cm DBH). However, there were some exceptions to the separation of treatments in the multivariate space, the most glaring of which included two disturbed plots that occurred among the control plots at quite a distance from the other disturbed plots (Figure 2 and Figure 3). These plots had the following characteristics which helps explain their similarity to the control plots:

- One of the plots had the least amount of mortality allowed for a disturbed sample (30%—we sampled sites with mortality between 30 and 70%)
- The other outlier plot was the driest plot sampled. This site had a soil moisture regime of subxeric, while the majority of the plots were mesic. The outlier plot still met our criteria for vegetation types of interest.

In addition to these two plots, the other three disturbed plots that occurred most deeply within the cloud of control plots on Figure 2 and Figure 3 were also drier than the rest of the beetle plots. These plots had lower amounts of CWD than characteristically occurred in the disturbed plots. Soil moisture regime is a ‘bottom up’ driver of productivity—a driver that exerts influence at a local scale (Lertzman and Fall, 1998); the lower levels of CWD may in part be due to the drier soil moisture conditions leading to lower amounts of live tree basal area (Bridge and Johnson, 2000), and therefore less CWD following disturbance.

As found in Waterton Lakes, in Kootenay, Banff and Yoho, the control and 1980s disturbance were clearly distinguished in the structural attribute ordination. The 1940s plots were intermediate between the control and the 1980s disturbance, and more closely related to the control plots (Figure 11 and Figure 13). The ordination attributed the greatest amount of variation to (in decreasing order of importance): three variables of live basal area, the number of stems of regeneration class three (stems ≤ 30 cm in height), two variables of vegetation biomass and maximum age. Two vegetation variables (graminoids and shrubs) and total live basal area (trees > 4 cm DBH) were common to the Kootenay, Banff and Yoho and the Waterton Lakes ordinations, although they differed in their relative contributions to the amount of variation represented—vegetation represented more variation in Waterton Lakes than it did in Kootenay, Banff and Yoho, and vice versa for total live basal area.

Overstory Basal Area

There were biologically significant differences between treatments in many of the variables found by the analyses to have statistical significance. In Waterton Lakes, total basal area of live trees (trees > 4 cm DBH), which explains the least variation of all the variables with r^2 values greater than 0.320 in the ordination, was about half of the amount in the disturbed stands compared to the control stands. In the ANOVA, this relationship had significance across the diameter classes analyzed (i.e., liveBA12, liveBA34).

The overall pattern of relationships between treatments of live basal area in Kootenay, Banff and Yoho were similar to those seen in Waterton Lakes. In Kootenay, Banff and Yoho, the basal area variables (liveBA34, live4BA, liveBA), which the greatest overall variation in the data according to the ordination, were greatest in the control, followed by the 1940s and then the 1980s disturbances; all treatments were significantly different from each other. As in Waterton Lakes, total live tree basal area (liveBA) and large (> 20 cm DBH) live tree basal area (liveBA34) had approximately twice the values in the controls compared to the 1980s disturbance; the 1940s disturbance is intermediate. Again, as in Waterton Lakes, the ANOVA for smaller diameter basal area (≤ 20 cm DBH; liveBA12) was also significant in Kootenay, Banff and Yoho, with the same relationship among treatments as occurred for the larger diameter classes.

Diameter classes 3 and 4 (DBH >20 cm) comprise those trees that would have been primarily susceptible at the time of the mountain pine beetle disturbance (Safranyik et al., 1980)—hence the lower live basal area of this diameter class in the disturbed stands compared to the controls. However, some smaller diameter trees (e.g., our basal area class 2, >10–20 cm DBH) were also susceptible and may have experienced mountain pine beetle mortality (Safranyik, 1989). During field sampling we observed that some of the downed smaller diameter trees (≤ 20 cm DBH) with no evidence of attack by mountain pine beetles were likely knocked down as larger trees that were killed by mountain pine beetles fell to the ground.

Several authors have documented growth releases in residual stands following disturbance by the mountain beetle (e.g., Cole and Amman, 1980; Romme et al., 1986; Alfaro et al., 2003). Romme et al. (1986) suggested that stands attacked by mountain pine beetle attain or exceed pre-disturbance productivity levels within 10–15 years following the disturbance. However not all trees in a stand, or all stands, will experience a release, possibly due to the poor health and / or vigour of the remaining stems (Alfaro et al., 2003). We did observe release in many of the overstory and understory tree cores following the timing of the disturbance, however it was beyond the scope and resources of this study to quantify release. However, the significant differences in basal area between the disturbed and control stands show that a recovery period of 25 years following disturbance by the mountain pine beetle in Waterton Lakes and Kootenay, Banff and Yoho, and of 65 years in Kootenay, Banff and Yoho, is insufficient for stand basal area to approach the levels observed in the controls. Further work on the cores will be necessary to determine whether and when productivity approached or exceeded pre-disturbance levels in the disturbed stands.

Coarse Woody Debris and Wildlife Trees

Coarse woody debris differences between treatments were also biologically significant in both ecosystems. In Waterton Lakes, where CWD explains most of the variation in the ordination, total CWD volume differed dramatically between disturbed and control stands. Disturbed stands had about 3.5 times the total CWD of control stands, with relatively fresh CWD (decay classes 1 and 2, [CWD12]) and well decayed CWD (decay classes 3, 4 and 5, [CWD345]) showing a similar magnitude of difference between disturbed and control, although for CWD345, the P-value was 0.06, whereas for CWD12 the P-value was < 0.05. Coarse woody debris in the less decayed classes (CWD12) dominated all disturbed sites, occurring at five times the abundance of the more decayed CWD. Based on our field observations, the volumes in CWD12 represent the CWD resulting from the 1980s beetle disturbance.

