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Overstory and understory dynamics of whitebark pine (*Pinus albicaulis*) ecosystems of Northwestern British Columbia

by

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) is declining across its range due to disturbances such as mountain pine beetle and white pine blister rust. In this thesis, I assess the response and vulnerability of whitebark pine ecosystems to multiple stressors and disturbances at the northern edge of *P.albicaulis'* range in the Coastal Mountains of British Columbia, Canada. Both the compositional change over time of overstory and understory communities as well as vegetation spatial patterns suggest that different sites or ecosystem types housing whitebark pine may differ in their response to disturbance and stress. Surveys conducted ~ 20 years apart indicate that overstory community change differed between site types following the decline of *P. albicaulis* over time, while the understory did not change significantly. The spatial pattern of overstory species and understory communities also indicates that site type may be important in determining forest change under ongoing disturbance to whitebark pine.

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CHAPTER 1. Introduction

While all ecosystems change over time, disturbance and stress can influence how this change occurs. Disturbance is an important component of forest ecosystems and influences plant communities at different scales. Disturbances such as fire, insect or disease outbreak often interact with pre-disturbance stand and abiotic conditions to determine the post-disturbance forest community (White and Pickett 1985). Insect and disease outbreaks are often species-specific, reducing the abundance of live trees of a particular species in the canopy or preventing recruitment. The overstory may become dominated by alternate tree species, in turn changing above- and below-ground resources for the understory plant community (Battle and Fahey 2000).

1.1 Community ecology

Plant community composition is a function of climate (temperature, precipitation), topography (slope, slope position, aspect, geomorphology), soil (organic, mineral, parent material, geology) (Boerner 2006), biotic interactions (Tilman 1985, Callaway and Walker 1997) and life history traits (Kolb and Diekmann 2005). Which of these factors contributes most to community composition, pattern or diversity has been an important focus of plant ecological research (Beatty 1984, Fajardo and McIntire 2007, Laughlin and Abella 2007). In forest ecosystems the nature and relative importance of these processes vary across scales (Levin 1992) and with stand age (Fajardo and McIntire 2007). Biotic interactions between plants and between plants and their environment may also vary according to the abiotic environment (Bertness and Callaway 1994, Maher et al 2005, Getzin et al 2008). These processes that drive community composition and pattern will then interact with patterns and the nature of forest disturbance to determine the post-disturbance community.

1.2 Understory communities

Understory plants are influenced not only by variation in resource availability, the physical environment and plant-plant interactions, but are also influenced by the overstory (Berger and Puettmann 2000). Canopy trees affect the understory through effects on below-ground resources and edaphic conditions (nutrients, moisture, pH, soil temperature; Anderson et al. 1969), and above-ground resources (light; Battaglia et al 2002, Chipman and Johnson 2002) and environmental conditions (microclimate, microsite; Beatty 1984). Disturbance that results in a change to the overstory then influences the understory community through changes in light levels, soil water, soil nutrients, the physical presence of litter and potential phytotoxic chemicals associated with overstory trees (Barbier et al 2008). Understory communities may, in turn, affect the overstory through influences on tree regeneration or indirectly through nutrient cycling and decomposition rates (Nilsson and Wardle 2005). Disturbance to the overstory that alters the understory may then have a significant effect on overall ecosystem vegetation composition.

1.3 Whitebark pine

Whitebark pine (*Pinus albicaulis* Engelm.) was recently assessed as ‘endangered’ (April 2010) in Canada due to threats from multiple disturbances (mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins.), white pine blister rust (WPBR; *Cronartium ribicola* J.C. Fisch)) and stress (fire suppression and climate change) (Cambell and Antos 2000, Zeglen 2002, COSEWIC 2010). These threats have resulted in massive declines of

P. albicaulis populations across its range, which may not only affect the ability of these trees to persist in the future, but may also influence the wider ecosystem (COSEWIC 2010). Whitebark pine seeds are an important food source for many wildlife species including grizzly bears, and there is a recognized mutualistic relationship between *P. albicaulis* and Clark's nutcracker (*Nucifraga Columbia*), which is crucial for the dispersal of seed (Hutchins and Lanner 1982, Tomback 1982). *P. albicaulis* may be considered a keystone species due to its importance as a nurse tree (Callaway 1998) and as a food source for wildlife (Tomback 2007).

Pinus albicaulis is a long-lived subalpine forest species that reaches its northern extent north of Smithers, British Columbia in the Coastal mountain range and northwest of Prince George, BC in the northern Rocky Mountains (Klinka et al 2000). *P. albicaulis* is an early successional species in many areas, but on environmentally harsh sites it is able to regenerate and persist over the longer term, even without major disturbances such as fire (Keane et al 1990, Banner et al 1993). Whitebark pine is often found on sites with low nutrient availability, low moisture, high occurrence of frost, a late-melting snowpack, short growing season and high winds (Arno and Hoff 1989, Klinka et al 2000).

Disturbance from MPB and WPBR in whitebark pine ecosystems reducing the abundance of *P. albicaulis* in the overstory will potentially cause a shift towards a different forest type by enabling other tree species to recruit into the canopy (Keane et al 1994), while inhibiting regeneration of whitebark pine. Less frequent fires due to climate change or human intervention, may increase competition from shade tolerant conifers (Keane et al 1990, Keane et al 1994). Clark's Nutcrakers have a reduced probability of caching *P. albicaulis* seeds in denser stands (Tomback et al 1990), following encroachment of shade tolerant conifers (Keane et al 1990). Climate change is also expected to shrink the range of suitable growing areas for *P. albicaulis* along an elevational gradient before the range expands northwards (Hamann and Wang 2006). This may result in shade tolerant conifers, such as *Abies lasiocarpa* and *Tsuga mertensiana* in Northwestern BC (Meidinger and Pojar 1990, Banner et al 1993), significantly increasing in abundance (Keane et al 1994, Campbell and Antos 2003, Kipfmueller and Kupfer 2005). Given its role as a keystone species and the current decline in abundance across its range, the loss of whitebark pine may result in significant ecosystem change (Ellison et al 2005).

1.4 Ecosystem change

Cumulative disturbances may lead to a regime shift, where ecosystems switch from one state to another (Scheffer and Carpenter 2003). If multiple disturbances to whitebark pine ecosystems result in a shift away from a community composition where *Pinus albicaulis* may be supported in the future, then this may represent a regime shift. Different ecosystem types may however, respond differently to cumulative disturbances, with some communities being more resilient to change than others. Resilience is defined here as the ability of a community to return to its original state following perturbations, such as multiple disturbance events (Holling 1973). The resilience of a system is then related to its proximity to a tipping point, where systems closer to a critical point of change may be pushed past this threshold by cumulative disturbance events, resulting in a significant regime shift. Others, further from the tipping point may not reach this threshold (Holling 1973, Pascual and Guichard 2005, Andersen et al 2009).

1.5 Temporal and spatial indicators of ecosystem change

Quantifying changes in forest communities over time under stress and/or disturbance may indicate their vulnerability (Andersen et al 2009, Guttal and Jayaprakash 2008). For example, examining changes in overstory and understory communities in whitebark pine ecosystems over time under the influence of stress and disturbance can help provide insight into their resilience. The abundance and composition of understory tree regeneration over time can also provide important insight into future stand structure and ecosystem resilience. In the absence of stand re-initiating disturbance, seedlings and advanced regeneration in the understory may eventually replace the current canopy (Battles and Fahey 2000). If shade tolerant conifers increasingly dominate understory regeneration, then it would be unlikely that *Pinus albicaulis* could re-establish without fire disturbance or active restoration. Changes in the abundance of different overstory species, combined with a significant change in understory plant communities over time, may indicate a regime shift if these systems are unlikely to recover a whitebark pine community in the future.

Long-term datasets often do not exist to study how ecosystems change over time. The spatial distribution of plants may then provide insight into the processes driving composition (Watt 1947, Kershaw 1963). Linking spatial pattern to process, or the factors influencing birth, death and growth of individual plants, has been an important development in understanding community dynamics (Watt 1947, Kershaw 1963, Levin 1992, van der Maarel 1996). Intra and inter-specific spatial pattern analysis is a useful tool to determine which processes may be responsible for community pattern. For instance, the nature of a repeated spatial arrangement of vegetation may suggest which factors acted on the vegetation to produce this pattern (Watt 1947, Kershaw 1963). The processes examined in forest ecosystems often include the importance of the physical environment (Beatty 1984), abiotic resource heterogeneity (Wijesinghe et al 2005, Getzin et al 2008), life history traits (Kolb and Diekmann 2005, Maher et al 2005) or biotic interactions across gradients in resource availability (Tilman 1985, Bertness and Callaway 1994, Callaway 1998) in structuring vegetative communities. For example, Fajardo and McIntire (2009) used the spatial patterns of overstory trees in Ponderosa pine stands of Patagonia, Chile, to determine the relative importance of microsites and competitive interactions between trees over the course of succession. Examining current overstory and understory spatial patterns may then provide insight into the processes controlling pattern in whitebark pine communities and as a result, suggest future directions of change under ongoing disturbance. This, combined with quantifying the overall change in forest communities over time will suggest resilience of whitebark pine ecosystems to multiple disturbances and stressors.

1.6 Influence of Site on Direction of Ecosystem Change

Different site characteristics may result in similar edaphic conditions (ie. moisture and nutrients) and thus similar vegetation communities (Getzin et al 2008). However, site conditions, such as the spatial variation in resource availability driven by topography, may result in different processes controlling forest change and ultimately ecosystem trajectory (Tilman 1985, Bertness and Callaway 1994, Maher et al 2005). For example, Getzin et al (2008), determined that environmentally heterogeneous sites (ie. variation in soil depth and associated resources caused by variation in geomorphology: rocky outcrops or depressions) compared to homogeneous sites with the same vegetation community, resulted in significant differences in plant community dynamics between sites, as a result of biological interactions with the abiotic environment.

1.7 Objectives

My objective was to assess resilience of whitebark pine ecosystems in Northwestern British Columbia under the recent history of stress and disturbance. I did this through examining changes in overstory and understory composition of two whitebark pine ecosystem types between the 1970/80's and the present. Further, to understand the successional future of these stands and how this may affect resilience, I looked at spatial pattern and overstory-understory relationships.

The remainder of the thesis is organized as follows:

Chapter 2: A simple, preliminary look at forest change by examining the change in diameter distributions of trees over time.

Chapter 3: A comprehensive analysis of overstory and understory community composition change over time

Chapter 4: Vegetation patterns and overstory-understory relationships

Chapter 5: General conclusions, management recommendations and suggested future research

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CHAPTER 2[1] - Canopy change in whitebark pine ecosystems of Northwestern British Columbia

2.1 Introduction

This MSc research on whitebark pine (*Pinus albicaulis*) ecosystems continues the work of the Bulkley Valley Research Centre in northwestern British Columbia (Haeussler 2008). Here, whitebark pine is at the northern extent of its range in the Coastal mountains and is subject to mountain pine beetle (MPB) and white pine blister rust (WPBR). Stresses such as climate change and the effects of fire suppression may also contribute to whitebark pine decline in this region.

Haeussler et al (2009) focused on rare whitebark pine-dominated stands on coarse-textured, nutrient-poor sites. They re-visited sites surveyed by the BC Ministry of Forests (BC-MOF) from 1978-85 to determine how they have changed over time. They thought that a warmer, wetter climate combined with canopy disturbance from MPB and WPBR would increase resource availability such that whitebark pine ecosystems would shift compositionally to resemble common, mesic ecosystems. Preliminary results did not fully support this hypothesis. The climate was warmer after the 1970s, but precipitation was highly variable. There was no uniform shift in understory composition; however, there were interesting differences in understory response between two different whitebark pine ecosystems surveyed: 'Moderately dry/poor' versus 'Dry/poor' (Haeussler et al 2009).

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[1] A version of this chapter has been published. Clason, A.J., Macdonald, S.E. and Haeussler, S., 2010. Nutcracker Notes. Spring/Summer 2010: 12-13

We followed up this preliminary study testing two possible hypotheses: (1) there was a homogenization of forest communities over time through a shift in both types of whitebark pine ecosystems towards a mesic ecosystem composition; or (2) there was a threshold response whereby 'Dry/poor' ecosystems demonstrate resilience to change, while 'Moderately dry/poor' ecosystems are more vulnerable. In 2009 we undertook further re-sampling of old BC-MOF plots in both whitebark pine ecosystem types, as well as surveying mesic, non-whitebark pine ecosystems as a reference. Here we present changes in forest structure over time.

2.2 Methods

We returned to sites surveyed in 1978-85 and followed the original BC-MOF survey methodology (Luttmerding et al. 1990). We were not always able to relocate the original plot markers, however, we navigated as geographically close to the original plots as possible and ensured placement of our plot was in an area with as similar site characteristics as possible. In total 5 'Dry/poor', 4 'Moderately dry/poor' and 5 'Mesic/medium' sites were surveyed in 1978-85 and 2007-2009, collecting basic mensuration data (Diameter at breast height (DBH), height class) for live and dead trees by species using a prism. In the 2007-09 surveys we also used 5.6 m radius plots to collect this same data.

2.3 Results and Discussion

There was a significant change in tree species composition and abundance over time in all three ecosystem types. The observed change supported Hypothesis 1. A decrease in live whitebark pine stems has driven these forests to more closely resemble 'Mesic/medium' reference stands (Figure 2-1). Our results suggest that absolute disturbance intensity was similar in 'Moderately dry/poor' and 'Dry/poor' ecosystem types (dead *Pinus albicaulis* by the second survey period: 'Moderately dry/poor'=88 snags/ha and 'Dry/poor' = 62 snags/ha)

Disturbance in the 'Dry/poor' ecosystem type decreased the number of large *P. albicaulis*, changing the diameter distribution for this species from a J-shaped to a unimodal distribution (Figure 2-1c). The decline in smaller live *P. albicaulis* trees is worrying for the conservation of this species, particularly in dry, exposed stands, where it would normally be expected to persist throughout the old growth successional stage (Keane et al 1990). We did find that *P. albicaulis* seedlings continue to regenerate in the driest stands, suggesting these are the most suitable sites for whitebark pine persistence (Figure 2-2).

'Moderately dry/poor' ecosystems showed a similar loss of large whitebark pines as well as a decrease in large *A. lasiocarpa* accompanied by a sharp increase in small *T. mertensiana* (Figure 2-1). There were few small *P. albicaulis* trees in 2007-09; this, combined with proportionally less *P. albicaulis* seedlings (Figure 2-2) suggests whitebark pine may not persist in these ecosystems. The lack of regeneration could be due to shading from the thickening canopy of hemlock and fir and also due to lack of seeds, as Clark's nutcrackers may be less likely to cache seeds in 'Moderately dry/poor' stands (Tomback et al 1990).

Our reference stands (the 'Mesic/Medium' ecosystem type) also changed over time, primarily through decreasing *A. lasiocarpa* in the canopy. This may have been due to balsam bark beetle (*Dryocoetes confusus*) disturbance, competition with more shade tolerant *A. amabilis* and *T. mertensiana*, or simply that there is a decline in density as stands age.

Disturbance and stand dynamics in whitebark pine ecosystems are complex. Whitebark pine continues to regenerate in ‘Dry/poor’ ecosystems; however, ongoing disturbance will further decrease its presence in the overstory and canopy recruitment in the future, resulting in a worsening outlook for this rare ecosystem.

2.4 Figures

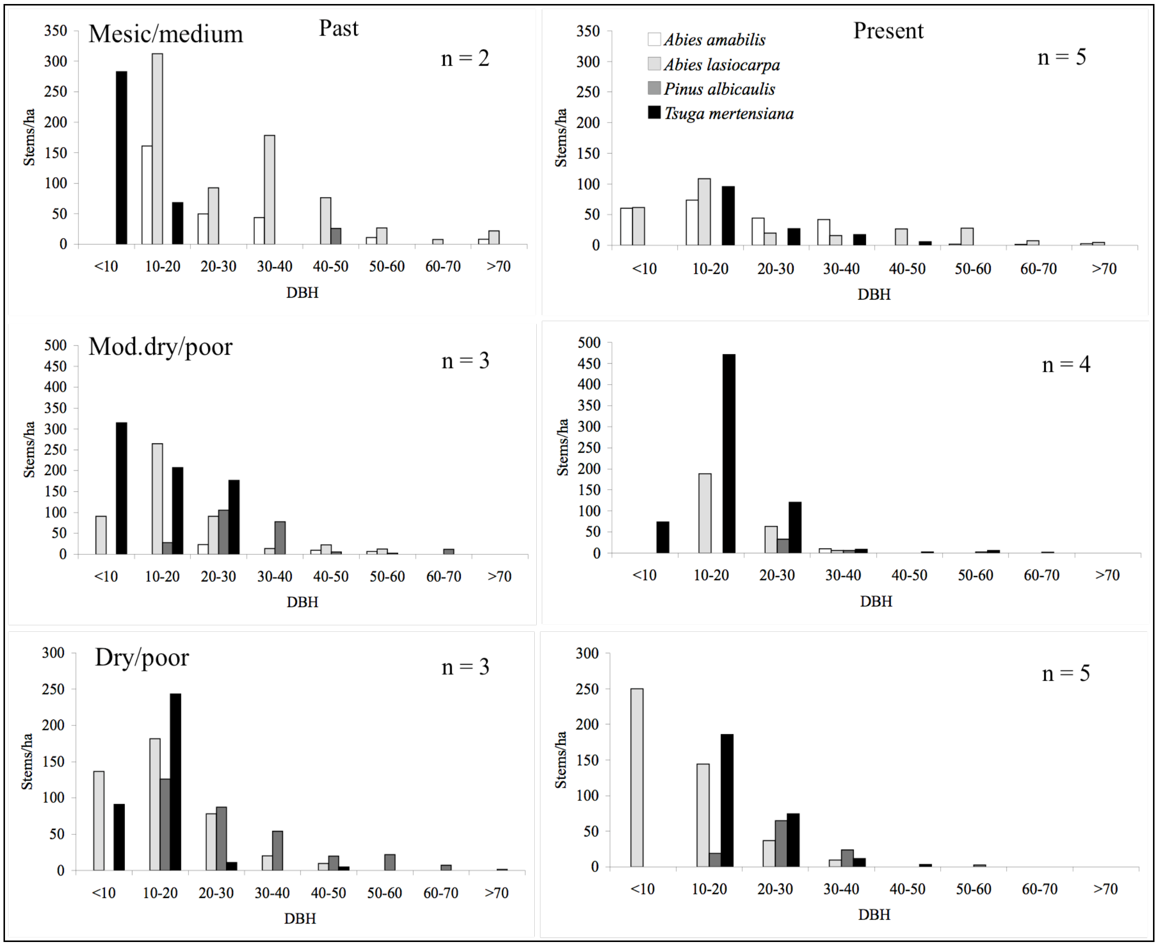

Figure 2-1 The number of live stems/ha by diameter at breast height (DBH) category for each species in the first survey period (left) and second survey period (right); A) ‘Mesic/medium’ reference stands; B) ‘Moderately dry/poor’ and C) ‘Dry/poor’ whitebark pine ecosystems.