In Kootenay, Banff and Yoho, CWD represented very little of the variation according to the ordination. However, according to the ANOVA results, CWD in the advanced decay classes (CWD345) in the 1940s disturbance was about two and a half times greater, and significantly different, than the control and the 1980s disturbance. We expected this trend, as beetle–killed logs have had sufficient time to reach a more advanced state of decay—approximately 65 years after the disturbance and about 50 years since these trees have fallen to the ground.

However, some trends in CWD between Waterton Lakes and Kootenay, Banff and Yoho differ. In Kootenay, Banff and Yoho, unlike in Waterton Lakes, the amount of all CWD and CWD in a less advanced state of decay (CWD12) in the 1980s disturbance compared to the control is not significantly different; although it is on average greatest in the 1980s, there is also large variation in the 1980s data. However, the amount of all CWD is significantly greater (volume greater by 1.5 times) in the 1940s compared to the controls in Kootenay, Banff and Yoho. In Waterton Lakes, the amount of CWD12 is greater in the 1980s than the control by 3.5 times, and comprises over 80% of the total volume of CWD in the disturbance. Conversely, in Kootenay, Banff and Yoho, where the effect test for

CWD12 is not significantly different, CWD in this state of decay comprises only 50% of the total volume of CWD in the 1980s, and only 20% of the total volume in the 1940s. The control values for CWD12 are also greater in Kootenay, Banff and Yoho (68 m3/ha) than they are for Waterton Lakes (47 m3/ha) Furthermore, in Kootenay, Banff and Yoho, CWD345 is significantly different and comprises 50% of the 1980s and 80% of the 1940s total volume of CWD; some of the CWD from the 1980s disturbance in Kootenay, Banff and Yoho appears to have moved into the more advanced decay classes. Finally, in the Waterton Lakes control stands, total CWD is present at less than half the amount of the values that occur in Kootenay, Banff and Yoho.

We attribute differences in the trends in comparable time periods between the Waterton Lakes and Kootenay, Banff and Yoho ecosystems to several factors. The greater values for control for fresh CWD in Kootenay, Banff and Yoho than for Waterton Lakes control (and the lack of significant differences between the 1980s disturbance and control in Kootenay, Banff and Yoho) indicates more tree fall may have occurred overall in the Kootenay, Banff and Yoho ecosystem. This overall greater tree fall accumulation could be because the stands were of slightly older stand origin dates in Kootenay, Banff and Yoho (between 1800–1833) than in Waterton (between 1833–1884). The differing distribution of CWD between ecosystems and time periods could also be because some of the CWD from the 1980s disturbance in Kootenay, Banff and Yoho is in the more advanced decay classes. The differences in the 1980s trends between ecosystems, and the similarities between trends in the 1940s disturbance in Kootenay, Banff and Yoho and in the 1980s in Waterton Lakes might also be due to the initial mountain pine beetle disturbance having the most pronounced effect on CWD. This effect could be the case if the first mountain pine beetle disturbance affects the cohort of lodgepole pine that established following stand initiating fire. In the case of CWD, the cumulative nature of additional disturbance doesn’t appear to have amplified the effects of the initial disturbance.

Taken together, the different patterns of CWD accumulations in the different stages of decay may also suggest that different decay rates occur in Waterton Lakes than in Kootenay, Banff and Yoho. Kootenay, Banff and Yoho is a wetter and more productive ecosystem; wood decay rates are likely higher there than in Waterton Lakes, which would explain why the pulse of CWD inputs from the 1980s mountain pine beetle disturbance appears to have moved into the more advanced decay classes. This difference between the ecosystems suggests that recruitment and persistence of CWD in the different stages of decay differs between ecosystems. Differential rates of decay between ecosystem types would lead to different habitat values occurring at different times in different ecosystems following the same disturbance event, increasing habitat heterogeneity at landscape and regional scales.

The mountain pine beetle is an important contributor to snag densities, with a consequent effect on organisms that utilize dead and dying lodgepole pine trees (Bull, 1983; Bull et al., 1997; Keisker, 2000; Lindgren and MacIsaac, 2002). However, the pulse of snags and the associated forage and nesting opportunities are ephemeral; the mountain pine beetle provides inputs to the detritus cycle in several pulses; soon after attack when needles fall; within 10 years, as bark sloughs off; and within 15 years, when most dead trees have fallen (Manning et al., 1982; Lotan et al., 1984; Bull et al., 1997; Mitchell and Preisler, 1998). The similarities between the control and disturbed stands in snag basal area 25 years following the disturbance in both ecosystems, and the differences between treatments in CWD suggest that most, if not all, of the mountain pine beetle mortality had passed through the snag stage to the CWD stage, as expected. The mountain pine beetle has historically been an important contributor of coarse woody debris in lodgepole pine forests (Steed and Wagner, 2002). Steed and Wagner (2002) predict that the relative importance of the beetle to the dead wood cycle will increase in the near future, due to the increased abundance of stands containing susceptible hosts, compared to historic landscapes, suggesting that a long–term shift in habitat value may occur at the stand and landscape levels over the long term.

Vegetation Volume

Vegetation volume, which explains the second greatest amount of variation in the ordination, differed dramatically between the treatments in Waterton Lakes. The disturbed plots had almost four times the total vegetation volume found in the control plots. The magnitude of the differences between the control and disturbed stands differed between strata: of the variables found by the ANOVA to be statistically significant, tall shrubs were about four times more abundant, dwarf shrubs were three times more abundant and forbs were one and a half times more abundant in the disturbed plots than in the controls. Tall shrubs also comprised the majority of the total vegetation, accounting for 57% in the control and 73% in the disturbed stands. Dwarf shrubs accounted for a further 20% and 18% of the totals in the control and disturbed plots respectively. Forbs accounted for 16% in the control and 8% in the disturbed stands and graminoids accounted for only 5 and 2% respectively. Moss volume was negligible. Other authors have documented a temporary redistribution of biomass production from overstory trees to understory vegetation in lodgepole pine ecosystems following disturbance by mountain pine beetles (Romme et al., 1986; Stone and Wolfe, 1993; Stone and Wolfe, 1996); however, the effect in Waterton Lakes appears to be sustained 25 years after the disturbance.

In Kootenay, Banff and Yoho, where the vegetation variables for graminoid and tall shrub explain a relatively low amount of the variation in the ordination, the greatest proportional change was in graminoid volume (logGram) (Figure 20). The 1980s disturbance had 10 times as much graminoid volume and was significantly different than the control and 1940s disturbance, which had very low amounts of graminoid volume. Similarly, dwarf shrub volume in the 1980s disturbance was two to three times greater than and significantly different than the 1940s disturbance and control volumes. Conversely, moss was approximately one third greater in the control and 1940s disturbance when compared to the 1980s disturbance, but only the 1940s and 1980s differences were significant. As in Waterton Lakes, tall shrubs accounted for the highest amount of vegetation volume in Kootenay, Banff and Yoho. However, while not significantly different, tall shrub volume in the 1980s disturbance plots was only 60% of that in the control. This was very different from Waterton where large shrubs show a fourfold increase in the 1980s disturbance compared to the control; likely affecting total vegetation volume differences in Waterton Lakes. In all ecosystems and treatments the tall shrub strata is comprised of several species. In Waterton, the dominant tall shrub is

Acer glabrum. *Acer* along with *Betula papyrifera* are the dominant species in the Kootenay, Banff and Yoho 1940s disturbance. *Acer* and *Betula* are virtually absent from the Kootenay, Banff and Yoho controls and 1980s disturbance.

Regeneration

There was no significant difference in counts for any regeneration count category between the controls and 1980s in either Waterton Lakes, or Kootenay, Banff and Yoho, and no significant difference in regeneration age in Waterton Lakes. However, small tree (≤ 30 cm in height; lgReg3) regeneration counts were significantly greater in the 1940s disturbance than in the control in Kootenay, Banff and Yoho, although numbers of small trees in Kootenay, Banff and Yoho were very low: 1305 stems/ha in the 1940s disturbance and 271 stems/ha in the control. In Kootenay, Banff and Yoho, regeneration was significantly older in the control than in the 1980s disturbance and 1940s disturbance. The average weighted age of the regeneration in the 1940s and 1980s disturbed plots, approximately 28 and 20 years respectively, indicated that a large portion of the smallest stems and seedlings originated post-mountain pine beetle disturbance. The regeneration response indicates that recruitment differs in the two ecosystems, and that establishment of regeneration may either experience a considerable delay, as shown by the weighted age of 1940s regeneration at only 28 years, approximately 65 years following the disturbance; or more immediate, as shown by the weighted age of 1980s regeneration at 20 years, approximately 25 years following the disturbance. Finally, although the age of regeneration may differ, as between the 1980s disturbance and controls in Kootenay, Banff and Yoho, a recruitment event may be insignificant in number. However, as time goes on and recruitment continues, differences in numbers may become significant, as seen in the 1940s.

Vegetation competition may influence recruitment of regeneration, depending on ecosystem type. In Kootenay, Banff and Yoho, there were not the dramatic differences in vegetation that occurred in Waterton Lakes. However, the cumulative effect of the results for other variables may reveal why a significant pulse of regeneration is absent or delayed after mountain pine beetle disturbance in Waterton Lakes stands. Live basal area is less than half in the disturbed than in the control stands, and similar basal areas of dead standing trees occur in control and disturbed stands. The vegetation and overstory numbers suggest that by 25 years following the disturbance, overstory live and dead trees are not impeding sunlight from reaching the forest floor (Coates and Hall, 2005). The redistribution of resources seen in the aggressive response of vegetation, and the appearance of different species in the disturbed stands (see below) may be in response to better light conditions in the disturbed than in the control stands, and / or to the increased availability of water and nutrients. The absence or delay of regeneration establishment could thus be partially attributed to competition with vegetation for occupancy, water and nutrients. Given that understory response to mountain pine beetle mortality can be both immediate (Kovacic et al., 1985) and sustained, as evidenced by the results in Waterton Lakes, silviculture strategies should consider vegetation competition effects in reforestation plans, regardless of whether reforestation is delayed or occurs soon after disturbance (Coates and Hall, 2005). However, Bunnell *et al.* (2004) prescribe the maintenance of vegetation in its natural state to enhance biodiversity following disturbance by the mountain pine beetle in managed stands.

For both ecosystems, maximum stand age follows the same trends, although with differing strength. For Waterton Lakes, maximum age was not significantly different (control = 131 years, 1980s disturbance = 126 years). For Kootenay, Banff and Yoho, all treatments are significantly different from each other; the controls had the oldest maximum age, followed by the 1940s and then the 1980s disturbance. The result in Kootenay, Banff and Yoho was as expected; other authors have documented a shift in the age-structure of stands following disturbance by the mountain pine beetle (Roe and Amman, 1970; Amman, 1977; Safranyik, 1981; McGregor and Cole, 1985; Safranyik, 1989).