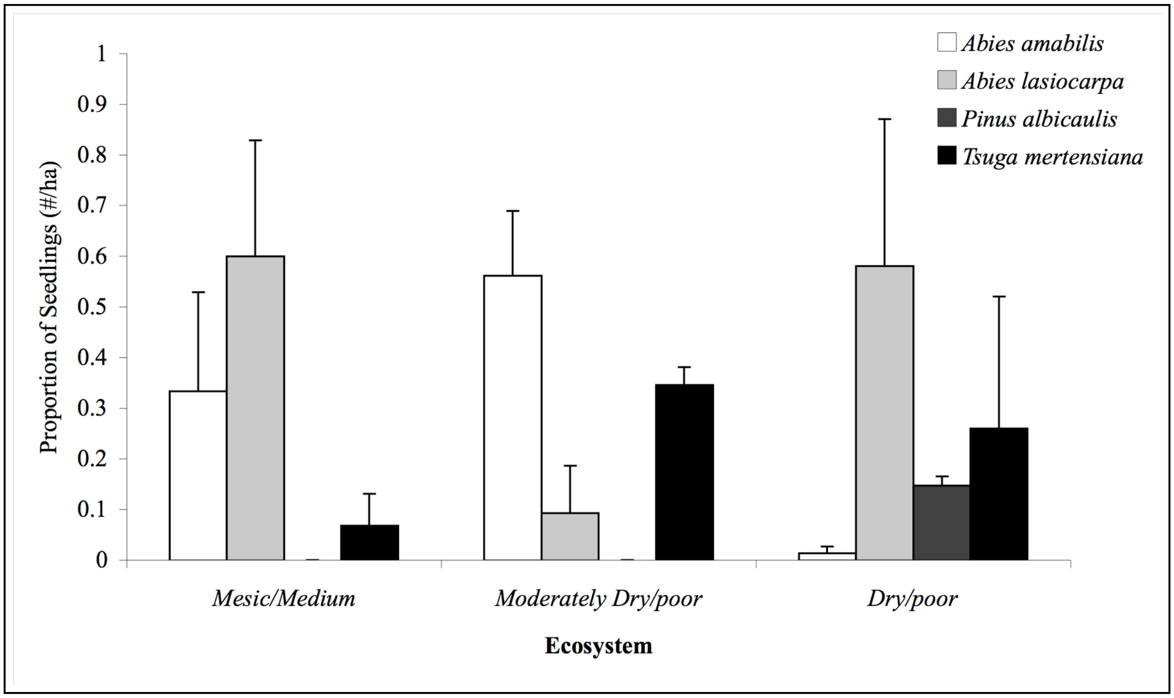

Figure 2-2 The proportional number (mean ± SE) of seedlings/ha (dbh < 5cm, height < 2m) for each species by ecosystem type ('Mesic/medium' n = 5; 'Moderately dry/poor' n = 2; 'Dry/poor' n = 3) from fixed plot (5.6m radius) surveys in the 2007/09 surveys

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CHAPTER 3: Ecosystem change under cumulative disturbance and stress: Vulnerability of whitebark pine ecosystems of northwestern British Columbia

3.1 Abstract

The response of forest communities to multiple disturbances can provide insight into the resilience of an ecosystem to change. Whitebark pine (*Pinus albicaulis*) is threatened due to its exposure to multiple stresses (fire suppression, climate change) and disturbances (white pine blister-rust, mountain pine beetle). We examined *P. albicaulis* ecosystems at the northern edge of the species' range in the Coastal mountains of British Columbia, Canada. Study sites surveyed in the 1970/80's were re-visited in 2007/09 to quantify changes in overstory and understory vegetation over this time period. Overstory and understory change in two *P. albicaulis* ecosystem types ('Moderately dry/poor' and 'Dry/poor') were compared to a reference ('Mesic/medium') non-whitebark pine ecosystem. We hypothesized that either: (1) both whitebark pine ecosystems would now resemble non-whitebark systems due to disturbance causing death of whitebark pine and the subsequent resource pulse in these nutrient poor systems; or (2) there is a threshold to change, whereby the 'Dry/poor' whitebark ecosystems would be resilient (ie. would remain compositionally distinct from non-whitebark ecosystems) while the 'Moderately dry/poor' systems vulnerable (ie. would become more similar to non-whitebark ecosystems) to the influence of stressors and disturbance. In contrast to our original expectation, the results indicate a shift in the overstory of 'Dry/poor' whitebark pine ecosystems towards a composition more similar to 'Mesic/medium' ecosystems over time. However, the understory in the ‘Dry/poor’ ecosystems did not change with the canopy. In ‘Moderately dry/poor’ ecosystems neither the overstory nor the understory changed significantly over time, but the overstory is trending towards increased abundance of *Tsuga mertensiana*. *P. albicaulis* continues to regenerate in both whitebark pine ecosystem types; however, it constitutes a significantly higher proportion of the subcanopy tree layer in the ‘Dry/poor’ ecosystem type. ‘Dry/poor’ stands may be more resilient to change due to the persistence of the understory vegetation community, including understory *P. albicaulis*, which may return the overstory to its original state over time. However, ongoing disturbance and increasing dominance by shade tolerant conifers may alter understory communities in both ‘Dry/poor’ and ‘Moderately dry/poor’ ecosystems in the future as a result of overstory effects on understory communities.

Keywords: Cumulative disturbance, Whitebark pine, Ecosystem change, Community ecology, Resilience, Overstory-Understory associations

3.2 Introduction

Disturbance is an integral process in forest ecosystems. Disturbance agents such as fire, insects and pathogens impact the forested landscape at different scales and interact with pre-disturbance stand conditions and environmental gradients to influence the re-arrangement and establishment of the post-disturbance forest community (White and Pickett 1985). The cumulative effects of multiple disturbances may cause a significant change in ecosystem trajectory and, in certain instances, may lead to irreversible regime shifts (Folke et al 2004). The loss of an important species, for instance, may have a large impact on the rest of the ecosystem (Ellison et al 2005).

Whitebark pine (*Pinus albicaulis*) was recently federally assessed as 'endangered' in Canada (COSEWIC 2010) due to threats from multiple disturbances (mountain pine beetle (MPB, *Dendroctonus ponderosae*), white pine blister rust (WPBR, *Cronartium ribicola*), and stress (fire suppression and climate change) (B.C. Conservation Data Centre 2010a, Alberta Sustainable Resource Development and Alberta Conservation Association 2007). *P. albicaulis* may be considered a keystone species due to its importance as a nurse tree, facilitating future community development (Callaway 1998) and importance as a food source for wildlife (Tomback 2007). *Pinus albicaulis* seeds are an important food source for many wildlife species including grizzly bears, and there is a recognized mutualistic relationship between *P. albicaulis* and Clark's nutcracker (*Nucifraga Columbia*), which is crucial for the dispersal of seed (Hutchins and Lanner 1982, Tomback 1982). Northwestern BC (NW BC), Canada houses the northern-most populations of *P. albicaulis* in the Coastal mountain range (Klinka et al 2000, Banner et al 1993).

Disturbance from MPB and WPBR in whitebark pine ecosystems reduces the abundance of *P. albicaulis* in the overstory and enables other tree species to recruit into the canopy (Keane et al 1994). These trees are often shade tolerant conifers (Keane et al 1994, Campbell and Antos 2003, Kipfmueller and Kupfer 2005), commonly *Abies lasiocarpa* and *Tsuga mertensiana* in whitebark pine ecosystems of NW BC (Meidinger and Pojar 1991, Banner et al 1993). Climate change and fire suppression may also increase the abundance of *Abies lasiocarpa* and *Tsuga mertensiana* within whitebark pine ecosystems. Climate change is expected to shrink suitable growing areas for *P. albicaulis* along an elevational gradient before the range expands northwards (Hamann and Wang 2006). Less frequent fires, either as a result of climate or human intervention, could change canopy composition in whitebark pine ecosystems through increased competition from shade tolerant conifers as well (Keane et al 1990, Keane et al 1994). Increasing prominence of these species can inhibit regeneration of the moderately shade-tolerant whitebark pine (Klinka et al 2000). There may also be reduced regeneration microsites for *P. albicaulis* under increasing canopy closure and Clark's Nutcrakers have a reduced probability of caching *P. albicaulis* seeds in denser stands (Tomback et al 1990).

P. albicaulis is able to persist on environmentally harsh sites (Keane et al 1990, Banner et al 1993) where other species cannot because of low nutrient availability, low moisture, high occurrence of frost, a late-melting snowpack, short growing season and high winds (Arno and Hoff 1989, Klinka et al 2000). Whitebark pine regenerates on these sites even in the absence of fire (Keane et al 1994) and shade tolerant conifers such as *A. lasiocarpa* and *T. mertensiana* may not succeed as well on these environmentally stressed sites (Klinka et al 2000, Maher et al 2005).

Cumulative disturbances may lead to a regime shift, where ecosystems switch from one state to another (Scheffer and Carpenter 2003). For example, the disturbances that alter vegetative composition in whitebark pine ecosystems, may result in areas that once sustained *P. albicaulis* no longer supporting this community type. Ecosystems may however, demonstrate variable responses to disturbance and stress, with some communities being more resilient to change than others (Holling 1973). Systems closer to a critical point of change could be pushed past a threshold by cumulative disturbance events, resulting in a significant ecosystem shift. Others, further from the tipping point may not reach this threshold (Holling 1973, Pascual and Guichard 2005, Andersen et al 2009). The loss of whitebark pine may not necessarily indicate a regime shift, however, as disturbances to this species may simply accelerate the 'natural' successional processes. However, on sites where whitebark pine is expected to persist through succession, a change in canopy composition away from *P. albicaulis* and towards other conifers would represent a significant shift in stand trajectory.

Understory plant communities are influenced by canopy composition through effects on light levels, soil water, soil nutrients, the physical presence of litter and potential phytotoxic chemicals associated with the presence of overstory trees (Barbier et al 2008). Altered canopy cover and composition due to the loss of whitebark pine may then also lead to significant alterations in understory plant communities.

Here, we evaluate the ecosystem trajectory of whitebark pine forests by testing whether the overstory and understory of two different whitebark pine ecosystems have homogenized with non-whitebark pine ecosystems over time. By comparing whitebark pine ecosystems to a reference system, we are able to assess the potential direction of change. We hypothesized that either: (1) the overstory and understory of both whitebark pine ecosystem types have compositionally homogenized with non-whitebark pine ecosystems over time; or (2) the driest whitebark pine ecosystems have not compositionally homogenized with non-whitebark pine ecosystems. In this case, the driest whitebark pine ecosystem may represent the condition furthest from the tipping point, and therefore the most resilient ecosystem.

3.3 Methods

3.3.1 Study Design

The study area was within the moist cool (mk) Engelmann Spruce-Subalpine fir (ESSF) zone in Northern British Columbia (Meidinger and Pojar 1991). This forested subzone occurs between 1000-1800m in elevation in a narrow band on the leeward side of the Coastal Mountains (Banner et al 1993). The ESSFmk has dry summers (average total precipitation 1000mm) and a high snowpack in the winter (>2m; Banner et al 1993, Coupé et al 1991 in Meidinger and Pojar 1991).

Three ecosystem types were surveyed for this study, described here by edaphic conditions and plant associations: '(02) Dry/poor – *Abies lasiocarpa*/*Pinus albicaulis* – *Cladonia*'; '(03) Moderately dry/poor – *A. lasiocarpa*/*Tsuga mertensiana* – *Cladonia*'; and '(01) Mesic/medium – *A. lasiocarpa*/*T. mertensiana* – *Streptopus*' (Banner et al 1993). These ecosystem names will be abbreviated to their edaphic conditions for brevity. *P. albicaulis* occurs only within 'Dry/poor' and 'Moderately dry/poor' ecosystems. The 'Mesic/medium' sites were used as a reference to help determine the direction of whitebark pine ecosystem change over time through comparison to a non-whitebark pine ecosystem.

Although these ecosystems are classified by a combination of environmental, climatic, soil and vegetation characteristics (Banner et al 1993, Meidinger and Pojar 1991), we focused solely on the change in vegetation as an indicator of overall ecosystem change. The 'Dry/poor' ecosystems are characterized during the old growth successional stage by abundant *Pinus albicaulis* and uncommon *Tsuga mertensiana* and *Abies lasiocarpa* in the overstory. The subcanopy tree layer in these systems is dominated by abundant *A. lasiocarpa* and common *T. mertensiana*, while the herb layer is sparse and the ground vegetation is characterized by abundant *Dicranum fuscescens*, less abundant, but still common *Cladina* spp., *Barbiliphozia* spp., *Pleurozium schreberi* and uncommon *Cladonia* spp. The 'Moderately dry/poor' ecosystem is characterized by abundant *P. albicaulis* and *A. lasiocarpa*, common *T. mertensiana* and uncommon *Abies amabilis* in the overstory during old growth. The subcanopy tree layer in these ecosystems is dominated by widespread *T. mertensiana*, abundant *A. lasiocarpa* and uncommon *A. amabilis*. The herb layer is also sparse and the forest floor in 'Moderately dry/poor' ecosystems is comprised of widespread *Dicranum fuscescens*, abundant *Cladina* spp., common *Barbiliphozia* spp. and uncommon *Cladonia* spp. and *Pleurozium schreberi* (Banner et al 1993).

For this study we re-surveyed 14 old growth plots in 2007/09 ('Present') that had been previously established by the BC Ministry of Forests from 1978-1988 ('Past'). S. Haeussler from the Bulkley Valley Research Centre surveyed two 'Dry/poor' and two 'Moderately dry/poor' sites in 2007, while A. Clason led surveys in 2009 in three 'Dry/poor', two 'Moderately dry/poor' and five 'Mesic/medium' sites. In order to re-locate each plot, we used a combination of plot descriptions, geographic coordinates, topographic maps, air photos and ground photos when available from the first survey period. However, not all plots could be precisely re-located. In the cases where the original plot markers could not be re-located, we surveyed as geographically close to the site as possible, where variables such as slope, aspect, slope position were the same as the original plot. Disturbance was not explicitly quantified at any site; however, in the second survey period we recorded cause of tree death when possible. Mountain pine beetle disturbance largely occurred during an outbreak in the 1980's in our study area except two 'Moderately dry/poor' and one 'Dry/poor' sites, which were disturbed during the more recent (~2005) attack (See Appendix 1 for detailed site descriptions). Whitepine blister rust was also present across the study area as seen in other studies (Zeglen 2002).

3.3.2 Survey Methods

In order to compare overstory and understory composition between the two survey periods, we followed the same methods used during the 1978-1988 survey period. Visual estimates of vegetation cover were made following Luttmerding et al (1990) and B.C. Ministry of Forests (1998). In order to determine the overall abundance of different species, surveyors walked a variable sized plot (~20 x 20m), recording each species encountered. Species found were given a percent cover within each height class in which it occurred (D = bryophytes/lichens, C = Forbs/dwarf shrubs, woody species: understory <2m, overstory >2m).

Two main datasets were used for analysis: understory species abundance (including height classes B2, C & D) and overstory species abundance (trees > 2m). Only live vegetation cover was included in analyses. Once separated into overstory and understory datasets, height classes were removed. We did analyses on overstory species by height class but we do not report all results from these analyses.

Species data were used when we were confident that identification would be similar for all observers; however, some species were grouped to genus to reduce error due to misidentification: (*Barbiliphozia* spp., *Brachythecium* spp., *Cladina* spp., *Cladonia* spp., *Dicranum* spp., *Peltigera* spp., *Racomitrium* spp., *Sorbus* spp.). In order to verify the consistency in estimating percent cover between observers over time we compared percent cover estimates for trees to mensuration data (stems/ha) and determined that trends between ecosystems and over time were the same. Soils were classified in the first survey period. In the second survey, due to time constraints, small soil pits were examined only to confirm soil moisture and nutrient regime. Site description data (slope, aspect, slope positions, elevation, soil moisture and nutrient regime, successional status, substrate cover) were recorded in both survey periods for all plots. Ground photos were taken at a subset of the plots during the 1978-88 surveys and every plot in the 2007/09 surveys.

3.3.3 Data Analysis

Multivariate Analyses

To compare community composition between ecosystem types and over time, we used ordination techniques including principal components analysis (PCA) and non-metric multi-dimensional scaling (NMDS). We then used multi-response permutation procedures (MRPP) to test for statistically significant differences between ecosystem types and over time. These analyses were applied separately to: 1) the overstory data set; 2) proportional overstory community (a dataset of proportional cover by species for overstory trees); and 3) the understory community datasets. We chose to analyse absolute overstory cover to determine the compositional similarity between ecosystems and between time periods. We also analysed the proportional cover of overstory species in order to remove the effect of changes in absolute canopy density while assessing changes in relative abundance of overstory trees between ecosystems and over time

All community datasets, except for proportional overstory cover, were log transformed prior to analysis in order to reduce the influence of highly abundant as well as rare species (McCune and Grace 2002). Proportional cover of overstory species was arcsine square-root transformed prior to analysis, a technique recommended for proportional data to compress middle values while spreading high and low values (Sokal and Rohlf 1995).

In order to determine if our datasets were appropriate for linear ordination methods (i.e PCA), we used detrended correspondence analysis (DCA) in PC-ORD (ver.5.0) (McCune and Mefford 2006) to determine the longest species gradient length. Species gradient lengths are a measure of the heterogeneity in community composition along the ordination axis (McCune and Grace 2002, Leps and Smilauer 2003). When a species gradient is long (values 4+), unimodal species responses are expected along that gradient (i.e. there is an optimum), however, when the gradient is short (values < 3), there is likely a linear species response (i.e. only an increase or a decrease along that gradient) (Leps and Smilauer 2003). We used PCA as a linear ordination method when the DCA species gradient length was < 3 and NMDS with a Bray-Curtis distance measure (McCune and Grace 2002) as a unimodal ordination technique when the gradient was close to 3 or a linear technique was inappropriate due to data structure (Leps and

Smilauer 2003). NMDS is a rank-based technique that has few assumptions about underlying community structure (Clarke 1993, McCune and Grace 2002). This technique has some disadvantages (see review in Kenkel 2006), so we only used NMDS when a linear method was not appropriate.

The absolute overstory and proportional overstory communities had short species gradient lengths (DCA gradient lengths: 1.8 and 1.9) so we used principal components analysis (PCA) in PC-ORD (v.5.0; McCune and Mefford 2006) to explore trends between ecosystem types and over time. The understory community dataset had a moderate species gradient length (DCA gradient length = 2.6), however linear ordination techniques were inappropriate due to outliers, which could not be corrected through transformations. Thus, we used NMDS in PC-ORD (ver.5.0) (McCune and Mefford 2006) to analyse the understory community dataset. The starting coordinates for NMDS analyses were generated from PCA scores, which produced a stable and repeatable solution (McCune and Grace 2002).