Overall, for Kootenay, Banff and Yoho, the placement of the 1940s plots in the multivariate space suggests similarities between the control and 1940s disturbance, indicating a recovery toward pre-disturbance conditions in the disturbance. The ANOVA results also suggest a close relationship between control plots and the 1940s disturbance plots (Table 6). The values for the 1940s disturbance are closest to the control values for the three vegetation variables estimated by the ANOVA to be significant ($P<0.05$). For seven variables related to live and dead trees, the values of the 1940s disturbance plots are intermediate to the other treatments. Conversely, for the two CWD variables found by the ANOVA to be significant, the 1980s disturbance and control are the most closely related, with the 1940s stands showing the greatest CWD volumes. Higher levels of CWD may benefit some organisms (Bull et al., 1997; Bunnell et al., 2004) while having a negative influence on others, such as ungulates if woody debris is a barrier to forage (Light and Burbridge, 1985). This latter finding suggests that although the values of other variables indicate a recovery toward control conditions in the 1940s stands, the presence of elevated levels of CWD creates a different type of habitat than that found in the controls.

Species Composition

No strong groupings of plots occur within the species ordination in Waterton Lakes; very few plots are consistently tightly grouped and related in three dimensions. The cloud of disturbed plots has greater dispersion compared to the control plot cloud, and disturbed plots often occur outside of the cloud of control plots (figure 9, figure 10, figure 11). The *Symporicarpos albus, Amelanchier alnifolia, Rubus parviflorus* species group is the only one that appears to be restricted to one treatment (disturbed). However, the plots that contain this species group are not related in the structural ordination.

In Waterton Lakes, rather than seeing a consistent successional change across the disturbed plots, and in addition to marginally significantly greater within–plot species richness (alpha diversity), greater between–plot species diversity (beta diversity) occurred in the disturbed plots compared to the controls.

In Kootenay, Banff and Yoho, although the 1940s disturbance has marginally significantly higher species richness than the 1980s (averaged across plots) and greater between plot variation in plant communities, the control has the highest number of total species (68). The 1980s disturbance has the fewest number of species (46) and the 1940s disturbance has 62 species (see Appendix 2 for species list). The greater number of species in the control may stem from the larger geographic range covered by the control plots than is covered by the disturbance plots.

The Kootenay, Banff and Yoho species ordination more clearly distinguishes between the treatments than in Waterton Lakes. However, the Banff and Yoho control plots, while belonging to the same ELC vegetation type, are sufficiently different to differentiate themselves on the species ordination (figure 18). Banff plots occur near the centre of the ordination graph and most Yoho plots occur in the upper left of the graph; there appears to be a geographic effect on species composition in the controls. This geographic effect makes it problematic to strictly attribute differences in species composition between controls and treatment in Kootenay, Banff and Yoho to disturbance.

However, as discussed above, the vegetation volumes for the 1940s disturbance are closest to the control values for the three vegetation variables that were estimated by the ANOVA to be significant. This similarity suggests an overriding effect of treatment over geography on biomass response; the 1980s and 1940s would be more similar than either of these treatments would be compared to the controls, if geography exerted a stronger influence over vegetation dynamics than did treatment. Additionally, species differences between the 1940s disturbance and 1980s disturbance show strong disturbance–related effects; if geographic affinity had a stronger influence on community composition than did treatment, we would expect greater similarity between the 1940s and 1980s disturbances than we observed.

In their model of natural disturbance and plant community succession, Platt and Connell (2003) suggest that episodic disturbance with high spatial and temporal variation, such as the mountain pine beetle disturbances studied here, will result in different successional trajectories of plant communities at different sites after disturbance. Although we do not see shifts in plant communities that are evident at the scale at which national parks ecosystems are described, the disturbed study sites in both ecosystems show higher beta, or landscape level, diversity. However, this effect is confined to the initial mountain pine beetle disturbance; in Kootenay, Banff and Yoho, similar to the pattern seen for CWD volumes, the second disturbance in the 1980s did not create additional diversity. Overall, the results for species composition show that the mountain pine beetle contributes to an increase plant diversity at the stand level, and community diversity at the landscape level following the initial disturbance by the mountain pine beetle.

Summary, Conclusions and Recommendations

Summary

The objective of this study was to establish baseline information on the ecological characteristics that occur at different stages of succession, resulting from mountain pine beetle disturbance at different time intervals. We measured overstory and understory structural attributes, gathered cross-sectional tree discs and cores from the boles of regeneration, and surveyed vegetation communities in 85 randomly located stands in two circum-mesic lodgepole pine ecosystem types—in Waterton Lakes national park and in Kootenay, Banff and Yoho National Parks. We performed multivariate ordination on the overstory and understory structural attributes and the vegetation data to describe the relationships in the data set, and used analysis of variance (ANOVA) on all data to examine treatment effects.

In Waterton Lakes and Kootenay, Banff and Yoho, considerable agreement occurred between the ANOVA and the multivariate ordination results in the selection and significance of variables that separated the treatments; the multivariate ordination for the two ecosystems well differentiated the treatments in multivariate space, while the majority of the attributes selected by the ordination to describe the greatest variation in the data showed statistically significant differences in the ANOVA.

The rank order of all variables according to the amount of variation they represented differed between ecosystems, although two vegetation variables (graminoids and shrubs) and total live basal area (trees > 4 cm DBH) were common to the Kootenay, Banff and Yoho and the Waterton Lakes ordinations. For these variables, vegetation represented greater variation in Waterton Lakes than it did in Kootenay, Banff and Yoho, and live basal area represented greater variation in Kootenay, Banff and Yoho than it did in Waterton Lakes.