We then used the multi-response permutation procedure (MRPP) (McCune and Grace 2002) in PC-ORD (v.5.0; McCune and Mefford 2006) on all three datasets (overstory, proportional overstory and understory) to statistically test compositional similarity between ecosystems and over time. This is a nonparametric technique for comparison between predefined groups when you have a multivariate dataset. For our study, these groups were defined by ecosystem type*year combinations, resulting in six predefined groups (‘Mesic/medium’-Past, ‘Mesic/medium’-Present, ‘Moderately dry/poor’-Past, ‘Moderately dry/poor’-Present, ‘Dry/poor’-Past, ‘Dry/poor’-Present). MRPP allows for an un-balanced study design, uses ecologically significant distance measures and provides both an indication of between group differences (T statistic) and homogeneity within groups (A statistic) (McCune and Grace 2002). As ‘T’ decreases, dissimilarity increases and as ‘A’ increases, within group homogeneity increases (McCune and Grace 2002). When the overall MRPP was significant ($P < 0.05$) we followed up with nine pairwise comparisons between particular ecosystem*year combinations: past *vs* present for each ecosystem type (3 comparisons), pairwise between ecosystem types in the past (3) and the present (3)). For these, we used a Benjamini-Hochberg α correction (Benjamini and Hochberg 1995, Waite and Campbell 2006). The Benjamini-Hochberg procedure maintains power and reduces the likelihood of a Type II error, while minimizing Type I error, compared to more traditional corrections such as the sequential Bonferroni. This method is especially suitable for small, variable ecological datasets (Waite and Campbell 2006). The alpha value is calculated sequentially as ip/m, where i is the ith comparison, multiplied by the starting alpha (p), divided by the total number of comparisons (m). In this way the first alpha value and the last remain the same as for a sequential Bonferroni correction, however, the intermediate alpha values are relaxed (Benjamini and Hochberg 1995; Waite and Campbell 2006).

Univariate Analyses

We used univariate mixed model analyses to compare the abundance (i.e., cover) of different species and groups of species between ecosystem types and over time. Our primary objective for univariate analyses was to quantify more specifically how the different tree species varied in abundance between ecosystems and over time and to assess the potential for forest change in the future. We also wanted to examine how the abundance of different species groups (e.g., lifeforms) have changed over time in the different ecosystem types. We did this through a comparison of the absolute and relative (proportional) cover of each tree species in the canopy and relative cover of each tree species in the understory (< 2m) between ecosystems and between survey periods. Lastly, we compared abundances of 11 selected understory species between ecosystems and over time using univariate analysis. These species were selected because they were highly correlated with at least of one the axes in the NMDS ordination ($\tau > 0.5$).

Our mixed model analysis of variance used the following statistical model:

$$Y_{ij} = \mu + T_i + S_j + TS_{ij} + P_k(T_i) + E$$

Where:

Y_{ij} = response; T_i = Ecosystem type ('Dry/poor'; 'Moderately dry/poor'; 'Mesic/medium') (Fixed effect); S_j = Survey Period (Past; Present) (Fixed effect); TS_{ij} = Ecosystem type*Survey period interaction; $P_k(T_i)$ = Plot(nested within Ecosystem type) (Random effect).

We used 'plot' as a blocking factor in this analysis as opposed to using a strict 'repeated measures' design. All variables were tested for normality and homogeneity of variance prior to analyses (Steel and Torrie 1997); the above mixed model was used for those that met the assumptions of normality. For those variables that could not be transformed to meet the assumptions of a parametric ANOVA we used the Scheirer-Ray-Hare Extension of Kruskal-Wallis (Sokal and Rohlf 1995) for non-parametric analyses. The SRH-extension of Kruskal-Wallis test uses rank-transformed data and critical values are compared to a Chi-square statistic (Sokal and Rohlf 1995). In both cases, Type III sums of squares (SS) were used due to unequal replication. Following a significant main effect, pairwise comparisons among levels were made using least square means comparisons for parametric ANOVA, while for non-parametric analyses we used Kruskal-Wallis comparisons. As we tested multiple species or groups within each dataset, we used a Benjamini-Hochberg α correction for multiple comparisons for the main effects in the ANOVA and for post-hoc comparisons (Benjamini and Hochberg 1995; Waite and Campbell 2006). All these analyses were conducted using SAS v 9.2 (SAS Institute 2007).

3.4. Results

3.4.1 Overstory change

The changes in absolute (Figure 3-1) and proportional cover (Figure 3-2) of overstory trees over time showed variability within and between the three different ecosystem types. Three of four 'Moderately dry/poor' sites shifted towards increased prominence of *T. mertensiana* in the second survey period, while the fourth shifted towards more *A. lasiocarpa* (Figure 3-1 & 3-2). Three of the 'Dry/poor' sites shifted towards more *T. mertensiana* in the second survey period (Figure 1) and this was more evident in the change in proportional cover (Figure 3-2). The other two shifted slightly towards *A. lasiocarpa* (Figure 3-1 & 3-2). The 'Mesic/medium' sites changed little over time (Figure 3-1 & 3-2).

MRPP verified these trends for change in absolute overstory cover over time and differences among the ecosystem types. There was a significant difference among our six pre-defined groups (ecosystem*survey period combinations) based on the MRPP (T = -

2.06, $A = 0.16$, $P = 0.03$). Pairwise comparisons indicated that overstory composition of the ‘Dry/poor’ whitebark pine ecosystem was significantly different from the reference ‘Mesic/medium’ ecosystem in the first survey period, but not in the second survey period (Past: $T = -4.24$, $A = 0.26$, $P = 0.002$; Present: $T = -2.06$, $A = 0.11$, $P = 0.05$). In contrast, the ‘Moderately dry/poor’ whitebark pine ecosystem was not significantly different from the ‘Mesic/medium’ ecosystem in the first survey period, but these two ecosystems were approaching a significant difference in the second survey period (Past: $T = -0.71$, $A = 0.04$, $P = 0.19$; Present: $T = -1.88$, $A = 0.16$, $P = 0.06$). The ‘Moderately dry/poor’ and ‘Dry/poor’ ecosystems were not significantly different in either survey period; however, these ecosystems were more different from one another in the first survey period (Past: $T = -1.38$, $A = 0.11$, $P = 0.09$; Present: $T = -0.58$, $A = 0.04$, $P = 0.22$). MRPP results for proportional overstory change followed the same trend, so we do not present results here.

There were significant differences among ecosystem types in terms of absolute overstory cover for each tree species but no significant differences over time and no ecosystem type * survey period interactions (Table 3-2). Overstory cover in the ‘Mesic/medium’ ecosystem type was dominated by *Abies lasiocarpa* followed by *Abies amabilis* and then *Tsuga mertensiana*; there was almost no pine in this ecosystem type (Table 3-3). In the ‘Moderately dry/Poor’ ecosystem, overstory cover was dominated by *T. mertensiana*, with *A. lasiocarpa*, *A. amabilis* and *Pinus albicaulis* as minor components. The ‘Dry/poor’ ecosystem was dominated in the overstory by *P. albicaulis*, *T. mertensiana* and *A. lasiocarpa*, with *Pinus contorta* as a minor canopy component. Total overstory cover was lowest in the ‘Dry/poor’ ecosystem and highest in ‘Moderately dry/poor’ ecosystems (Table 3-3).

For proportional overstory cover there was a significant difference among ecosystem types for *Pinus albicaulis* and a significant effect of survey period for *Tsuga mertensiana* (Table 3-2). The proportional cover of *P. albicaulis* was greater in both the 'Dry/poor' and 'Moderately dry/poor' ecosystems compared to 'Mesic/medium' (Table 3-3). The proportional cover of *Tsuga mertensiana* was greater in the second compared to the first survey (Table 3-2 & 3-3). There were no other significant differences in proportional overstory cover. While not significant, there was a trend of decreasing absolute and proportional overstory cover of *P. albicaulis* over time in both the 'Moderately dry/poor' and 'Dry/poor' ecosystems (Table 3-3).

3.4.2 Understory change

A three-axis NMDS produced the lowest stress solution for understory composition change over time between ecosystems (Final stress = 7.18, Instability = 0.00001 with 55 iterations; Figure 3-3a & 3-3b). Axis 1 separated plots along a moisture gradient from the right (moist) to the left (dry). We did not see a shift in understory communities over time along this moisture gradient, nor did understory communities in different ecosystems become more similar over time. MRPP results support our findings from this unconstrained ordination; there were no significant differences in understory composition between the two time periods for any of the three ecosystem types (Table 3-1). In terms of understory composition, the 'Dry/poor' and 'Moderately dry/poor' ecosystems were both significantly different from the 'Mesic/medium' ecosystem in both survey periods (Table 3-1). However, these two whitebark pine ecosystem types were not significantly different from one another in either time period (Table 3-1).

The results (NMDS, MRPP) suggested that the 'Dry/poor' and 'Mesic/medium' understory communities became more different over time (in MRPP the *T* value decreased and *A* value increased). In contrast, some 'Moderately dry/poor' sites became more similar to the 'Dry/poor' ecosystem over time, while others became more similar to the 'Mesic/medium' ecosystem in the second survey period (Figure 3-3a & 3-3b). This may indicate greater between site variability in understory communities of the 'Moderately dry/poor' ecosystem in the second survey period (Table 3-1).

For the 11 understory species that were strongly correlated with at least one NMDS axis (Table 3-4) there were no significant changes over time in any of the ecosystem types (Table 3-2). However, differences in cover of understory species between ecosystem types indicated that the 'Mesic/medium' and 'Dry/poor' ecosystem types had several distinguishing understory vegetation features compared to the 'Moderately dry/poor' ecosystem. The 'Mesic/medium' ecosystem had the greatest cover of *Vaccinium ovalifolium*, *Streptopus lanceolatus*, *Rubus pedatus* and *Viola lansdorfii*. The 'Dry/poor' ecosystem had the greatest cover of *Cassiope mertensiana*, *Cladina* spp., *Cladonia* spp., understory *Pinus albicaulis* and *Racomitrium* spp., while the 'Moderately dry/poor' ecosystem had the greatest cover of understory *Tsuga mertensiana* (Table 3-3). There was also no significant change over time for any lifeforms, but several were different between ecosystem types (Table 3-2 & 3-3). The 'Dry/poor' ecosystem had the greatest cover of dwarf shrubs and lichens, while the 'Mesic/medium' ecosystem had the greatest cover of herbs. The 'Dry/poor' and 'Mesic/medium' ecosystems also had a significantly greater cover of ferns and fern allies compared to the 'Moderately dry/poor' ecosystem, which had none.

There was a significant difference between ecosystem types for the proportional understory tree cover (i.e., subcanopy trees < 2 m in height) of *Pinus albicaulis* (Table 3-2). The proportion of regenerating *P. albicaulis* was greater in 'Dry/poor' ecosystems than in either the 'Moderately dry/poor' or 'Mesic/medium' types (Table 3-3).

3.5. Discussion

Based on overstory composition, our results support the hypothesis that homogenization of whitebark pine and non-whitebark pine ecosystems has occurred over the time period from the 1970/80s to the present. However, in contrast to our second hypothesis, it was the 'Dry/poor' whitebark pine ecosystem, not the 'Moderately dry/poor' that became more compositionally similar to the 'Mesic/medium' ecosystem type. Understory communities did not follow the same trends as the overstory. Both whitebark pine ecosystems maintained fairly similar understory communities over time regardless of overstory change. The persistence of the understory community may eventually return the 'Dry/poor' ecosystem its original state through ongoing regeneration of whitebark pine and its associated community. However, as the overstory continues to change due to ongoing disturbance, understory communities may eventually change due to overstory effects on understory composition across both whitebark pine ecosystem types.

3.5.1 Overstory change

Decreased cover of *Pinus albicaulis* and increased cover of either *Tsuga mertensiana* or *Abies lasiocarpa* drove overstory compositional homogenization between the 'Dry/poor' and 'Mesic/medium' ecosystem types. This was apparent in our multivariate analyses, which showed changes in composition over time shifting 'Dry/poor' sites towards increased cover of these shade tolerant conifers, while changes over time in absolute and proportional cover of overstory trees were largely not significant. The lack of significant overall changes for individual species is attributable to the fact that *Abies lasiocarpa* increased on some 'Dry/poor' sites while *Tsuga mertensiana* increased on others. This variation in overstory change is likely a result of site conditions in the 'Dry/poor' ecosystem. Sites on exposed rocky outcrops/south-facing slopes shifted towards *A. lasiocarpa* while those on a north-facing upper slope or glacio-fluvial fans shifted towards *T. mertensiana*. This distinction between site types is partially recognized in the classification system as two different phases within the 'Dry/poor' ecosystem type. However, the north-facing upper slope site would have been classified with the rocky outcrops as the 'Lithic' phase, and the glacio-fluvial fans as the 'Fluvial' phase (Banner et al 1993). Our results suggest that forest change on the most exposed sites may follow a different trajectory than in the less stressful environments.

The overstory in the 'Moderately dry/poor' ecosystem type did not become more similar to the 'Mesic/medium' ecosystem over time. The loss of whitebark pine in this ecosystem resulted in a trend towards increased overstory *Tsuga mertensiana* over time. The 'Moderately dry/poor' ecosystem is expected to have a greater abundance of *T. mertensiana* compared to either the 'Mesic/medium' or 'Dry/poor' ecosystems (Banner et al 1993), and we see this even in the first survey period. Further increases in cover of *T. mertensiana* by the second survey period may therefore be what underlies the greater dissimilarity between 'Moderately dry/poor' and 'Mesic/medium' ecosystems. *Tsuga mertensiana* could have out competed the less shade tolerant *A. lasiocarpa* over time

(Alexander et al 1990, Klinka et al 2000). The trend towards *T. mertensiana* was not uniform across all four 'Moderately dry/poor' ecosystems, however, with one site trending towards *Abies lasiocarpa* over time. This site had the highest proportional abundance of *Pinus albicaulis* (76.6%) and the least proportional abundance of *Tsuga mertensiana* (2.1%) of all 'Moderately dry/poor' ecosystems in the first survey period. In contrast to the 'Dry/Poor' type, the influence of site characteristics on overstory change patterns were not as clear in the 'Moderately dry/poor' ecosystem where two upper slope, more exposed sites followed the same temporal change trends as two flat, lower slope sites.

The success of *Abies lasiocarpa* and *Tsuga mertensiana* on different sites may be related to life history adaptations. *Abies lasiocarpa* is more tolerant of water deficits and frost damage compared to *T. mertensiana* (Klinka et al 2000). On very dry sites, high summer temperatures and lack of growing season soil moisture limit *A. lasiocarpa* growth, while a deeper winter snowpack results in elevated summer soil moisture supporting increased growth (Peterson et al 2002). These very dry sites are likely to experience drought, which does not affect mature *A. lasiocarpa* trees, but may reduce seedling establishment and survival (Peterson et al 2002). For *T. mertensiana* on the other hand, a deep spring snowpack and low summer temperatures shorten the growing season and limit its growth across most of its range in the northern coastal mountains of the USA (Peterson and Peterson 2001). On slightly wetter sites, a deep snowpack and low summer temperatures will also limit *A. lasiocarpa* growth due to the shortened growing season (Peterson et al 2002).

Our results support these concepts about climatic adaptation of these species. The overstory on our driest (rocky/south-facing) 'Dry/poor' sites is shifting towards *A. lasiocarpa* with the decline of *Pinus albicaulis*. These sites would have faster snowmelt and greater likelihood of summer drought compared to less exposed (glacio-fluvial/north-facing) 'Dry/poor' or 'Moderately dry/poor' sites. *T. mertensiana* and *A. lasiocarpa* would be equally affected by a shortened growing season on glacio-fluvial/north-facing 'Dry/poor' sites and on 'Moderately dry/poor' sites, and there *T. mertensiana* may out compete *A. lasiocarpa* over time as it is more shade tolerant (Alexander et al 1990).

As we have seen in our study, subalpine ecosystems may follow different successional trajectories across the landscape (Donnegan and Rebertus 1999). Whitebark pine ecosystems, in particular, have been shown to follow complex successional pathways depending on site conditions or stand composition immediately following large-scale disturbance (Campbell and Antos 2003, Kipfmueller and Kupfer 2005). Differences in overstory community change over time between 'Dry/poor' and 'Moderately dry/poor' ecosystems could be a result of differences in successional development due to differences in site productivity (Donnegan and Rebertus 1999).

Our results also show that *Pinus albicaulis* has continued to regenerate in the absence of fire in the open stand condition of the 'Dry/poor' ecosystem, as seen in other harsh environments (Keane et al 1990). This species may establish on sites that are inhospitable to other species given the tolerance of *P. albicaulis* to high winds, frost and a short growing season (Klinka et al 2000). The greater abundance of whitebark pine on environmentally stressed 'Dry/poor' sites compared to 'Moderately dry/poor' may then be due to less competition from other species on the harsher sites or to availability of suitable regeneration microsites in open stands for the moderately shade-tolerant *P. albicaulis* (Klinka et al 2000). White pine blister rust was present on many *P. albicaulis* seedlings and saplings in this study, however, indicating that disturbance to this species is ongoing and will continue to affect the direction of change in these ecosystems in the future.

In our study area, mortality to *P. albicaulis* was likely due to mountain pine beetle and white pine blister rust. We did not attempt to distinguish the impact of a particular disturbance agent or event on overstory and understory communities, but rather looked at the trajectory of the system as a whole under past and ongoing disturbances. We did not conduct detailed stand reconstruction, so we could not evaluate the role of other disturbance agents, such as drought, in influencing tree mortality across the different ecosystem types. Drought may be an important factor influencing mortality and succession in subalpine ecosystems (Donnegan and Rebertus 1999). The main disturbances affecting the overstory in our study system were targeted at *Pinus albicaulis*; however, balsam bark beetle (*Dryocoetes confusus*) was also present in the study area.

3.5.2 Understory change

Understory communities in 'Dry/poor' and 'Moderately dry/poor' ecosystems did not become more compositionally similar to 'Mesic/medium' ecosystems over time. Rather, there were differences between ecosystem types that were maintained over time. 'Dry/poor' sites had greater ground lichen cover than both 'Moderately dry/poor' and 'Mesic/medium' ecosystems in both survey periods. This high abundance of terrestrial lichens may be related to poor nutrient conditions (Beaudry et al 1999) or reduced competition from mosses that cannot tolerate desiccation in open stand conditions

(Williston and Cichowski 2006, Fenton and Frego 2005). Bryophytes, liverworts in particular, are sensitive to water stress (Fenton and Frego 2005) that may be common in the summer in low canopy density whitebark pine ecosystems. Lichen communities that dominate ‘Dry/poor’ ecosystems may also have allelopathic effects that inhibit seed germination (Sedia and Ehrenfeld 2003) for many vascular plants, including trees. However, other studies have found that there is no allelopathic effect of lichens such as *Cladonia* on seedling growth (Kytöviita and Stark 2009). Another unique characteristic of the ‘Dry/poor’ compared to ‘Moderately dry/poor’ and ‘Mesic/medium’ ecosystems was the greater total dwarf shrub cover, including *Cassiope mertensiana* and *Phyllodoce empetriformis*. Both these species are often found in the open on nitrogen poor sites with deep snowpacks (Beaudry et al 1999). Herbs were virtually absent from both whitebark pine ecosystems compared to ‘Mesic/medium’ ecosystems, which may be related to poor nutrient and moisture conditions in whitebark pine stands (Banner et al 1993).

3.5.3 Overstory-understory relationships

Our results suggest that overstory and understory communities may not always be strongly correlated across a range of environmental conditions and disturbance regimes. Even in old stands, the composition of the overstory may be more related to time since disturbance while understory composition is related to variation in soil moisture and nutrient conditions (Campbell 1998, Chipman and Johnson 2002, Del Moral and Watson 1978). Understory community response to overstory change may also be slow, particularly in subalpine ecosystems. For instance, the understory may not respond to the short term pulse in above and below-ground resources following death of a canopy tree, but the increased litter input over time from dead overstory trees may alter understory composition (Laughlin and Abella 2007). Terrestrial lichen communities in particular, such as those common in our 'Dry/poor' sites, may not respond quickly to the death of an overstory tree (Williston and Cichowski 2006), but increased litterfall from these dead trees may reduce ground lichen abundance over time (Coxson and Marsh 2001). The understory in the whitebark pine ecosystems here may then still change in the future with ongoing canopy disturbance.