Overall in Waterton Lakes, the ordination attributed the greatest amount of variation to (in decreasing order of importance): three CWD variables comprising all decay classes of CWD; five vegetation volume variables and total live basal area. There were statistically ($P<0.05$) and biologically significant differences in these variables; CWD and vegetation were significantly greater and basal area less, in the treatments compared to the control areas, with several variables showing doubling or even greater difference in values. No significant differences occurred between treatments for regeneration age or amount in Waterton Lakes. The disturbed stands in Waterton Lakes showed marginally significantly greater (P-value between 0.05 and 0.1) species richness than the control stands. Beta diversity was also higher in the disturbed stands than in controls, although a separate community type did not emerge.

Overall in Kootenay, Banff and Yoho, the ordination attributed the greatest amount of variation to (in decreasing order of importance): three variables of live basal area, the number of stems of small regeneration (stems ≤ 30 cm in height), two variables of vegetation volume and maximum stand age (age of the largest tree). Similar to the effects in Waterton Lakes, differences were statistically and biologically significant, with several variables showing doubling or even greater difference in values. Basal area was greatest in the controls, followed by the 1940s disturbance and then the 1980s disturbance; all treatments were significantly different from each other. Small regeneration was significantly greater in the 1940s disturbance than in the control, but not significantly greater than in the 1980s disturbance. All regeneration (≤ 4 cm DBH) combined was significantly older in the controls than in the 1940s and the 1980s. Controls also had the greatest maximum age, followed by the 1940s and 1980s disturbances; all treatments differed significantly from each other. Basal area of dead trees was marginally significantly greater in the controls than in the 1980s disturbance, and CWD was significantly greater in the 1940s than in the controls. Vegetation volume was generally significantly greater in the 1980s disturbance than in both the 1940s and the control. The 1940s disturbed stands showed marginally significantly greater species richness than the 1980s stands. Beta diversity was also higher in the 1940s disturbed stands than in controls, and clear compositional differences occurred between all treatments.

In the ordination for Kootenay, Banff and Yoho, the 1940s plots were intermediate between the control and the 1980s disturbance, and more closely related to the control plots, revealing a gradual recovery of disturbed stands taking place over 65 years. However, the significant differences that still exist between the control and 1940s disturbed stands suggest that the mountain pine beetle has altered the trajectory of these stands for both community and structural attributes. This altered trajectory suggests that the mountain pine beetle increases heterogeneity, and creates unique post-disturbance assemblages of species and habitat attributes, enhancing habitat values at stand and landscape levels.

We can summarize our study findings to date by returning to the study objectives. Regarding the ecological character of stands and ecological legacies following mountain pine beetle disturbance—first, we saw that CWD, vegetation and basal area accounted for the greatest variation between treatments, but that the rank order of their contribution to the variation in the data differed between the two ecosystems. Second, the mountain pine beetle stimulated understory vegetation productivity—a sustained re-distribution of resources between stands that persisted into the mid term. Third, the mountain pine beetle increased stand and landscape heterogeneity in three ways: via increased beta diversity of understory vegetation; by creating stands in the advanced recovery stage that have different habitat elements than control stands; and by initiating different trajectories of ecological legacies in different ecosystems. The latter finding shows that different habitat values occur over time across the landscape, originating from mountain pine beetle disturbance of similar timing.

Regarding the maintenance of ecological integrity in beetle-affected landscapes, the results clearly showed that ecological legacies existed and persisted following disturbance by the mountain pine beetle, and that recovery does gradually occur in disturbed stands, suggesting that an important ‘life-boating’ function exists for these legacies to help maintain ecological integrity in managed landscapes. However, we found a different recovery response between ecosystems, which may indicate that resilience to mountain pine beetle and to any additional disturbance differs between ecosystems. The success at maintaining ecosystem integrity will likely also differ, and be contingent upon the way in which additional disturbance (i.e., salvage) occurs.

Finally, we found either no notable pulse of regeneration or a delay in regeneration following disturbance.

Conclusion

Diversity characterizes many components of the mountain pine beetle–lodgepole pine systems that we studied, creating heterogeneity at multiple scales. This study showed that the mountain pine beetle strongly influenced the structure and composition of two ecosystems. The mountain pine beetle stimulated understory vegetation productivity, causing a re-distribution of resources within stands. The mountain pine beetle increased the heterogeneity of stands and landscapes and created diverse pathways of stand development. This diversity created unique ecological legacies and post-disturbance assemblages of species across landscapes. Accordingly, the mountain pine beetle influences process and function in these ecosystems.

Although many effects of the mountain pine beetle were similar in the two ecosystems, there were important differences in the relative contribution of different attributes to the overall variation between the treatments, and also differences in the trends for some variables. The similarities between findings in the two ecosystems suggest that some management interpretations about how to retain ecological functioning may be ubiquitous across ecosystems. However, some of the differences between findings in the two ecosystems suggest that rates of recruitment and persistence of ecological legacies vary between ecosystems, with consequent differences in the habitat values that different ecosystems would provide at different times following a widespread disturbance. Therefore, some management strategies should be adapted to suit local conditions.

Ecosystem recovery was apparent over the long term in Kootenay, Banff and Yoho. However, because ecosystem recovery from mountain pine beetle disturbance appears to vary in different ecosystems, resilience to post beetle management actions such as salvage logging will likely also vary between ecosystems; the type and intensity of rehabilitation should reflect the sensitivity of ecosystems to additional disturbance.

Recommendations

The study results suggest the following recommendations:

- To preserve beta vegetation diversity (landscape level diversity) and the successional potential of vegetation communities, maintain a range of intact ecosystem types (i.e., site series) within stands and across landscapes in salvage areas.
- Consider the potential effect of vegetation competition at the site and landscape level on the timing of reforestation activities, as interspecies competition for resources may strongly influence reforestation success over the short *and* mid-term.
- Plan for snag attrition and recruitment in salvaged stands; retain snags and live trees > 20 cm DBH.