3.5.4 Ecosystem Resilience

Our study suggests that only a subset of ecosystems housing *Pinus albicaulis* in Northwestern BC may continue to house this threatened tree species in the future. The overstory in the 'Moderately dry/poor' ecosystem was not significantly different from the 'Mesic/medium' ecosystem in the first survey period, and although the overstory communities of these two ecosystem types became less similar over time, this was due to the increased dominance of *Tsuga mertensiana* in the 'Moderately dry/poor' ecosystem. We had hypothesized that the 'Moderately dry/poor' ecosystem would be vulnerable to change (become compositionally similar to the 'Mesic/medium' ecosystem over time), so the lack of statistically significant overstory and understory change, may suggest that the 'Moderately dry/poor' ecosystem was more resilient than expected. However, the direction of overstory change towards *T. mertensiana*, the lower cover of canopy and regenerating *P. albicaulis* and greater cover of total overstory in the 'Moderately dry/poor' compared to the 'Dry/poor' ecosystem, and the low probability of Clark's nutcrackers caching *P. albicaulis* seeds in these dense stands (Tomback et al 1990), leads us to conclude that the ‘Moderately dry/poor’ ecosystem is likely the least resilient whitebark pine ecosystem.

In contrast to our hypotheses we would conclude that the overstory in the ‘Dry/poor’ ecosystem becoming increasingly similar to the ‘Mesic/medium’ ecosystem over time indicates greater vulnerability. However, as the understory in the ‘Dry/poor’ ecosystem did not change and *P. albicaulis* seedlings are a significant characteristic of the understory, the ‘Dry/poor’ ecosystem may be more resilient than the ‘Moderately dry/poor’ ecosystem; i.e., it is able to sustain the whitebark pine community in the future. Our results also suggest however, that particularly on glacio-fluvial fans, the significant change in the overstory and the ongoing disturbance of WPBR affecting *P. albicaulis* regeneration, ‘Dry/poor’ ecosystems may still require active restoration. This would reduce the abundance of *A. lasiocarpa* and *T. mertensiana* and increase the abundance of rust-resistant *P. albicaulis* in the canopy for successful whitebark pine conservation in the ‘Dry/poor’ ecosystem.

3.6 Conclusion

The decline of whitebark pine in the overstory of the whitebark pine ecosystem types we studied has resulted in homogenization of overstory communities in NW BC. Canopy change was not consistent across our study area, stands in these subalpine whitebark pine ecosystems changed in different directions depending on ecosystem type and site conditions. While there is evidence that the 'Dry/poor' ecosystem is resilient to change, as indicated by the persistence of a distinct understory community and continued regeneration of *Pinus albicaulis*, further change in the overstory may yet result in altered understory communities and a significant change in overall ecosystem trajectory. The 'Moderately dry/poor' ecosystem type may exhibit more rapid change due to the lack of whitebark pine regeneration, further changing canopy composition. Ongoing disturbances targeting *P. albicaulis* coupled with increasing dominance of shade tolerant conifers, will continue to threaten whitebark pine in the future. Restoration, such as planting rust-resistant *Pinus albicaulis* seedlings, even in sites that may be more resilient (the 'Dry/poor' ecosystem), is a necessary action to ensure the survival of this important subalpine tree species and its associated community.

3.7 Tables

Table 3-1 - Results of Multi-Response Permutation Procedure (MRPP) tests examining pairwise comparisons between ecosystem types and survey periods for overstory and understory composition. 'T' describes the difference between groups (the more negative T, the greater the difference) and 'A' describes the within group agreement (the greater A, the greater the homogeneity within groups). * indicates significant P values (after Benjamini-Hochberg correction for multiple comparisons).

		Overstory			*Understory*		
		T	*A*	*P*	*T*	*A*	*P*
Mesic/medium	Mod dry/poor - PAST	-0.71	0.04	0.19	-3.66	0.15	0.004*
Mesic/medium	Mod dry/poor - PRESENT	-1.88	0.16	0.06	-3.25	0.15	0.009*
Mesic/medium	Dry/poor - PAST	-4.24	0.26	0.002*	-4.61	0.15	0.001*
Mesic/medium	Dry/poor - PRESENT	-2.06	0.11	0.04	-4.83	0.21	0.001*
Mod dry/poor	Dry/poor - PAST	-1.38	0.11	0.09	-1.93	0.07	0.04
Mod dry/poor	Dry/poor - PRESENT	-0.58	0.04	0.22	-1.86	0.09	0.05
Mesic/medium - PAST	Mesic/medium - PRESENT	0.51	-0.04	0.61	0.49	-0.07	0.64
Mod dry/poor - PAST	Mod dry/poor - PRESENT	0.62	-0.05	0.71	0.96	-0.05	0.83
Dry/poor - PAST	Dry/poor - PRESENT	-0.78	0.05	0.19	0.47	-0.02	0.63

Table 3-2 - Results of parametric (F values given) and non-parametric (H values given) analyses of variance testing for the effects of ecosystem type, survey time period and their interaction. Tests were conducted for: overstory cover by species, proportional overstory cover by species, cover by lifeform; cover for selected understory species, and proportional cover by species for understory trees. Individual understory species reported were those highly correlated with each axis in understory NMDS. * indicates a significant P value. † indicates a non-parametric test. All tests were α corrected (Benjamini-Hochberg) except for individual understory species.

	Ecosystem		**Survey Period**		**Ecosystem*Survey Period**	
	F/H	*P*	*F/H*	*P*	*F/H*	*P*
Absolute Overstory Cover						
Abies amabilis†	6.21	0.04*	0.44	0.37	0.01	1.00
Abies lasiocarpa†	11.08	<0.01*	1.80	0.18	2.02	0.36
Pinus albicaulis†	15.31	<0.001*	3.00	0.08	0.70	0.70
Pinus contorta†	8.04	0.02*	0.00	0.94	0.01	0.99
Tsuga mertensiana†	7.53	0.02*	0.26	0.61	0.13	0.94
Proportional Overstory Cover						
Abies amabilis†	6.21	0.04	0.75	0.39	0.07	0.97
Abies lasiocarpa	3.03	0.09	0.01	0.94	1.22	0.33
Pinus albicaulis†	16.54	<0.001*	2.22	0.14	0.45	0.80
Pinus contorta†	8.04	0.02	0.00	1.00	0.00	1.00
Tsuga mertensiana	1.50	0.27	23.15	<0.001*	5.69	0.02
Totals by Lifeform						
Overstory trees	4.91	0.03	3.20	0.10	0.52	0.61
Understory trees	1.24	0.33	5.06	0.05	0.04	0.96
Shrubs	0.76	0.49	0.07	0.79	0.22	0.81
Dwarf shrubs†	12.52	<0.01*	0.13	0.72	0.11	0.95
Ferns & allies†	8.92	0.01*	<0.01	0.96	0.02	0.99
Graminoid†	4.21	0.12	1.03	0.31	1.45	0.48
Herbs	18.45	<0.001*	0.27	0.61	0.78	0.48
Lichen	5.69	0.02*	0.41	0.53	4.96	0.03
Liverworts	1.47	0.27	0.94	0.35	2.12	0.17

Mosses	0.99	0.40	6.26	0.03	1.39	0.29
Select Understory Species						
Cassiope mertensiana	10.57	<0.01*	0.28	0.59	0.27	0.88
Cladina spp.[†]	14.75	<0.001*	0.57	0.45	0.55	0.76
Cladonia spp.[†]	16.67	<0.001*	0.36	0.55	0.72	0.70
Paxistima myrsinites[†]	5.93	0.05	<0.001	0.98	<0.01	0.10
Pinus albicaulis[†]	19.79	<0.0001*	0.03	0.87	0.44	0.80
Racomitrium spp.[†]	13.01	<0.01*	<0.001	0.98	<0.01	0.10
Rubus pedatus[†]	18.77	<0.0001*	0.18	0.67	0.38	0.83
Streptopus lanceolatus[†]	20.16	<0.0001*	0.24	0.63	0.14	0.93
Tsuga mertensiana[†]	3.99	0.14	0.55	0.46	0.95	0.62
Vaccinium ovalifolium[†]	11.42	<0.01*	<0.01	0.95	0.10	0.95
Viola langsdorfii[†]	8.29	0.02	2.58	0.11	1.89	0.39
Proportional Understory Tree Cover						
Abies amabilis[†]	7.18	0.03	0.28	0.59	0.21	0.90
Abies lasiocarpa	0.72	0.51	0.79	0.39	0.55	0.59
Pinus albicaulis[†]	19.91	<0.0001*	0.03	0.86	0.67	0.72
Pinus contorta[†]	8.04	0.02	0.02	0.89	0.04	0.98
Tsuga heterophylla[†]	1.81	0.40	0.87	0.35	1.81	0.40
Tsuga mertensiana[†]	6.10	0.05	0.05	0.82	0.74	0.69

Table 3-3 - Mean % cover (+/- Standard Error) for the three ecosystem types surveyed in the two time periods (past = 1978-1988; present = 2007 or 2009) for: overstory cover by species, proportional overstory cover by species, cover by lifeform, cover for selected understory species (<2m in height), and proportional cover by species for understory trees. Individual understory species reported were those highly correlated with the axes of the NMDS ordination of the understory data. Letters indicate significant differences between ecosystems (†) and survey periods (‡) after Benjamini-Hochberg correction for multiple comparisons (starting α = 0.05/# of comparisons), with † and ‡ indicating whether the letters beside the means represent differences in ecosystems or differences between survey periods for that species or lifeform.

	(01) - Mesic/Medium		**(03) - Moderately dry/Poor**		**(02) - Dry/Poor**	
	Past	***Present***	***Past***	***Present***	***Past***	***Present***
	Mean % ± SE	*Mean % ± SE*	*Mean % ± SE*	*Mean % ± SE*	*Mean % ± SE*	*Mean % ± SE*
Absolute Overstory Cover						
Abies amabilis†	18.40 ± 12.35	8.40 ± 4.74^{a}	9.00 ± 5.21	14.25 ± 8.23^{ab}	0.00 ± 0.00	0.20 ± 0.20^{b}
Abies lasiocarpa†	45.4 ± 8.75	33.62 ± 6.41^{a}	29.75 ± 7.60	11.25 ± 4.89^{ab}	11.80 ± 2.18	13.40 ± 4.39^{b}
Pinus albicaulis†	1.00 ± 1.00	0.00 ± 0.00^{a}	14.38 ± 7.83	5.50 ± 3.33^{b}	18.40 ± 2.50	4.60 ± 2.04^{b}
Pinus contorta†	0.00 ± 0.00	0.00 ± 0.00^{a}	0.00 ± 0.00	0.00 ± 0.00^{ab}	4.00 ± 3.10	5.60 ± 3.66^{b}
Tsuga mertensiana†	12.40 ± 7.37	9.00 ± 6.84^{a}	34.75 ± 13.46	44.00 ± 14.75^{b}	11.00 ± 8.82	14.40 ± 6.77^{a}
Proportional Overstory Cover						
Abies amabilis	16.99 ± 10.60	15.96 ± 7.43	9.19 ± 5.30	16.59 ± 9.66	0.00 ± 0.00	0.50 ± 0.50
Abies lasiocarpa	68.60 ± 17.25	70.50 ± 14.17	32.70 ± 6.44	19.69 ± 12.10	32.42 ± 9.37	42.26 ± 16.99
Pinus albicaulis†	1.30 ± 1.30	0.00 ± 0.00^{a}	24.19 ± 17.69	10.48 ± 7.72^{b}	42.99 ± 4.87	13.83 ± 5.91^{b}

Pinus contorta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	7.56 ± 5.64	11.25 ± 6.89
Tsuga mertensiana‡	13.11 ± 8.12^{a}	13.54 ± 7.57^{b}	33.92 ± 12.13^{a}	53.24 ± 16.52^{b}	17.03 ± 12.64^{a}	32.16 ± 15.52^{b}
Total cover by Lifeform						
Overstory trees	77.60 ± 14.65	52.02 ± 11.05	87.88 ± 14.07	75.00 ± 10.40	45.20 ± 7.93	39.20 ± 8.45
Understory trees	14.52 ± 5.38	8.58 ± 1.55	24.13 ± 7.86	17.50 ± 5.19	20.24 ± 4.21	15.34 ± 3.74
Shrubs	38.80 ± 10.67	39.37 ± 9.85	31.28 ± 6.78	32.55 ± 7.94	28.54 ± 11.19	22.81 ± 3.60
Dwarf shrubs†	0.02 ± 0.02	0.00 ± 0.00^{a}	0.50 ± 0.50	0.75 ± 0.75^{a}	8.90 ± 4.43	4.63 ± 2.38^{b}
Ferns & Allies†	0.86 ± 0.57	1.24 ± 0.96^{a}	0.00 ± 0.00	0.00 ± 0.00^{b}	0.10 ± 0.10	0.02 ± 0.02^{a}
Graminoids	0.58 ± 0.36	0.06 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.30 ± 0.30	0.00 ± 0.00
Herbs†	16.70 ± 3.35	17.77 ± 4.10^{a}	1.20 ± 1.04	0.32 ± 0.24^{b}	1.74 ± 0.78	0.05 ± 0.03^{b}
Lichens†	0.72 ± 0.20	0.10 ± 0.04^{a}	18.68 ± 8.26	12.75 ± 7.01^{a}	25.52 ± 8.26	36.32 ± 10.24^{b}
Liverworts	8.80 ± 3.15	1.40 ± 0.68	16.18 ± 4.08	15.15 ± 2.04	11.36 ± 7.43	13.80 ± 6.31
Mosses	32.34 ± 4.06	19.87 ± 2.79	35.60 ± 4.94	35.02 ± 7.36	34.80 ± 9.23	18.02 ± 5.81
Select Understory Species						
Cassiope mertensiana†	0.00 ± 0.00	0.00 ± 0.00^{a}	0.25 ± 0.25	0.00 ± 0.00^{a}	6.00 ± 3.52	3.42 ± 2.35^{b}
Cladina spp.†	0.00 ± 0.00	0.00 ± 0.00^{a}	10.03 ± 8.41	6.75 ± 5.11^{b}	13.60 ± 7.37	17.00 ± 7.09^{b}
Cladonia spp.†	0.58 ± 0.22	0.08 ± 0.05^{a}	8.45 ± 0.54	6.00 ± 2.49^{b}	11.18 ± 3.67	19.32 ± 8.20^{b}
Paxistima myrsinites	0.52 ± 0.38	0.64 ± 0.59	0.00 ± 0.00	0.00 ± 0.00	0.80 ± 0.49	0.80 ± 0.49
Pinus albicaulis†	0.00 ± 0.00	0.00 ± 0.00^{a}	0.38 ± 0.13	0.50 ± 0.50^{b}	2.14 ± 0.72	2.80 ± 0.92^{c}
Racomitrium spp.†	0.00 ± 0.00	0.00 ± 0.00^{a}	0.00 ± 0.00	0.00 ± 0.00^{a}	7.20 ± 5.77	3.62 ± 2.22^{b}
Rubus pedatus†	3.10 ± 1.12	5.40 ± 2.77^{a}	0.00 ± 0.00	0.00 ± 0.00^{b}	0.00 ± 0.00	0.00 ± 0.00^{b}
Streptopus lanceolatus†	2.70 ± 1.16	2.82 ± 1.01^{a}	0.13 ± 0.13	0.00 ± 0.00^{b}	0.00 ± 0.00	0.00 ± 0.00^{b}
Tsuga mertensiana	5.28 ± 3.85	1.70 ± 1.14	15.50 ± 5.25	7.00 ± 3.39	6.70 ± 5.98	5.70 ± 4.84
Vaccinium	6.60 ± 2.98	2.84 ± 1.58^{a}	0.88 ± 0.72	1.50 ± 1.19^{ab}	0.10 ± 0.10	0.02 ± 0.02^{b}

ovalifolium†						
Viola langsdorfii†	0.32 ± 0.18	0.14 ± 0.09^{a}	0.00 ± 0.00	0.00 ± 0.00^{b}	0.20 ± 0.09	0.00 ± 0.00^{ab}
Proportional Understory Tree Cover						
Abies amabilis	23.00 ± 12.26	28.45 ± 13.63	8.41 ± 5.12	20.00 ± 11.55	0.59 ± 0.59	0.08 ± 0.08
Abies lasiocarpa	54.42 ± 19.00	55.62 ± 21.17	30.43 ± 12.40	27.05 ± 20.92	60.32 ± 16.19	49.90 ± 12.83
Pinus albicaulis†	0.00 ± 0.00	0.00 ± 0.00^{a}	3.46 ± 2.57^{b}	2.94 ± 2.94^{b}	11.40 ± 3.41^{c}	22.21 ± 7.96^{c}
Pinus contorta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	6.00 ± 4.06	1.80 ± 1.77
Tsuga heterophylla	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.95 ± 0.95	0.00 ± 0.00
Tsuga mertensiana	22.58 ± 10.23	15.93 ± 8.47	57.70 ± 13.55	50.01 ± 20.80	20.75 ± 17.40	26.02 ± 17.72

Table 3-4 – Correlation values for understory species (<2m in height) that were highly correlated (τ > 0.5) with at least one of the axes from NMDS. Values of τ > 0.5 are bolded.