- Consider ecosystem abundance and resilience in salvage planning. Where ecosystems occur in lower proportions in landscapes, or where site conditions suggest longer recovery times (for example, due to lower productivity), avoid salvage harvesting or use a lighter touch than in more productive or resilient stands. Where ecosystems occur in lower proportions *and* site conditions suggest longer recovery times, avoid salvage harvesting.
- Different ecological attributes respond differently to disturbance in different landscapes. In salvaged landscapes, use existing knowledge of past response to disturbances to identify local rehabilitation and recovery plans that reflect management opportunities, potential future ecological deficits and the resilience or sensitivity of individual ecosystem attributes to management.
- Because salvage harvesting is impractical in all stands and landscapes affected by the mountain pine beetle, there is an opportunity to enhance ecosystem recovery in these landscapes by emphasizing retention objectives.
- This report represents preliminary analysis of the data. Data gathered in this study could be used to advance management goals in the rehabilitation of landscapes disturbed by mountain pine beetle by:
    - quantifying management guidelines for dead wood retention and other attributes;
    - further interpretation and synthesis of the study findings to date;
    - further analyzing structural, compositional and tree core data to improve understanding of stand dynamics, productivity release and regeneration recruitment; and
    - further analyzing plant community dynamics.

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Appendix 1. Waterton Lakes Vegetation Summary

	disturbance	1980s beetle			Control		
Genus	**Species**	**Average Volume index**	**Count**	**% Frequency**	**Average Volume index**	**Count**	**% Frequency**
Abies	lasiocarpa	7.198	7	41.18	6.415	7	41.18
Acer	glabrum	8.324	9	52.94	0.084	3	17.65
Allium	cernuum	0.001	2	11.76	0	0	0
Alnus	viridis	2.284	5	29.41	0.527	3	17.65
Amelanchier	alnifolia	2.026	11	64.71	0.555	8	47.06
Angelica	dawsonii	0.114	1	5.88	0.116	3	17.65
Apocynum	androsaemifolium	0.007	1	5.88	0	0	0
Arctostaphylos	uva-ursi	0.002	1	5.88	0	0	0
Arnica	cordifolia	0.757	13	76.47	0.786	15	88.24
Aster	ciliolatus	0.006	2	11.76	0.008	2	11.76
Aster	conspicuus	0.973	16	94.12	0.608	12	70.59
Aster	foliaceus	0.001	1	5.88	0	0	0
Betula	papyrifera	0.049	1	5.88	0	0	0
Brachythecium	sp.	0.004	4	23.53	0.005	5	29.41
Bromus	ciliatus	0.011	5	29.41	0.102	4	23.53
Bromus	vulgaris	0.006	1	5.88	0	0	0
Calamagrostis	canadensis	0.265	2	11.76	0.024	1	5.88
Calamagrostis	rubescens	0.241	7	41.18	0.546	10	58.82
Campanula	rotundifolia	0.008	3	17.65	0.009	4	23.53
Carex	sp.	0.208	4	23.53	0.006	3	17.65
Chimaphila	umbellata	0.014	6	35.29	0.05	9	52.94
Cladonia	sp.	0.002	3	17.65	0.001	2	11.76
Clematis	sp.	0	0	0	0.005	2	11.76
Clematis	occidentalis	0.018	1	5.88	0.015	2	11.76
Clintonia	uniflora	0.081	11	64.71	0.084	11	64.71
Corallorhiza	sp.	0	0	0	0.001	1	5.88
Cornus	canadensis	0.052	4	23.53	0	0	0
Cornus	stolonifera	0.066	1	5.88	0	0	0
Dicranum	sp.	0	0	0	0.005	3	17.65
Dryopteris	filix-mas	0.059	1	5.88	0	0	0
Elymus	glaucus	0.02	4	23.53	0.001	1	5.88

	disturbance	1980s beetle			Control		
Genus	**Species**	**Average Volume index**	**Count**	**% Frequency**	**Average Volume index**	**Count**	**% Frequency**
Leymus	innovatus	0	0	0	0.004	1	5.88
Elymus	sp.	0.009	1	5.88	0	0	0
Epilobium	angustifolium	0.208	8	47.06	0.026	5	29.41
Erigeron	peregrinus	0.003	1	5.88	0	0	0
Erythronium	grandiflorum	0.079	3	17.65	0	0	0
Festuca	occidentalis	0.005	1	5.88	0.001	1	5.88
Fragaria	virginiana	0.032	6	35.29	0.021	4	23.53
Galium	boreale	0.007	2	11.76	0.005	3	17.65
Galium	triflorum	0.001	1	5.88	0	0	0
Geranium	viscosissimum	0.014	1	5.88	0	0	0
Goodyera	oblongifolia	0.004	5	29.41	0.009	8	47.06
Hedysarum	sulphurescens	0.031	1	5.88	0.395	5	29.41
Hieracium	albiflorum	0.015	2	11.76	0.005	1	5.88
Hieracium	umbellatum	0.044	1	5.88	0.003	1	5.88
Juniperus	communis	0.179	2	11.76	0	0	0
Lathyrus	ochroleucus	0.156	6	35.29	0.118	6	35.29
Lilium	philadelphicum	0.001	1	5.88	0.001	1	5.88
Linnaea	borealis	0.004	3	17.65	0.006	1	5.88
Listera	cordata	0.001	1	5.88	0	0	0
Lonicera	involucrata	0	0	0	0.052	1	5.88
Lonicera	utahensis	0.214	3	17.65	0.037	3	17.65
Mahonia	repens	0.153	10	58.82	0.226	10	58.82
Maianthemum	racemosum	0.031	3	17.65	0.082	8	47.06
Melica	subulata	0.002	1	5.88	0	0	0
Menziesia	ferruginea	0.228	2	11.76	0.275	1	5.88
moss		0.002	1	5.88	0.003	2	11.76
Orthilia	secunda	0.007	6	35.29	0.012	9	52.94
Osmorhiza	berteroi	0.038	10	58.82	0.009	6	35.29
Paxistima	myrsinites	0.002	1	5.88	0	0	0
Pedicularis	bracteosa	0.011	2	11.76	0	0	0
Picea		3.481	2	11.76	0.473	3	17.65
Pleurozium	schreberi	0	0	0	0.001	1	5.88
Populus	balsamifera	0.191	1	5.88	0	0	0
Prosartes	hookeri	0.056	3	17.65	0	0	0
Prosartes	trachycarpa	0.052	3	17.65	0.001	2	11.76
Prunus	virginiana	0.235	1	5.88	0	0	0
Pseudotsuga	menziesii	3.191	5	29.41	0	0	0
Pteridium	aquilinum	0.468	2	11.76	0	0	0
Ptilium	crista-castrensis	0	0	0	0.001	1	5.88
Pyrola	asarifolia	0	0	0	0.005	2	11.76
Pyrola	chlorantha	0	0	0	0.002	2	11.76
Racomitrium	sp.	0.001	1	5.88	0	0	0
Rosa	acicularis	0.076	3	17.65	0.029	5	29.41
Rubus	parviflorus	6.397	14	82.35	2.571	12	70.59

	disturbance	1980s beetle			Control		
Genus	**Species**	**Average Volume index**	**Count**	**% Frequency**	**Average Volume index**	**Count**	**% Frequency**
Salix	sp.	0.919	1	5.88	0	0	0
Shepherdia	canadensis	1.354	6	35.29	0.891	5	29.41
Solidago	canadensis	0	0	0	0.003	1	5.88
Sorbus	scopulina	0.794	4	23.53	0	0	0
Spiraea	betulifolia	1.386	17	100	0.856	15	88.24
Stenanthium	occidentale	0.001	1	5.88	0.002	1	5.88
Symphoricarpos	albus	1.001	10	58.82	0.035	3	17.65
Thalictrum	occidentale	0.904	14	82.35	0.323	11	64.71
Vaccinium	caespitosum	0.015	4	23.53	0.014	6	35.29
Vaccinium	membranaceum	0.111	5	29.41	0.029	1	5.88
Vaccinium	myrtillus	0.232	6	35.29	0.163	7	41.18
Veratrum	viride	0.038	3	17.65	0	0	0
Viola	canadensis	0.001	1	5.88	0	0	0
Viola	orbiculata	0.001	2	11.76	0.003	2	11.76
Xerophyllum	tenax	0.237	4	23.53	0.023	4	23.53

Appendix 2. Kootenay, Banff, Yoho Vegetation Summary

	Disturbance	1940s beetle			1980s beetle			Control		
Genus	**Species**	**Average Volume index**	**Count**	**% Freq.**	**Average Volume index**	**Count**	**% Freq.**	**Average Volume index**	**Count**	**% Freq.**
Abies	lasiocarpa	0.118	6	35.29	0	0	0	0.147	2	11.76
Acer	glabrum	15.998	8	47.06	2.721	1	5.88	1.084	1	5.88
Achillea	millefolium	0.002	1	5.88	0.008	7	41.18	0	0	0
Alnus	viridis	4.049	4	23.53	0	0	0	6.483	3	17.65
Amelanchier	alnifolia	0.869	7	41.18	0.746	12	70.59	0.632	6	35.29
Aralia	nudicaulis	0.058	3	17.65	0	0	0	0.084	2	11.76
Arctostaphylos	uva-ursi	0	0	0	0.029	2	11.76	0	0	0
Arnica	cordifolia	0.026	7	41.18	0.002	1	5.88	0.104	12	70.59
Aster	ciliolatus	0.001	2	11.76	0	0	0	0	0	0
Aster	conspicuus	0.469	9	52.94	0.419	11	64.71	0.769	12	70.59
Aster	foliaceus	0.014	4	23.53	0.08	8	47.06	0.008	3	17.65
Barbilophozia	sp.	0	0	0	0	0	0	0.006	3	17.65
Betula	papyrifera	26.316	6	35.29	19.118	1	5.88	0	0	0
Brachythecium	sp.	0.002	1	5.88	0.015	5	29.41	0.006	2	11.76
Calamagrostis	canadensis	0	0	0	0	0	0	0.003	1	5.88
Calamagrostis	rubescens	0.171	10	58.82	0.93	15	88.24	0.121	7	41.18
Campanula	rotundifolia	0	0	0	0.002	1	5.88	0	0	0
Carex	vaginata	0.002	1	5.88	0	0	0	0	0	0
Carex	sp.	0	0	0	0	0	0	0.001	2	11.76
Chimaphila	umbellata	0.001	1	5.88	0	0	0	0.001	1	5.88
Cladonia	sp.	0.004	3	17.65	0	0	0	0.001	1	5.88
Clintonia	uniflora	0	0	0	0	0	0	0.012	5	29.41
Cornus	canadensis	0.348	15	88.24	0.104	5	29.41	0.315	15	88.24
Cornus	stolonifera	0.216	1	5.88	0	0	0	0	0	0
Dicranum	sp.	0.034	8	47.06	0.01	5	29.41	0.039	6	35.29
Elymus	glaucus	0.006	1	5.88	0	0	0	0.002	1	5.88
Leymus	innovatus	0.194	10	58.82	2.941	13	76.47	0.193	9	52.94
Epilobium	angustifolium	0	0	0	0	0	0	0.004	3	17.65
Equisetum	arvense	0	0	0	0	0	0	0.002	1	5.88
Fragaria	virginiana	0.012	6	35.29	0.199	12	70.59	0.017	8	47.06
Galium	boreale	0.004	3	17.65	0.022	7	41.18	0	0	0
Gentianella	amarella	0	0	0	0.001	2	11.76	0	0	0
Geocaulon	lividum	0.002	2	11.76	0.004	2	11.76	0.008	2	11.76
Goodyera	oblongifolia	0	0	0	0	0	0	0.001	2	11.76
Hedysarum	sulphurescens	0.001	1	5.88	0.049	6	35.29	0	0	0
Hylocomium	splendens	0.717	17	100	0.492	16	94.12	0.421	14	82.35
Juniperus	communis	1.048	7	41.18	3.625	9	52.94	0.019	3	17.65
Ledum	groenlandicum	0.194	2	11.76	0	0	0	0.016	3	17.65
Lilium	philadelphicum	0	0	0	0.012	3	17.65	0	0	0
Linnaea	borealis	0.055	16	94.12	0.056	17	100	0.046	16	94.12
Lonicera	involucrata	0.147	4	23.53	0.003	1	5.88	0.046	2	11.76
Lonicera	utahensis	0.184	5	29.41	0.012	4	23.53	0.258	6	35.29
Lycopodium	annotinum	0.023	4	23.53	0.009	4	23.53	0.048	2	11.76
Maianthemum	dilatatum	0	0	0	0	0	0	0.002	1	5.88