	Axis 1 (τ)	**Axis 2 (τ)**	**Axis 3 (τ)**
Pinus albicaulis	**-0.65**	-0.07	0.33
Cladonia spp.	**-0.55**	0.07	0.36
Racomitrium spp.	**-0.54**	-0.13	-0.17
Cladina spp.	-0.48	0.30	**0.59**
Cassiope mertensiana	-0.41	0.06	**0.56**
Paxistima myrsinites	-0.12	-0.46	**-0.56**
Tsuga mertensiana	0.16	**0.66**	0.19
Viola langsdorfii	0.26	**-0.51**	-0.19
Rubus pedatus	**0.63**	-0.29	-0.20
Vaccinium ovalifolium	**0.65**	0.06	-0.01
Streptopus lanceolatus	**0.65**	-0.34	-0.28

3.8 Figures

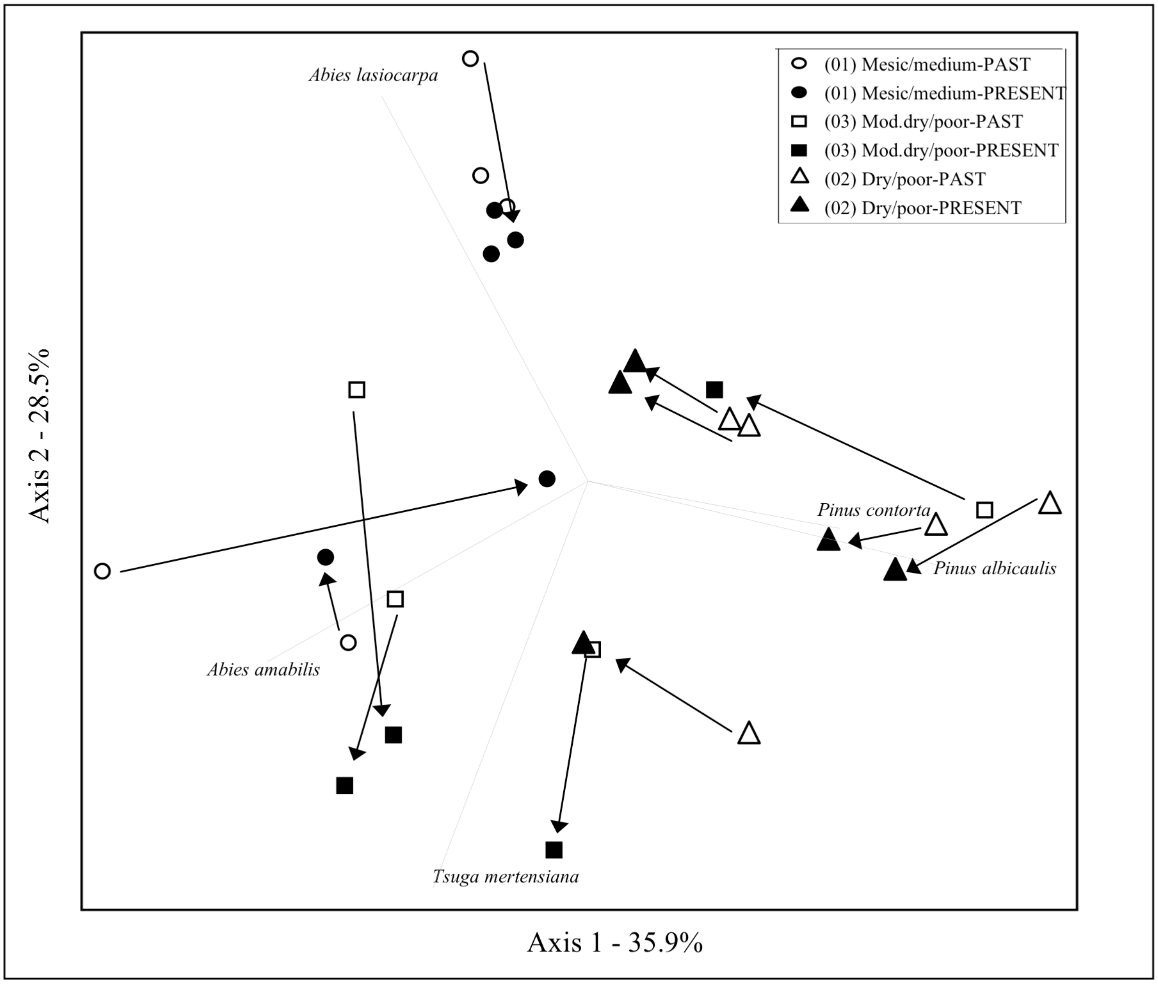

Figure 3-1- Results of unconstrained ordination (PCA) showing the change in cover of overstory communities over time between the three ecosystem types (Dry/poor, Moderately dry/poor and Mesic/medium). Open symbols indicate the location in ordination space of each surveyed site from the 1970/80's and closed symbols the location of surveys in 2007/09. Arrows show the change in composition over time for each site (unless site scores were too close to fit an arrow). The five overstory species names represent species coordinates (eigenvectors) in ordination space, used in this ordination biplot to indicate the association between sites and species.

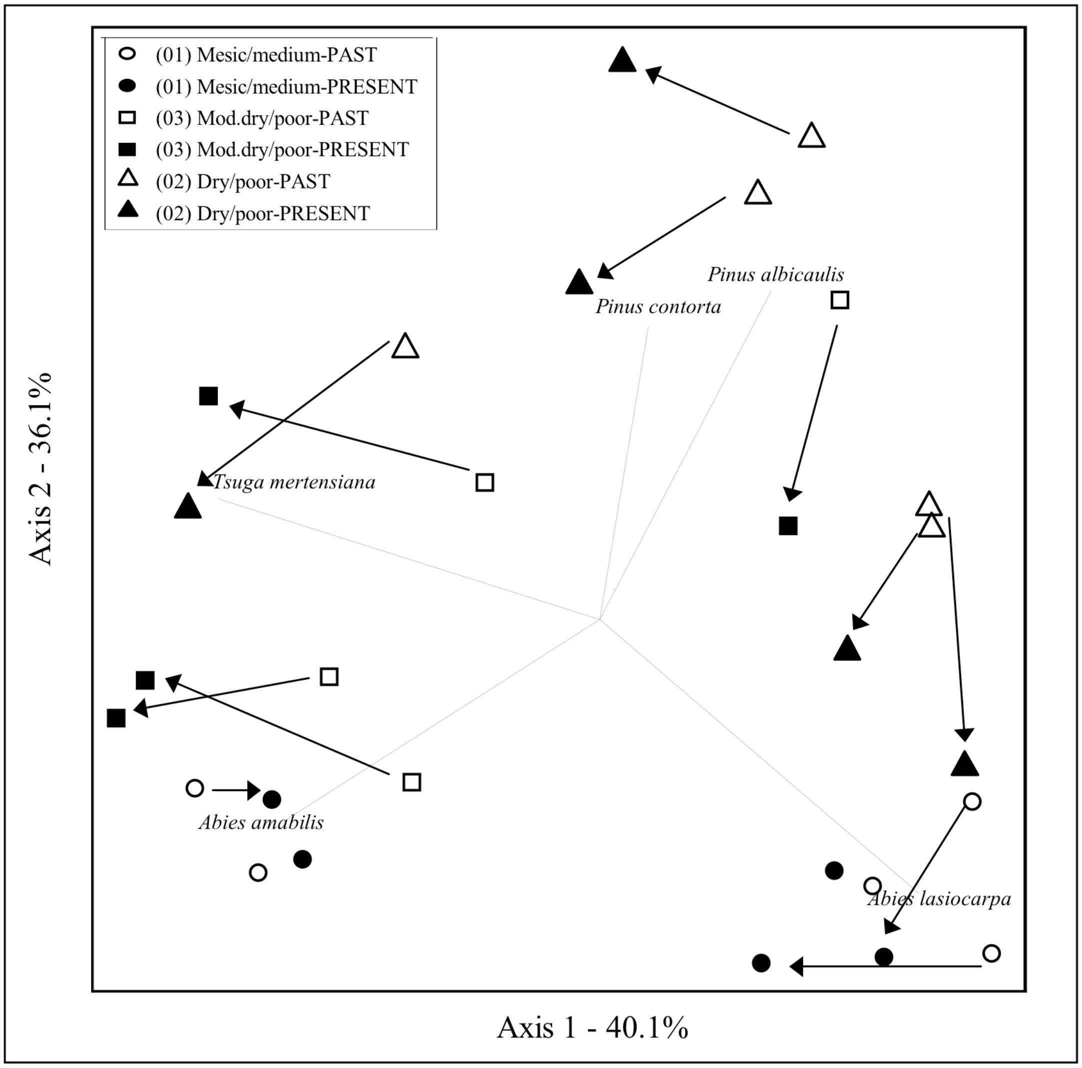

Figure 3-2 Results of unconstrained ordination (PCA) showing the change in proportional cover of overstory trees over time between the three ecosystem types (‘Dry/poor’, ‘Moderately dry/poor’ and ‘Mesic/medium’). Open symbols indicate the location in ordination space of each surveyed site from the 1970/80’s and closed symbols the location of surveys in 2007/09. Arrows show the change in composition over time for each site (unless site scores were too close to fit an arrow). The five overstory species names represent species coordinates (eigenvectors) in ordination space, used in this ordination biplot to indicate the association between sites and species.

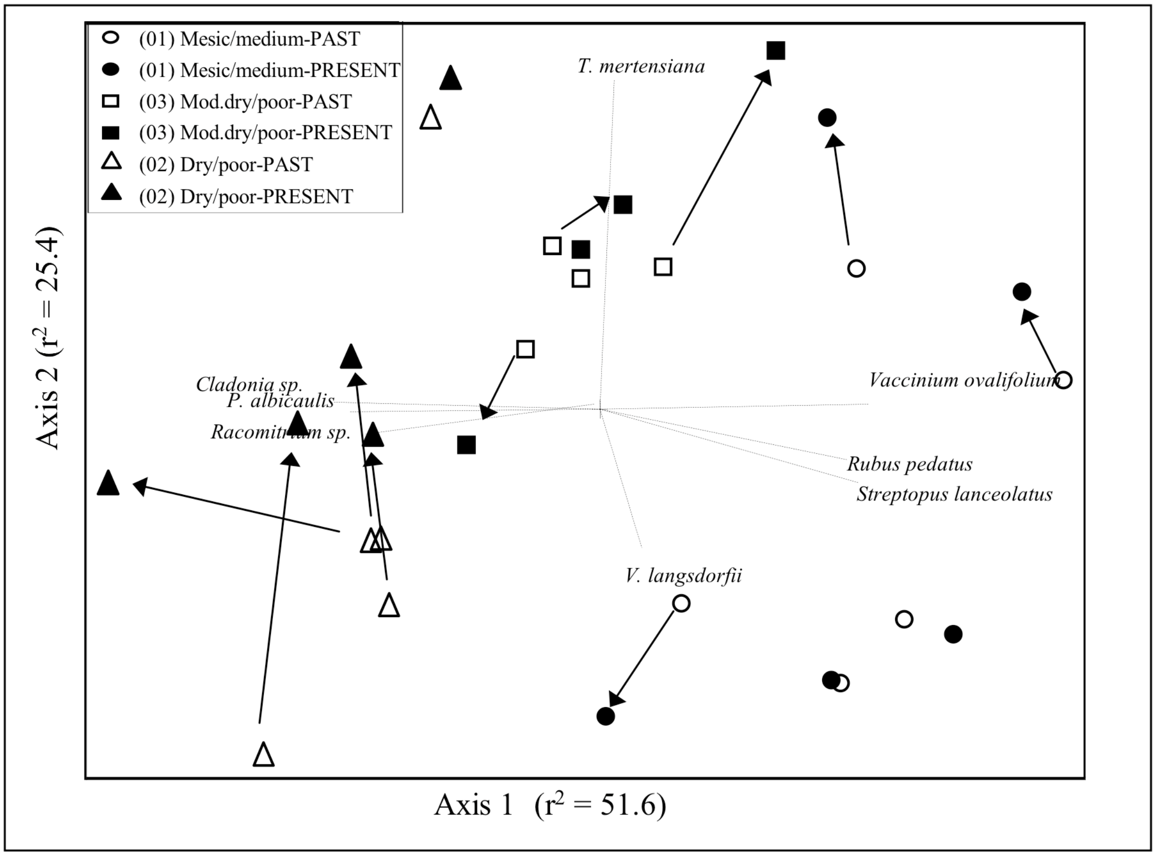

Figure 3-3a - Results of the unconstrained ordination (NMDS, axis 1 *versus* axis 2) of the change in understory communities over time between the three ecosystems (‘Dry/poor’, ‘Moderately dry/poor’ and ‘Mesic/medium’). Open symbols indicate the location in ordination space of each surveyed site from the 1970/80’s and closed symbols the location of surveys in 2007/09. Arrows show the change in composition over time for each site. The understory species names represent species coordinates (eigenvectors) in ordination space, used in this ordination biplot to indicate the association between sites and species. Understory species shown are those that were highly correlated (τ > 0.5) with at least one of the axes from NMDS.

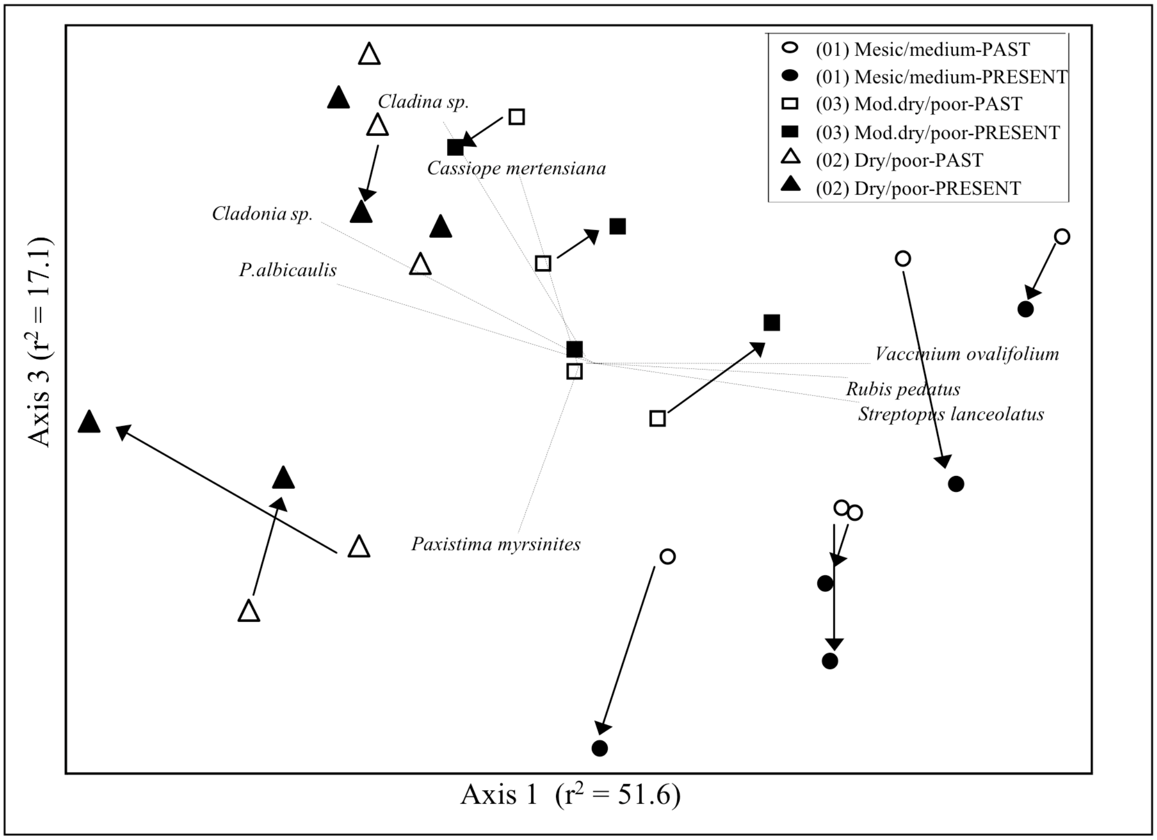

Figure 3-3b Results of the unconstrained ordination (NMDS, axis 1 *versus* axis 3) of the change in understory communities over time between the three ecosystems ('Dry/poor', 'Moderately dry/poor' and 'Mesic/medium'. Open symbols indicate the location in ordination space of each surveyed site from the 1970/80's and closed symbols the location of surveys in 2007/09. Arrows show the change in composition over time for each site. The understory species names represent species coordinates (eigenvectors) in ordination space, used in this ordination biplot to indicate the association between sites and species. Understory species shown are those that were highly correlated ($\tau > 0.5$) with at least one of the axes from NMDS.

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CHAPTER 4: Vegetation patterns in threatened whitebark pine ecosystems of Northwestern British Columbia

4.1 Abstract

Questions: What is the spatial pattern of canopy, of understory vegetation communities, and of their relationships to one another in threatened whitebark pine (*Pinus albicaulis*) ecosystems? What do these patterns suggest about the process of *Pinus albicaulis* replacement by shade tolerant conifers over time and future overstory and understory composition on different site types?

Location: Northern extent of *Pinus albicaulis*' range on the leeward side of the coastal mountains, Northwestern British Columbia

Methods: Understory and overstory species abundance was collected along 7 -100m transects using a modified line intercept method in five *P. albicaulis* stands on either rocky and exposed, or glacio-fluvial fan sites. Abundance data in 0.1m continuous linear 'quadrats' was used for analysis. We used indicator species analysis (ISA) to prune a cluster analysis and classify understory communities along transects. We used wavelet analysis to determine patterns and bivariate wavelet analysis to determine relationships between canopy trees and between the overstory and understory.

Results: Glacio-fluvial sites had stronger overstory spatial pattern than rocky outcrop sites. There was a negative relationship between shade tolerant conifers (*Abies lasiocarpa* and *Tsuga mertensiana*) and positive relationship between *A. lasiocarpa* and dead *P. albicaulis* on glacio-fluvial sites, but no relationship on rocky outcrops. Overstory cover was negatively associated with understory cover on all but the harshest sites. *Cladina* communities were negatively associated with total overstory cover but positively associated with dead *P. albicaulis* at small scales. *Dicranum*/liverwort understory community was positively associated with total overstory cover and *Tsuga mertensiana*.

Conclusions: Shade tolerant conifers will likely replace *Pinus albicaulis* under ongoing disturbance even on sites where *P. albicaulis* is normally expected to be an important component of late successional stands. *Tsuga mertensiana* and *Abies lasiocarpa* may establish in sheltered microsites on rocky outcrops, while the ability for either species to succeed on glacio-fluvial fans may be influenced by interactions with their environment and other vegetation. Overstory-understory relationships indicate that decreased cover of canopy whitebark pine followed by an increase in *T. mertensiana* or *A. lasiocarpa* may decrease the abundance of the understory *Cladina* community, which includes regenerating *P. albicaulis*. Replacement of whitebark pine by shade tolerant conifers on these sites may significantly affect vegetation composition both in the overstory and in the understory in the future.

Keywords: Spatial patterns, overstory, understory, overstory-understory relationships, wavelet analysis, Whitebark pine ecosystems

4.2 Introduction

Whitebark pine (*Pinus albicaulis*) is an important component of high-elevation forests in western North America. Whitebark pine forests are under threat throughout their range from disturbance (mountain pine beetle (MPB), white pine blister rust (WPBR)) and stress (fire suppression and climate change) (Sustainable Resource Development and Alberta Conservation Association 2007, B.C. Conservation Data Centre 2010a). Whitebark pine is considered a keystone species due to its importance as a nurse tree and food source for wildlife (Ellison et al. 2005, Tomback 2007) including grizzly bears (Mattson et al. 1991) and the Clark's nutcracker (*Nucifraga Columbia*) upon which it depends for seed dispersal (Hutchins and Lanner 1982, Tomback 1982). *Pinus albicaulis* is an early successional species, which, at lower elevations, is typically replaced by shade tolerant species later in succession (Keane et al. 1990). However, in some lower elevation exposed sites and most higher elevation sites it may persist throughout the old growth successional stage (Keane et al. 1990). Disturbances targeting *P. albicaulis* may cause the overstory to become dominated by shade tolerant species even on these high elevation and exposed sites (Ch. 2). Given ongoing disturbances to *Pinus albicaulis* in areas where it is expected to persist in the overstory, it is important to understand the relationships among canopy trees across different site types to determine potential future stand trajectories. It is also important to examine how changing overstory conditions may affect understory communities and regeneration in the future.

Linking pattern to process may significantly advance our understanding of ecosystems (Watt 1947, Kershaw 1963, Levin 1992, van der Maarel 1996). The analyses of spatial patterns in plant communities, in particular, can provide insight into the processes responsible for vegetation composition and distribution (Dale 1999, Keitt and Urban 2005, Kembel and Dale 2006). For instance, the presence of a repeated spatial arrangement of vegetation may suggest which factors acted on the vegetation to produce this pattern (Watt 1947). While pattern alone does not indicate process definitively (Cale et al. 1989), vegetation pattern analysis can reflect the combined influence of abiotic and biotic drivers and their interactions (Keitt and Urban 2005, Fajardo and McIntire 2007). Biotic interactions, such as competition, may yield a regularly spaced pattern (Stoll and Berguis 2005, Fajardo and McIntire 2007), while microsite influence on pattern may primarily result in spatial autocorrelation at small scales (Fajardo and McIntire 2007).