	Disturbance	1940s beetle			1980s beetle			Control		
Genus	**Species**	**Average Volume index**	**Count**	**% Freq.**	**Average Volume index**	**Count**	**% Freq.**	**Average Volume index**	**Count**	**% Freq.**
Maianthemum	racemosum	0.048	5	29.41	0.009	1	5.88	0.006	1	5.88
Menziesia	ferruginea	0.346	2	11.76	0	0	0	1.596	7	41.18
Mitella	nuda	0.006	7	41.18	0.002	1	5.88	0	0	0
Orthilia	secunda	0.011	9	52.94	0.014	10	58.82	0.005	6	35.29
Oryzopsis	asperifolia	0.092	4	23.53	0.665	9	52.94	0.038	2	11.76
Osmorhiza	berteroi	0.014	2	11.76	0	0	0	0.004	1	5.88
Peltigera	sp.	0.016	6	35.29	0.009	5	29.41	0.018	9	52.94
Petasites	frigidus	0.004	3	17.65	0	0	0	0.01	2	11.76
Picea		0.001	1	5.88	0.001	1	5.88	0.006	1	5.88
Platanthera	obtusata	0.002	2	11.76	0	0	0	0	0	0
Pleurozium	schreberi	0.214	16	94.12	0.326	17	100	0.463	17	100
Populus	tremuloides	0.006	2	11.76	0.211	5	29.41	0	0	0
Prosartes	trachycarpa	0	0	0	0.009	1	5.88	0	0	0
Pseudotsuga	menziesii	0.005	1	5.88	0	0	0	0.002	1	5.88
Ptilium	crista-castrensis	0.238	14	82.35	0.032	5	29.41	0.223	15	88.24
Pyrola	asarifolia	0.001	1	5.88	0	0	0	0	0	0
Pyrola	chlorantha	0.003	4	23.53	0.002	4	23.53	0.001	2	11.76
Rhododendron	albiflorum	0	0	0	0	0	0	0.039	1	5.88
Rhytidiadelphus	triquetrus	0.018	3	17.65	0	0	0	0	0	0
Ribes	lacustre	0.016	2	11.76	0	0	0	0.037	1	5.88
Rosa	acicularis	0.371	16	94.12	1.046	16	94.12	0.095	10	58.82
Rubus	parviflorus	0.334	6	35.29	0	0	0	0.279	3	17.65
Rubus	pedatus	0	0	0	0.018	1	5.88	0.002	1	5.88
Rubus	pubescens	0.051	9	52.94	0	0	0	0	0	0
Salix	sp.	0.098	1	5.88	0.074	1	5.88	0	0	0
Senecio	pseudaureus	0	0	0	0	0	0	0.001	1	5.88
Shepherdia	canadensis	3.676	14	82.35	8.042	16	94.12	4.868	13	76.47
Spiraea	betulifolia	0.145	12	70.59	0.082	8	47.06	0.296	9	52.94
Stenanthium	occidentale	0	0	0	0	0	0	0.003	1	5.88
Symphoricarpos	albus	0.039	2	11.76	0.629	8	47.06	0.029	1	5.88
Taxus	brevifolia	0	0	0	0	0	0	0.088	1	5.88
Thalictrum	occidentale	0	0	0	0	0	0	0.021	1	5.88
Vaccinium	caespitosum	0.03	8	47.06	0.114	6	35.29	0.004	3	17.65
Vaccinium	membranaceum	0.28	4	23.53	0	0	0	1.318	9	52.94
Vaccinium	myrtilloides	0	0	0	0	0	0	0.185	3	17.65
Vaccinium	myrtillus	0	0	0	0	0	0	0.139	9	52.94
Oxycoccus	oxycoccos	0	0	0	0	0	0	0.007	2	11.76
Vaccinium	scoparium	0	0	0	0	0	0	0.006	2	11.76
Vaccinium	vitis-idaea	0.001	1	5.88	0	0	0	0	0	0
Viburnum	edule	0.247	8	47.06	0.024	1	5.88	0.003	1	5.88
Viola	adunca	0	0	0	0.009	3	17.65	0	0	0
Viola	orbiculata	0.001	1	5.88	0	0	0	0.001	1	5.88

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