Canopy tree and overstory-understory relationships may differ by site due to the interactions between abiotic and biotic factors controlling the spatial arrangement of vegetation. The abiotic environment shapes patterns of both the canopy (Woodward 1998, Getzin et al 2008, Elliott and Kipfmueller 2010) and understory forest communities (Wijesinghe et al. 2005, Bengston et al. 2006). Topography (slope and aspect; Woodward 1998, Resler 2006) and microtopography (Beatty 1984) affect vegetation composition through effects on climate, microclimate, edaphic conditions and below-ground resources (Robertson et al. 1988, Lechowicz and Bell 1991, Bruckner et al. 1999). These ‘site’ or ‘microsite’ effects can influence vegetation patterns directly (Fajardo and McIntire 2007) or through interactions with biotic factors.

Biotic processes, in turn, such as dispersal, regeneration strategies and plant-plant interactions are also important drivers of vegetation pattern (Kolb and Diekmann 2005). Patterns of forest understory plant communities are then a function of the pattern of abiotic resources (Wijesinghe et al. 2005, Bengston et al. 2006), biotic interactions among understory plants (van Andel 2005) and are also influenced by overstory trees (Beatty 1984, Crozier and Boerner 1984, Berger and Puettmann 2000, Battaglia et al. 2002, Abella and Springer 2008, Barbier et al. 2008). The canopy affects understory plants through effects on below-ground resources (nutrient, moisture, pH; Anderson et al. 1969), above-ground resources (light; Battaglia et al. 2002, Chipman and Johnson 2002), environmental conditions (microclimate, microsite; Beatty 1984) and tree species differ in their effects (Crozier and Boerner 1984, Kembel and Dale 2006, Abella and Springer 2008).

Whitebark pine reaches its northern limit in the Northern Rocky and Coastal Mountain ranges of northern British Columbia (BC), Canada (Klinka et al. 2000). In northwestern BC, it occurs on several different site types in the subalpine zone of the Coast Mountains. We focused our study on sites where *P. albicaulis* is expected to persist throughout succession on two edaphically similar, but topographically different areas: rocky outcrops ('Lithic'), and glacio-fluvial deposits ('Fluvial') (Banner et al. 1993). We used spatial patterns to examine (1) how replacement of *Pinus albicaulis* by shade tolerant conifers may be influenced by site type and (2) given a change in the canopy, what overstory and understory patterns suggest about future overstory and understory composition on these sites.

4.3 Methods

4.3.1 Study Area

The study area was within the moist cool (mk) Engelmann Spruce-Subalpine fir (ESSF) zone in Northern British Columbia (Meidinger and Pojar 1991). This forested subzone occurs between 1000-1800m in elevation in a narrow band on the leeward side of the Coastal Mountains (Banner et al. 1993). The ESSFmk has dry summers (average total precipitation 1000mm) and a high snowpack in the winter (>2m; Meidinger and Pojar 1991, Banner et al. 1993).

Study sites were located in the ESSFmk '(02) Dry/poor – *Abies lasiocarpa*/*Pinus albicaulis – Cladonia*' ecosystem described by the British Columbia biogeoclimatic ecosystem classification system (BEC; Banner et al. 1993). During the old growth successional stage the overstory of this ecosystem type is characterized by abundant *Pinus albicaulis*, uncommon *Tsuga mertensiana* and *Abies lasiocarpa*. Regeneration in these systems is dominated by abundant *A. lasiocarpa* and common *T. mertensiana*, while the herb layer is sparse and the forest floor is characterized by abundant *Dicranum fuscescens*, less abundant *Cladina* spp., *Barbiliphozia* spp., *Pleurozium schreberi* and uncommon *Cladonia* spp.

Within 'Dry/poor' whitebark pine ecosystems, there are two recognized site types: 'Lithic', found on upper slopes and rocky outcrops, and 'Fluvial', on fluvial/glaciofluvial fans or terraces on flat areas at mid/lower slope positions. 'Lithic' sites have shallow soils over bedrock and moderate to steep slope gradients, while 'Fluvial' sites have deeper soils over gravel deposits with little slope (Banner et al. 1993).

Like most of the Whitebark pine forests within the study area, our studied stands were affected by the mountain pine beetle (MPB, *Dendroctonus ponderosae*) and White pine blister rust (WPBR, *Cronartium ribicola*). An outbreak of MPB in the 1980's affected several of our stands, while others were attacked by MPB during the more recent (c.2005) outbreak.

4.3.2 Survey Methods

In total, we surveyed seven 100m transects, four at 'Fluvial' sites and three at 'Lithic' sites. One 'Lithic' site was too small to fit a full 100m transect, so we divided it into an 80m and 20m section, which were analysed separately. Three 'Fluvial' transects were located at the same general location, each line 10m apart. We used a modified line intercept technique (Chambers and Brown 1983, Resource Information Branch 2004) to estimate cover of species (according to MacKinnon et al 1992) along each transect. For the line intercept, where a species is present directly over the transect line, the position and distance along the transect was recorded. However, due to the difficulty in estimating exact distances covered by small (e.g. bryophytes) or large (e.g. overstory trees) species, we modified this technique by visually estimating percent cover of each species within variably sized segments (dependent on size of species) along the transect. These estimates were then converted to continuous 0.1m linear "quadrats" for analysis, for a total of 1000 contiguous segments along each 100m of transect. We identified the most common bryophytes to species and grouped others into acrocarpous mosses, pleurocarpous mosses, rock moss (mosses often growing on bedrock) and liverworts. Likewise, the most common lichens were identified to genus and other species were grouped as "foliose lichens" or "crustose lichens". Woody species were classified as understory (<2m) or overstory (≥ 2m height). The datasets used for analysis were: understory (bryophyte/lichen, forbs, woody species < 2m height) and overstory (woody species > 2 m height). We also categorized trees as 'healthy, 'sick', 'recently dead' or 'dead'. Some species had very few individuals in some categories. Thus in our analyses we only considered: live *Abies lasiocarpa*, live *Tsuga mertensiana*, dead *Pinus albicaulis* and total overstory cover (all health categories of all overstory trees combined). We were often not able to determine the cause of tree mortality so we were unable to distinguish between *P. albicaulis* killed by MPB or other causes (including WPBR).

4.3.3 Data Analysis

Understory community types

We used cluster analysis on the entire understory dataset to create a classification of understory plant community types prior to spatial analysis (McCune and Grace 2002) in PC-ORD (McCune and Mefford 2006). We pruned the cluster dendrogram using indicator species analysis (Dufrêne and Legendre 1997), minimizing average indicator species p-values and maximizing the number of significant indicator species (McCune and Grace 2002). This resulted in five understory communities, described here by the most significant indicator species: (1) *Cladina*, (2) *Dicranum*/liverworts, (3) *Cladonia*/rock moss, (4) *Vaccinium membranaceum* and (5) *Pleurozium schreberi* (Table 4-1). Following this classification, the understory community type for each 0.1m segment along each transect was used for subsequent analyses.

Spatial Analysis

To determine spatial patterns of understory communities, overstory species and overstory-understory relationships across multiple scales, we used wavelet analysis (Dale and Mah 1999, Fortin and Dale 2005) in PASSAGE software (v. 2.0, Rosenberg 2009). We applied this pattern exploration technique to the data for: total overstory cover (including live and dead); overstory cover for each of the three tree species (live *Abies lasiocarpa* or *Tsuga mertensiana* or dead *Pinus albicaulis*); total understory cover; and the five understory community types. We used bivariate wavelet analysis to examine relationships between: overstory cover of the three trees; total overstory and total understory cover; each understory community type with total overstory cover; each understory community type with overstory cover for each of the three tree species. For all but the latter analyses we compared spatial patterns between the ‘Lithic’ and ‘Fluvial’ site types. It is often recommended for spatial analysis to examine patterns using several techniques (Fortin and Dale 2005, Saunders et al. 2005). Thus, we also used three-term local quadrat variance and covariance analysis (3TLQV/3TLQC) to confirm spatial pattern results from wavelet analysis (Dale 1999, Fortin and Dale 2005) but we do not present those results here as they indicated the same trends as wavelet analysis.

Wavelets are a family of discrete functions applied to a series of continuous data (Dale and Mah 1999). A wavelet transform is fitted to the data at a range of sizes and moved along the data series in a method similar to quadrat variance techniques (Bradshaw and Spies 1992, Fortin and Dale 2005, Kembel and Dale 2006). The general wavelet transform equation contains the wavelet function and the size and position of the transform along the data series (Eq. 1)

$$T(b,u_i) = \frac{1}{b}\sum_{j=1}^{n} y(u_j)g\left[(u_j - u_i)/b\right]$$

Equation 1 – The general wavelet transform for a wavelet function *g*, with a width *b* and a value of $y(u_j)$ at position u_j (Fortin and Dale 2005)

The transform moves along the data series as a ‘window’ of different sizes. When data fit the shape of the wavelet function, the value of the transform is high (Dale 1999). Variance can then be calculated from the wavelet transform (Eq. 2), which is used to determine pattern. Low variance across all scales indicates a lack of spatial pattern, whereas one with peaks and shoulders in variance indicates the average scale of patches and gaps (Dale and Mah 1999, Fortin and Dale 2005). When used for bivariate analysis, wavelet covariances indicate scale-specific relationships between two variables. Peaks in covariance indicate the scales of positive or negative relationships (Kembel and Dale 2006). We did not test the statistical significance of wavelet variance and covariance peaks, so patterns discussed here are based on the consistency in scale of variances or direction of covariances between transects.

$$V(b) = \sum_{i=1}^{n} \frac{T^2(b, u_i)}{n}$$

Equation 2 – Wavelet variance $V_w(b)$ where T is the transform for a width of b at position u_i (Fortin and Dale 2005)

An advantage of wavelets over other ‘moving window’ and spectral analysis techniques is that they do not require stationarity (Bradshaw and Spies 1992); i.e., the properties being studied need not be independent of location (Fortin and Dale 2005). Here, we use the Mexican hat wavelet transform (Eq.3), which is commonly used in ecological applications (Bradshaw and Spies 1992, Dale et al. 2002, Fortin and Dale 2005, Mi et al. 2005, Kembel and Dale 2006), and is useful in detecting patterns with symmetrical peaks and troughs (Bradshaw and Spies 1992) and in smoothing noisy data (Dale and Mah 1999).

$$g(u) = \frac{2}{\sqrt{3}}\pi^{-\frac{1}{4}}(1 - 4u^2)e^{-2u^2}$$

Equation 3 – Mexican hat wavelet where *g* is the wavelet function at position *u* (Fortin and Dale 2005)

4.4 Results

4.4.1 Overstory Patterns

Results suggest that there were stronger spatial patterns for total overstory cover in the 'Fluvial' compared to the 'Lithic' sites (Figure 4-1A), as indicated by greater amplitude of wavelet variance (Bradshaw and Spies 1992). The difference between 'Fluvial' and 'Lithic' sites was also seen in the analysis of overstory cover of the three tree species. 'Fluvial' sites had greater variance amplitudes than the 'Lithic' sites for both (live) *Abies lasiocarpa* and *Tsuga mertensiana* (Figure 4-2A & C). Dead *P. albicaulis* had weak spatial pattern in both site types (Figure 4-2B). Overstory *Abies lasiocarpa* had strong spatial pattern on 'Fluvial' sites, but there was no obvious dominant scale in the pattern (Figure 4-2A). *Tsuga mertensiana* had spatial pattern on both site types, but no one scale of pattern emerged from wavelet analysis (Figure 4-2C). Wavelet covariance analysis indicated that significant spatial relationships between canopy species existed only on 'Fluvial' sites. *Abies lasiocarpa* and dead *Pinus albicaulis* had positive covariance while *Abies lasiocarpa* and *Tsuga mertensiana* were negatively associated (Figure 4-3A & B). Dead *Pinus albicaulis* and live *Tsuga mertensiana* had no obvious pattern of association on either site type (Figure 4-3C).

4.4.2 Understory patterns

There was a spatial pattern in total understory cover on both site types (Figure 4-1B). There was a difference in scale, with a ~1 m dominant scale on ‘Fluvial’ sites, compared to ~3m scale on ‘Lithic’ sites (Figure 4-1B). When the understory was separated into the five community types (Table 4-1), patterns were less clear (Figure 4-4). Overall, the *Cladina* community had a strong spatial pattern on both site types, but with varying scales of pattern between transects (Figure 4-4A). The *Dicranum*/liverwort community appeared to have some small-scale pattern (~0-4m), but this was not consistent between transects on either site type (Figure 4-4B). The *Cladonia*/rock moss community had a stronger spatial pattern on ‘Lithic’ compared to ‘Fluvial’ sites (Figure 4-4C). The *Vaccinium membranaceum* community did not appear to have a spatial pattern on either site type (Figure 4-4D). The *Pleurozium schreberi* community exhibited small-scale spatial pattern (~0-5m) on ‘Lithic’ sites, while ‘Fluvial’ sites had greater wavelet variance amplitude but with different scales on different transects (Figure 4-4E).

4.4.3 Overstory-Understory

For most transects total overstory cover had a negative covariance with total understory cover (Figure 4-1C). However, the two most exposed (i.e south-facing rocky outcrops) ‘Lithic’ sites had a positive covariance (Figure 4-1C). One transect at a ‘Fluvial’ site showed negative covariance at smaller scales but positive covariance at a scale of ~13 – 20m (Figure 4-1C).

Total overstory cover had a negative covariance with the *Cladina* community but covaried positively with the *Dicranum*/liverwort and *Vaccinium membranaceum* community types on both site types (Figure 4-5A, B, D). There was little covariance between total overstory and the *Cladonia*/rock moss community type on either site

(Figure 4-5C). There was also little covariance between total overstory and the *Pleurozium schreberi* community on 'Lithic' sites, but there was stronger covariance (both negative and positive) on 'Fluvial' sites (Figure 4-5D).

Cover of overstory *Abies lasiocarpa* had a negative relationship with the *Cladina* community at small scales (~0-10m) (Figure 4-6A). Cover of dead overstory *Pinus albicaulis* covaried positively with the *Cladina* community at small scales (~1- 3m), and had a negative relationship with the *Pleurozium schreberi* understory community at small scales (Figure 4-6A, E). Overstory *Tsuga mertensiana* had an overall negative relationship with the *Cladina* community but a positive association with the *Dicranum*/liverwort understory community (Figure 4-6A, B).

4.5 Discussion

Spatial patterns in both the overstory and understory were variable among transects. Due to the weak overstory and understory patterns across 'Lithic' sites and the positive overstory-understory relationships on the harshest 'Lithic' sites, we find that microtopography may be important in determining pattern on these sites. 'Fluvial' sites often had stronger spatial patterns than 'Lithic' sites and this plus the relationships among overstory trees suggests to us that pattern on these sites may be related to more factors than microtopography alone. The relationship among different tree species and certain understory communities also varied among transects, but covariance of the *Cladina* community with total overstory cover and with both shade tolerant conifers was consistently negative.

The variability in strength and scale of spatial pattern among transects may be due to the complexity of factors interacting to control overstory and understory pattern. There is often variation in the results of wavelet analyses for understory communities (e.g., Kembel and Dale 2006). The lack of a strong or consistent pattern for the understory community, in particular, could be a result of multiple controlling factors including: overstory pattern (Crozier and Boerner 1984, Houle 2007, Moora et al. 2007, Barbier et al. 2008), below-ground resources (Lechowicz and Bell 1991, Wijesinghe et al. 2005, Bengtson et al. 2006) and microtopography (Beatty 1984, Roiloa and Retuerto 2007). Our study then does not indicate which of these factors are most important in determining understory community structure in whitebark pine ecosystems.

Pattern when present, however, may suggest process. For instance, biotic interactions, such as competition, may yield a regularly spaced pattern (Stoll and Berguis 2005, Fajardo and McIntire 2007), which would result in a strong wavelet variance signal at the scale of pattern (Bradshaw and Spies 1992). In contrast, patterns controlled by microsite may result in strong small-scale spatial autocorrelation (Fajardo and McIntire 2007) or weak wavelet variances due to the inconsistency in scale (Bradshaw and Spies 1992). While our results do not unequivocally support the dominance of any one controlling factor on overstory or understory patterns, we did find evidence that the strength or nature of the processes controlling pattern on 'Fluvial' sites were different than on 'Lithic' sites.

4.5.1 Overstory Patterns

Lower magnitude overstory wavelet variances and variability in scale among transects on 'Lithic' compared to 'Fluvial' sites indicates that pattern was weak and inconsistent on 'Lithic' sites. In harsh environments, such as those with thin soils, frequent exposure to high winds and summer moisture deficits, the soils that develop in sheltered microsites of geomorphic features are critically important for seedling establishment and in turn vegetation pattern (Resler 2006, Hiers et al. 2007). Tree species on 'Lithic' sites were not consistently in any spatial arrangement, which may indicate that microtopography or microsite conditions, rather than biotic interactions may be important in determining tree pattern (Resler 2006, Fajardo and McIntire 2007). It is also possible that our survey transects were not of adequate length to capture the scale of overstory pattern on the 'Lithic' sites. If tree pattern were at larger scales, which were repeated less frequently, longer transects would be required to describe this pattern (Fortin and Dale 2005). There was also no evidence of spatial covariance between the different tree species on 'Lithic' sites, which may also support that overstory pattern on these sites is determined by microtopography. For instance, trees on these sites establish in sheltered microsite positions regardless of interactions with other tree species or species-specific regeneration characteristics.

The greater magnitude of overstory wavelet variances on 'Fluvial' sites indicates a significant spatial pattern in those areas (Bradshaw and Spies 1992). The 'Fluvial' sites did not have a consistent scale of overstory pattern, however, which make inference into process difficult. Still, the presence of a pattern other than simply small-scale spatial autocorrelation, indicates that processes such as biotic interactions may be important in shaping these 'Fluvial' communities (Fajardo and McIntire 2007). This is further supported by the presence and consistency of wavelet covariances across transects on 'Fluvial' sites (eg. Tilman 1985, Callaway 1998). Microsite may still be an important driver of overstory pattern on these sites, however. Compared to the 'Lithic' sites, trees on 'Fluvial' sites establish in a more consistent pattern in relation to other tree species

(Maher et al 2005). For instance, the negative covariance between canopy *Abies lasiocarpa* and *Tsuga mertensiana* could suggest competition for resources between the two on 'Fluvial' sites (Tilman 1985). If competition is an important process between these two shade tolerant tree species, *T. mertensiana* may have a competitive advantage over *A. lasiocarpa* as it is more shade tolerant (Franklin and Dyrness 1967, Alexander et al 1990). *A. lasiocarpa* was also positively associated with dead *P. albicaulis* on 'Fluvial' sites, which support other studies in high elevation systems where a positive association between these species has been found (Callaway 1998, Maher and Germino 2006). This positive wavelet covariance could suggest that there was a facilitative relationship between these species at some prior point during their establishment and growth on 'Fluvial' sites (Callaway 1998, Maher et al 2005). The spatial relationships we found between these overstory species may also be a result of variation in microsite and germination requirements (Maher and Germino 2006, Maher et al 2005). For instance, microsite requirements of *A. lasiocarpa* may be more similar to *P. albicaulis* than *T. mertensiana.* The consistent direction of covariance between different tree species on 'Fluvial' sites, which was not seen on 'Lithic' sites, suggests that some biological traits of these trees are important on 'Fluvial' sites (Maher et al 2005). These species-specific environmental requirements or biotic interactions do not appear to be important on 'Lithic' sites.

4.5.2 Overstory-Understory Relationships

While there are multiple biotic and abiotic factors contributing to understory community structure, we focused on isolating the influence of overstory cover and composition on understory communities, because it is the canopy environment that will change under ongoing disturbance. Our study supports the idea that on all but the two most environmentally stressed sites, overstory species cover negatively affects understory biomass (Pugnaire and Luque 2001, Tewksbury and Lloyd 2001). There was generally weak or negative covariance between total overstory and total understory cover, but there was a strong positive relationship on the two most exposed, south-facing, rocky 'Lithic' sites. One explanation for this is that the overstory provides shelter and facilitates growth of understory vegetation on these harsh sites (Bertness and Callaway 1994, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001). In this case, there is likely a positive feedback, where the understory is able to succeed in the sheltered and ameliorated soil conditions beneath the overstory (Maher and Germino 2006, Resler 2006, Butterfield 2009) and overstory trees in turn benefit from increased litter deposition, decomposition, lowered soil temperatures and reduced nutrient leaching due to the understory (Pugnaire and Luque 2001). Another explanation may be that high vales of understory and overstory cover are simply found in similar favourable microsites in this harsh environment without any beneficial relationship between the two.

Our study also suggests that certain understory community types in 'Dry/poor' whitebark pine ecosystems are spatially associated with different overstory trees and total canopy cover. The life history or species traits of understory plants in each community type are important as this determines understory response to overstory composition and density (Kolb and Diekmann 2005, Butterfield 2009, Maestre et al. 2009). The *Cladina* community, which contains regenerating *Pinus albicaulis*, was negatively associated with overstory cover and *Abies lasiocarpa* or *Tsuga mertensiana* in the overstory. This community type contains species adapted to low nutrient conditions that can also tolerate the high light and low moisture conditions (Table 4-1, Beaudry et al. 1999) present in canopy gaps. The *Cladina* community may then be associated with dead *Pinus albicaulis* at small scales due to higher light conditions under a pine canopy compared to fir or hemlock (Canham et al. 1999). Understory communities on dry sites, however, are often influenced more by differences in overstory throughfall and moisture conditions beneath different canopy species rather than by light intensity (Anderson et al. 1969, Crozier and Boerner 1984, Andersson 1991). Understory community covariance patterns with overstory species in our study may then be a function of the moisture requirements of species within each understory community. For instance, the *Cladina* community may be excluded from beneath canopies that increase understory moisture conditions.

Although covariance between the *Dicranum*/liverwort community and the overstory was not strong, it was consistently positively associated with total overstory cover and with cover ob *Tsuga mertensiana* across transects. This may indicate a greater tolerance or ability to succeed on wetter microsites. *Dicranum* species and liverworts may occur across a wide range of moisture conditions in the subalpine areas of our study (Beaudry et al. 1999), however our results suggest that they are more associated with wetter microsites in these 'Dry/poor' ecosystems. The *Pleurozium schreberi* community was negatively associated with dead *Pinus albicaulis* at small scales. This may also be due to the moisture requirements of the species within this community (Table 4-1), with the conditions under dead *P. albicaulis* being too dry or exposed. The *Vaccinium membranaceum* community was positively associated with total overstory cover across both site types. Species in this community also cover a wide range of moisture and nutrient conditions in subalpine forests of northwestern BC (Beaudry et al. 1999), but may be found more commonly under the shelter of the canopy, on microsites with greater moisture in these 'Dry/poor' ecosystems.

4.5.3 Implications for future forest composition

Our results suggest that if overstory *Pinus albicaulis* continues to decline and *Abies lasiocarpa* and *Tsuga mertensiana* increase in relative abundance in 'Dry/poor' ecosystems of NW BC (Ch.2, Ch.3), the forest community on 'Lithic' sites may change in different ways than those on 'Fluvial' sites. For instance, the establishment of either of these shade tolerant trees on 'Lithic' sites may depend primarily on the availability of sheltered microsites, whereas on 'Fluvial' sites factors such as the life history attributes of *A. lasiocarpa* and *T. mertensiana* will affect whether these trees succeed or dominate under different abiotic conditions (Tilman 1985). If species-environment relationships or interactions between trees are important on 'Fluvial' sites, the outcome may also be influenced by climate (Taylor 1995, Peterson et al. 2001, Peterson and Peterson 2001, Heegaard and Vandvik 2004). For example, we may expect greater establishment and growth rates of *A. lasiocarpa* compared to *Tsuga mertensiana* on 'Fluvial' sites following years of low snow-fall and summer precipitation that results in growing season moisture deficits (Peterson and Peterson 2001). However, we may expect to see a dominance of *T. mertensiana* in the absence of moisture deficits, as it is more shade tolerant than, and may therefore outcompete *A. lasiocarpa* (Alexander et al. 1990, Franklin and Dyrness 1967) on 'Fluvial' sites when snowmelt is not a limiting factor (Heegaard and Vandvik 2004).

Our results also suggest that if total overstory cover increases in the future, total understory cover will decrease on all but the most environmentally severe sites. Increasing canopy cover may be associated with increases in understory cover on harsh sites but the number of suitable microsites will likely limit both overstory and understory cover. Increasing canopy cover would also potentially alter understory community structure. For instance, the *Cladina* community would likely decrease while the *Dicranum* spp./Liverwort and *Vaccinium membranaceum* communities would likely increase with increasing canopy cover in both site types.

The relationships between different overstory tree species and understory communities may also provide insight into how 'Dry/poor' whitebark pine ecosystems may change in the future. Our results suggest that if the relative cover of overstory *Tsuga mertensiana* or *Abies lasiocarpa* increases or *Pinus albicaulis* decreases in the future, this could result in an increased presence of the *Dicranum*/liverwort and *Pleurozium schreberi* community and decreased presence of the *Cladina* community. These results have important implications for future forest composition. For example, the *Cladina* community contains regenerating *P. albicaulis*, so a decrease in this community with increased canopy cover or a shift towards *T. mertensiana* or *A. lasiocarpa* may also decrease the amount of *P. albicaulis* regeneration. Our study indicates that overstory-understory relationships may contribute to the decline of whitebark pine. Understory response may be slow in high elevation forests (Kreyling et al. 2008), so it is unclear how long it would take for overstory change to alter understory communities.

Although this study provides new information on spatial patterns in two whitebark pine sites and we have made some inferences about processes, it is important to note that our data present only a snapshot at a single point in time (Cale et al. 1989). The intensity and direction of biotic interactions and the relative importance of abiotic and biotic controls on pattern may change over time throughout the course of succession

(Malkinson et al. 2003). Pattern alone may also not be sufficient to describe process, as different processes may result in similar spatial patterns (Cale et al. 1989). While acknowledging these limitations, we find that patterns strongly suggest that there are different factors controlling overstory pattern and overstory-understory relationships on our two site types. This is an important contribution to understanding forest change in whitebark pine ecosystems.

4.6 Conclusion

Vegetation patterns were variable both in the overstory and understory in our study suggesting that there may be many factors structuring plant communities in whitebark pine ecosystems. However, as *Pinus albicaulis* continues to be affected by disturbance and the overstory becomes increasing dominated by *Abies lasiocarpa* and *Tsuga mertensiana*, the establishment and relative abundance of these two shade tolerant species may be affected by different processes in the two site types. Microsite constraints on the harshest 'Lithic' sites will likely limit the extent of canopy cover, with many microsites remaining unsuitable for tree establishment. Those trees that do establish will likely be limited to particular favorable microsites such that species-specific interactions with the environment or with other vegetation are not very important in shaping the future canopy. On the more favourable 'Fluvial' sites, we may expect a shift in the canopy towards shade tolerant conifers to be more of a function of the biological characteristics of these species and their interactions with other trees and their environment. Certain understory communities were associated with different canopy trees. Based on overstory-understory relationships we would expect a decrease in the *Cladina* community and an increase in the *Dicranum* spp./liverwort, *Vaccinium membranaceum* and *Pleurozium schreberi* communities to accompany the decline of *Pinus albicaulis* and increased relative abundance of shade tolerant conifers or an increase in total canopy cover. Our study demonstrates that sites with similar forest communities, experiencing similar disturbances, may respond to disturbance differently according to site type.

4.7 Tables

Table 4-1 – Results of the classification of understory vegetation community types showing results of the indicator species analysis (ISA) used to prune the cluster dendrogram. Indicator values, and their significance, are given for ach species (or genus/group) by community type. Each community type is defined by the species with the largest indicator values: (A) *Cladina*, (B) *Dicranum*/Liverworts, (C) *Cladonia*/Rock moss, (D) *Vaccinium membranaceum*, (E) *Pleurozium schreberi.*

Species	Indicator Value	*P*
(A) *Cladina*		
Abies lasiocarpa (sick)	0.7	<0.001
Acrocarpous moss	0.6	0.01
Arctostaphylos uva-ursi	2.1	<0.001
Cassiope mertensiana	1.1	<0.001
Cladina spp.	42.7	<0.001
Unidentified *Cladina/Cladonia* spp.	14.2	<0.001
Cryptogramma crispa	0.1	0.21
Empetrum nigrum	1.1	<0.001
Foliose lichens	0.5	<0.001
Menziesia ferruginea	2	<0.001
Peltigera spp.	1.3	<0.001
Pinus albicaulis	2.3	<0.001
Pinus contorta	0.7	<0.001
Selaginella spp.	0.6	<0.001
Stereocaulon	7.6	<0.001
(B) *Dicranum*/Liverworts		
Dicranum spp.	34.6	<0.001
Liverworts	44.9	<0.001
(C) *Cladonia*/Rock moss		
Carex spp.	0.1	0.73
Cladonia spp.	38.7	<0.001
Crustose lichen	2.1	<0.001
Elliottia pyroliflorus	10.5	<0.001
Juniperus communis	0.1	0.14
Phyllodoce empetriformis	0.4	0.00

Pinus albicaulis (sick)	0.1	0.39
R*acomitrium spp.*/rock moss	39.7	<0.001
Sorbus spp.	0.3	0.14
Tsuga mertensiana	22.2	<0.001
(D) *Vaccinium membranaceum*		
Abies lasiocarpa (dead)	0.2	0.08
Lycopodium spp.	0.1	0.33
Pleurocarpous moss	1.1	<0.001
Vaccinium membranaceum	78.2	<0.001
(E) *Pleurozium schreberi*		
Abies lasiocarpa	25.3	<0.001
Cassiope stelleriana	1.4	<0.001
Pleurozium schreberi	52.9	<0.001

4.8 Figures

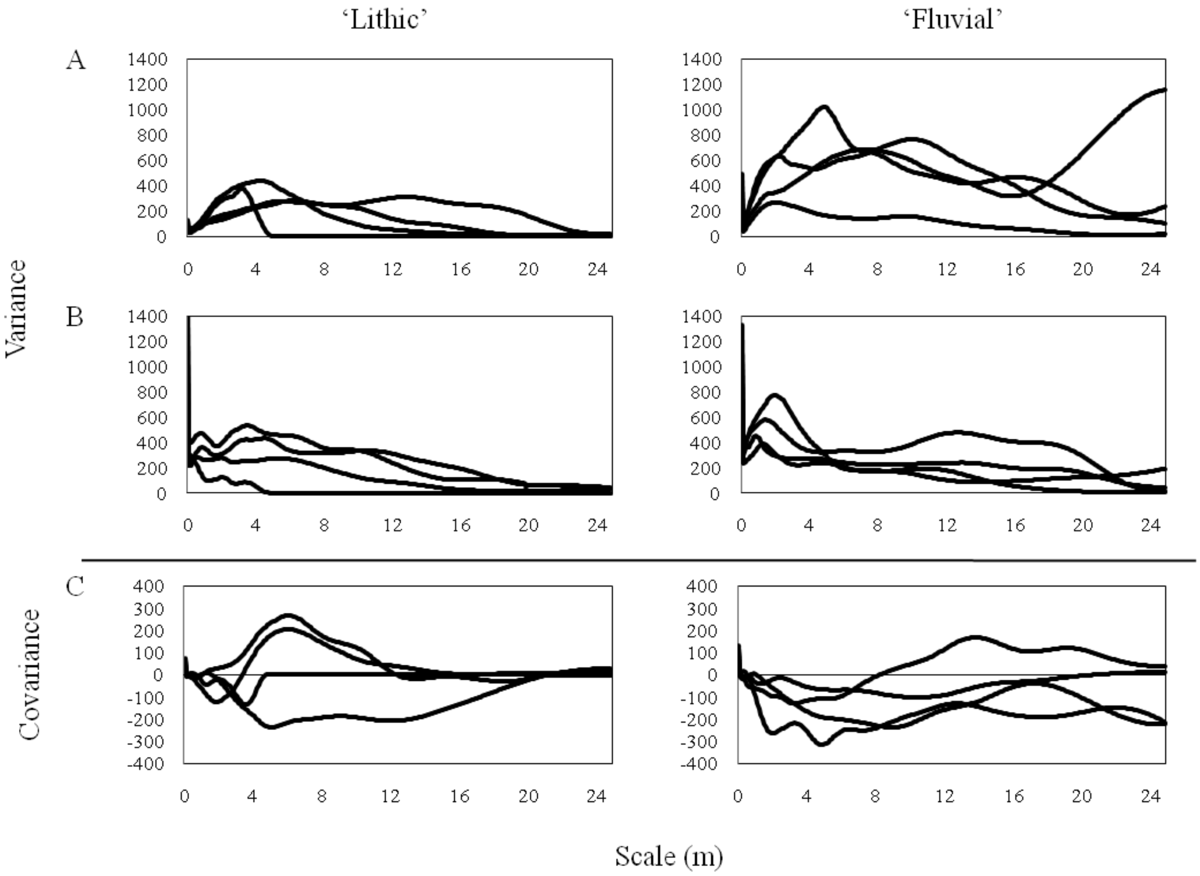

Figure 4-1 - Results of Wavelet analyses for A) total overstory cover, B) total understory cover, and C) wavelet covariance of total overstory and total understory. The Y-axis represents wavelet variance/covariance and the X-axis represents scale (m). Peaks and shoulders in variance/covariance indicate non-random spatial structure at a given scale, with higher variance/covariance vales representing a stronger pattern. Lines below the X-axis represent negative and above represent positive associations for wavelet covariances.

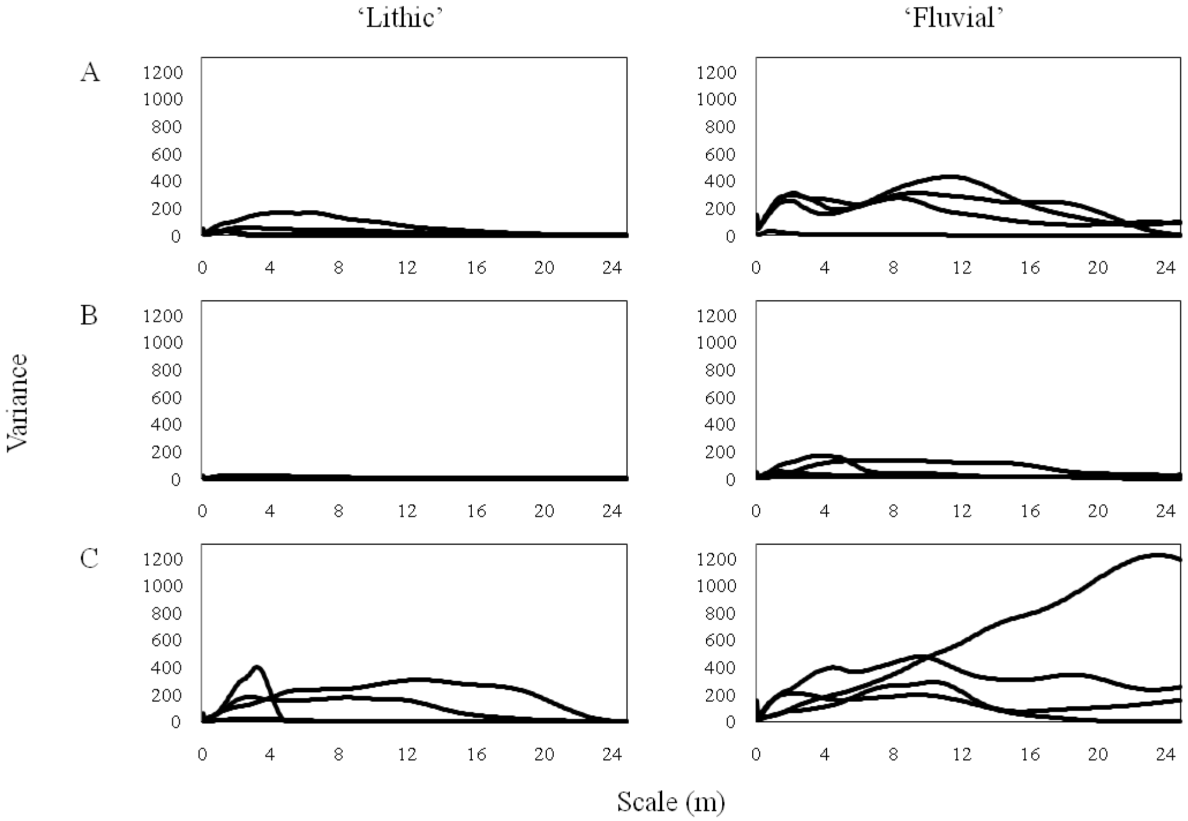

Figure 4-2 Results of wavelet analysis showing variances for cover of overstory A) *Abies lasiocarpa*, B) dead *Pinus albicaulis*, C) *Tsuga mertensiana*

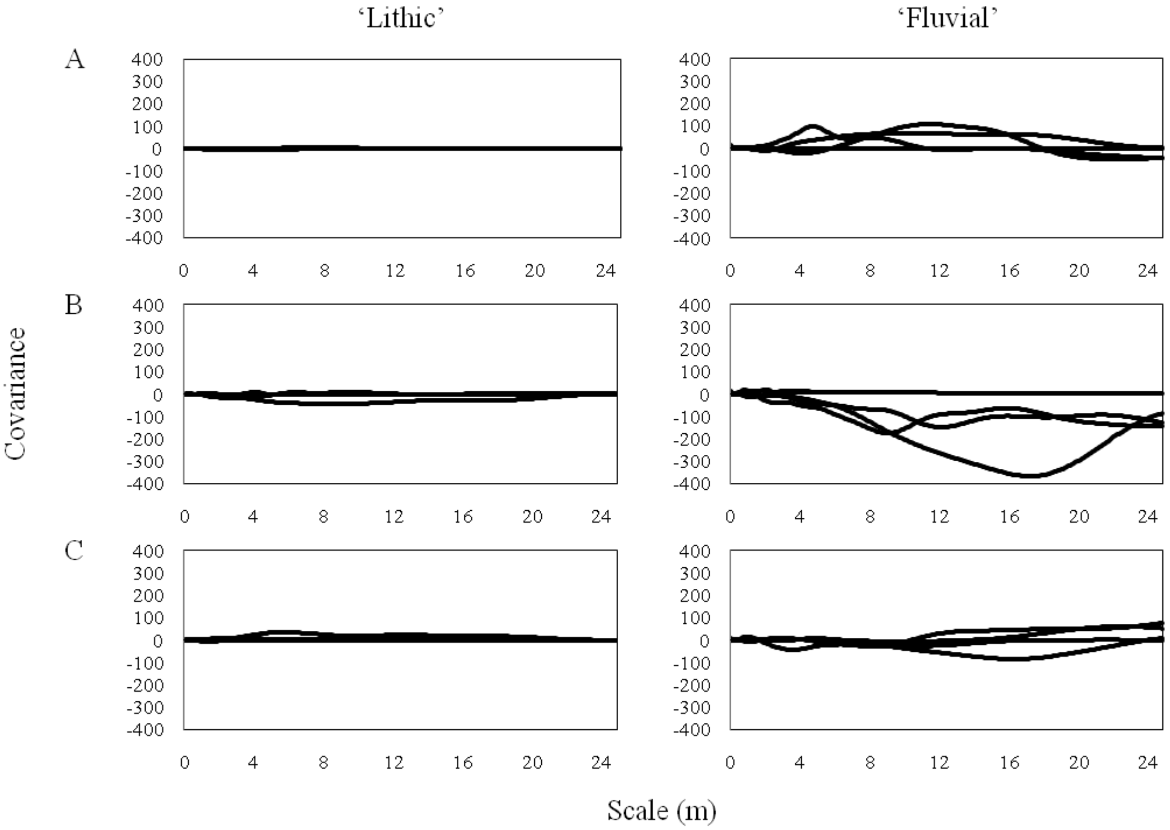

Figure 4-3 Results of bivariate wavelet analysis showing covariances for overstory cover of: A) *Abies lasiocarpa* x dead *Pinus albicaulis*, B) *Abies lasiocarpa* - *Tsuga mertensiana*, C) dead *Pinus albicaulis* - *Tsuga mertensiana*

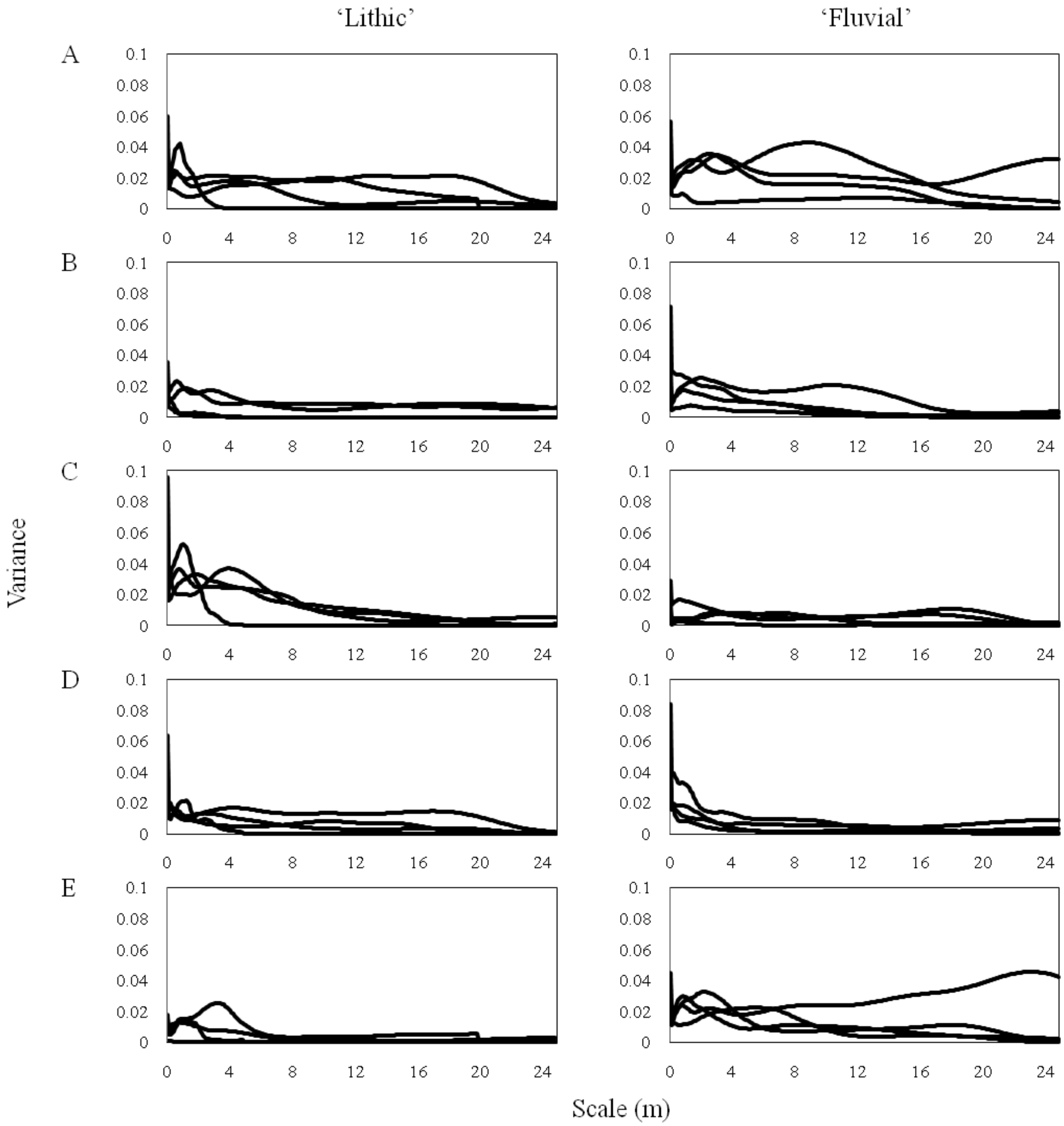

Figure 4-4 Results of wavelet analysis showing variances for understory community types: A) *Cladina*, B) *Dicranum* spp./liverworts, C) *Cladonia*/rock moss, D) *Vaccinium membranaceum*, E) *Pleurozium schreberi*

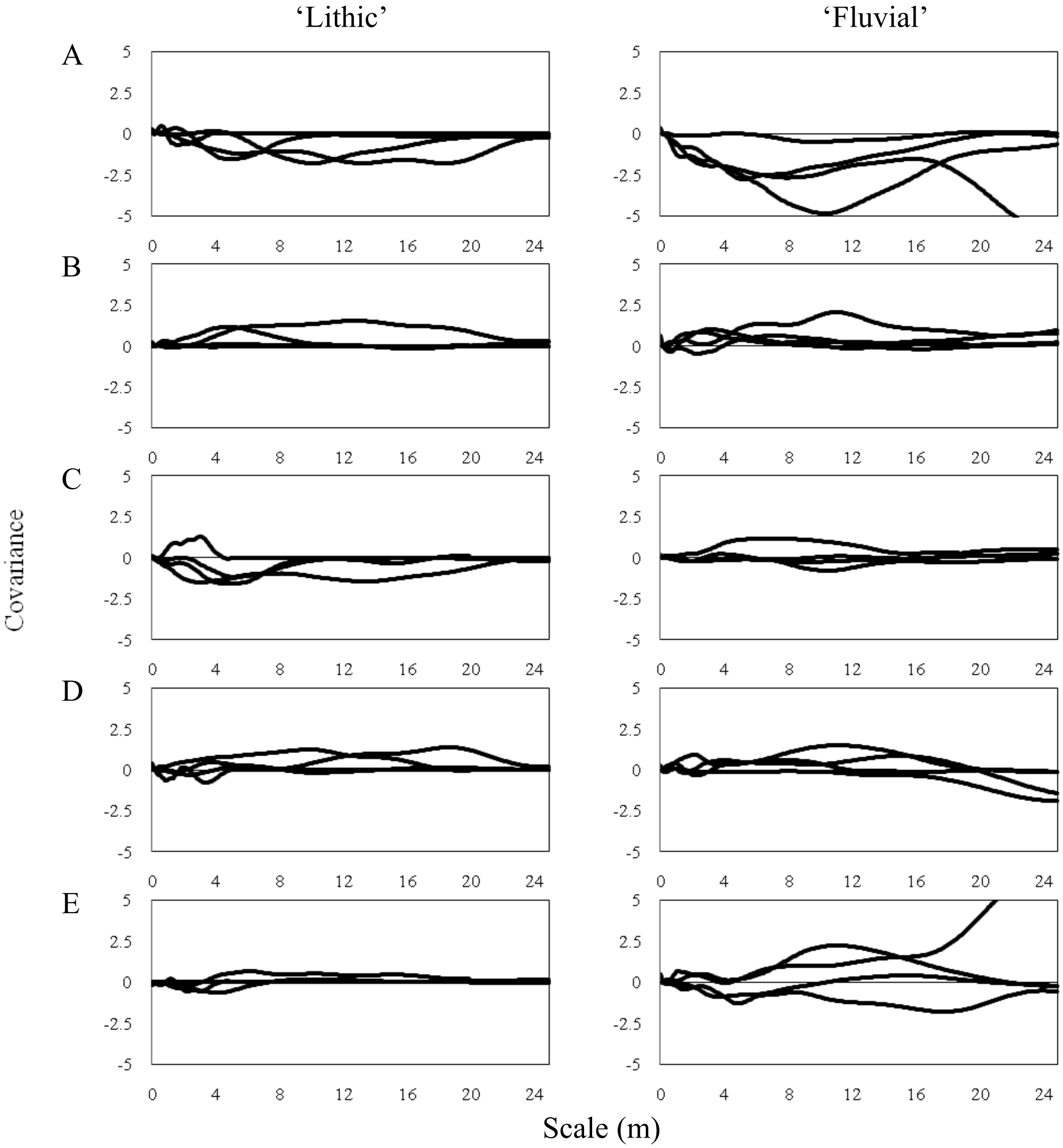

Figure 4-5 Results of bivariate wavelet analysis showing covariances for total overstory cover with each of the understory community types: A) *Cladina*, B) *Dicranum* spp./liverworts, C) *Cladonia*/rock moss, D) *Vaccinium membranaceum*, E) *Pleurozium schreberi*

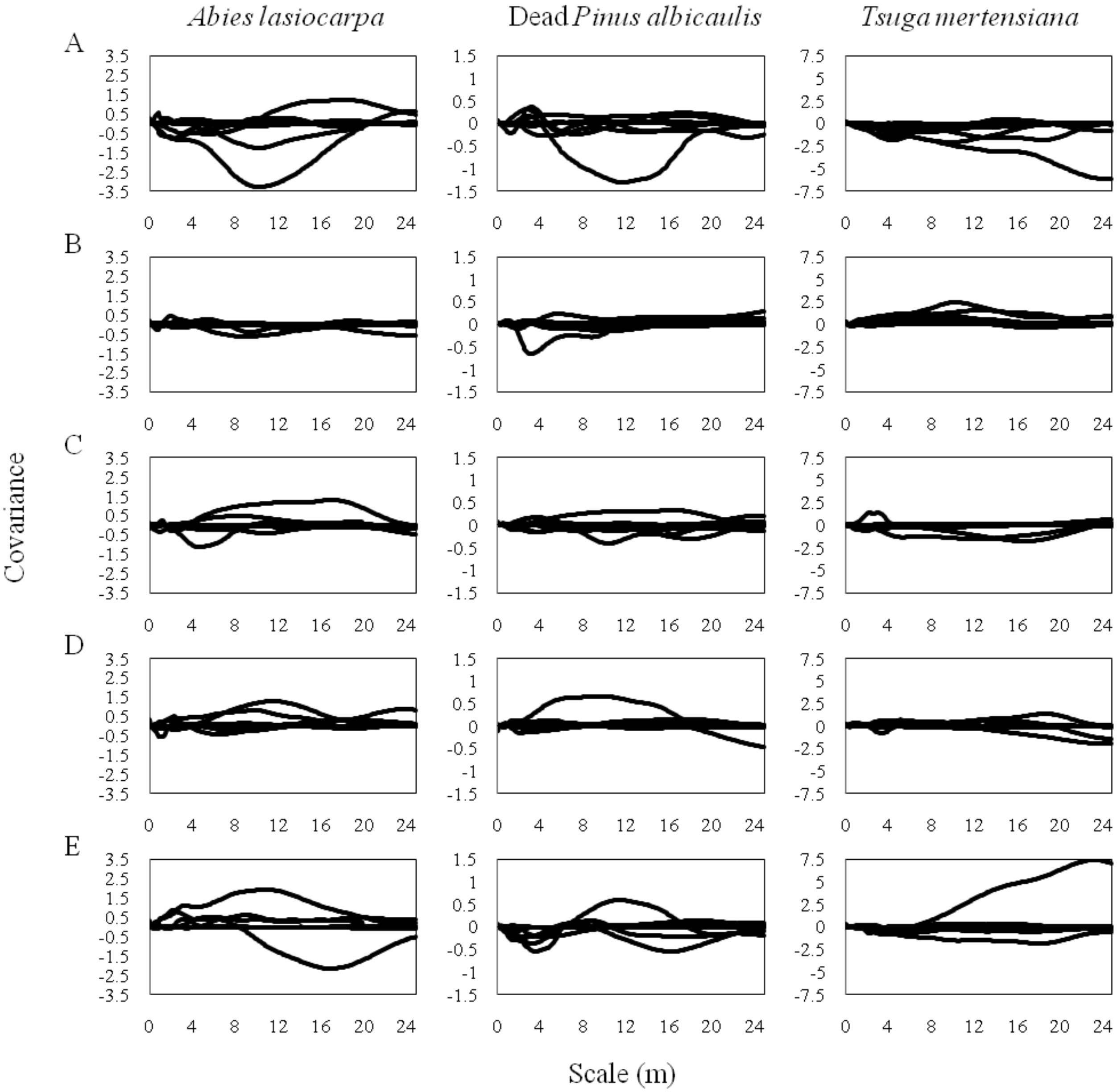

Figure 4-6 Results of bivariate wavelet analysis showing covariances for overstory cover of the three species (*Abies lasiocarpa*, dead *Pinus albicaulis*, *Tsuga mertensiana*) with each of the understory community types: A) *Cladina*, B) *Dicranum* spp./liverworts, C) *Cladonia*/rock moss, D) *Vaccinium membranaceum*, E) *Pleurozium schreberi*

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CHAPTER 5: General Discussion

In this thesis I examined: (1) how two whitebark pine (*Pinus albicaulis*) ecosystems (‘Dry/poor’ and ‘Moderately dry/poor’) have changed over time in the overstory and understory under disturbance; and (2) how spatial patterns of trees and between overstory and understory communities varied between two different site types in the ‘Dry/poor’ ecosystem

5.1 The Overstory Community

The overstory in the ‘Dry/poor’ ecosystem type shifted towards a composition more similar to the ‘Mesic/medium’ ecosystem over time. Sites on exposed rocky outcrops separated from the rest of our ‘Dry/poor’ sites, shifting towards a greater abundance of *Abies lasiocarpa*, while the other sites shifted towards a greater abundance of *Tsuga mertensiana* over time. The canopy may be influenced by greater environmental stress on our exposed ‘Dry/poor’ sites compared to less exposed sites. On harsh sites, variation in the physical environment could be important for providing sheltered regeneration sites, in turn determining overstory spatial pattern (Resler 2006). Weak spatial patterns in the overstory on exposed sites for the ‘Dry/poor’ ecosystem type suggested that such variation could be important in determining where overstory trees established on these harsh sites. *Abies lasiocarpa* may be better adapted to the summer moisture deficits and frequent frosts on our exposed ‘Dry/poor’ sites (Klinka 2000, Peterson et al 2002) than is *Tsuga mertensiana* (Klinka 2000, Peterson and Peterson 2001). This may also explain why there was a trend towards *Abies lasiocarpa* over time on these sites (Ch. 2& Ch.3).

In contrast to the results for the rocky outcrop sites, spatial patterns on glacio-fluvial fan sites of the ‘Dry/poor’ ecosystem, suggested that either life history traits or between tree interactions were important in determining spatial pattern on these sites. The observation of negative spatial covariance between *Abies lasiocarpa* and *Tsuga mertensiana* suggested either that these species compete for resources on glacio-fluvial sites (Tilman 1985) or that they select different microsites based on biological traits. If competition is an important process between these species, *T. mertensiana* may have an advantage over *A. lasiocarpa* as it is more shade tolerant (Franklin and Dyrness 1973, Alexander et al 1990) which could explain the trend towards *T. mertensiana* over time both on ‘Moderately dry/poor’ sites and glacio-fluvial ‘Dry/poor’ sites. On glacio-fluvial sites, *Abies lasiocarpa* was also consistently spatially located near dead *Pinus albicaulis* trees, which may indicate a facilitative relationship between these species at some prior successional stage (Callaway 1998).

5.2 Overstory-understory relationships in whitebark pine ecosystems

Understory communities changed little over time in both ‘Dry/poor’ and ‘Moderately dry/poor’ ecosystems, regardless of changes to the overstory. They also had weak spatial patterns, particularly in the exposed, rocky outcrops of the ‘Dry/poor’ ecosystem. However, interpretation of the relationships between overstory and understory communities over time and in space may suggest future forest composition in whitebark pine ecosystems.

In the ‘Dry/poor’ ecosystem we found that overstory change was not mirrored by understory change, which could imply resilience of the understory community. For instance, as the understory community remains intact and contains species such as regenerating *Pinus albicaulis*, it is possible that this ecosystem will eventually return to its original state through regeneration of whitebark pine and the associated community (Holling 1973). This is likely not a realistic scenario as we found many regenerating *Pinus albicaulis* seedlings infected with white pine blister rust, suggesting they are unlikely to recruit into the canopy.

We found that although the overstory changed, but the understory did not, there were strong relationships between overstory and understory composition, which is common in environmentally stressed sites (Michalet et al 2009), such as that found in the 'Dry/poor' ecosystem. The spatial analyses showed that some understory communities were positively or negatively associated with different overstory species across multiple scales. For instance, the *Cladina* community was positively associated with dead *Pinus albicaulis* and negatively associated with total canopy cover, *Tsuga mertensiana* and *Abies lasiocarpa*. This suggests that if overstory density increases, or the abundance of *A. lasiocarpa* or *T. mertensiana* increases in the canopy, there will likely be a decrease in the abundance of the *Cladina* community and an increase in *Dicranum*/liverwort and *Vaccinium membranaceum* or *Pleurozium shreberi* communities.

Exposed sites on rocky outcrops/south-facing slopes (classified as the 'Lithic' phase in BC (Banner et al 1993)) of the 'Dry/poor' ecosystem had different overstory-understory relationships than those on glacio-fluvial fans ('Fluvial', Banner et al 1993). Non-spatial analyses indicated that the understory communities on the most exposed 'Lithic' sites were associated with low overstory cover, whereas spatial analysis revealed a positive spatial association between cover of understory and overstory. This is a result of little overall overstory cover on an exposed rocky outcrop site, but the understory vegetation found there, commonly clusters around trees. This may have been due to a positive effect of overstory on understory in harsh environments (Tewksbury and Lloyd 2001) or both overstory and understory are located on the most favourable microsites on these exposed sites.

Despite this apparent association between overstory and understory cover on the 'Lithic" sites, there were differences among understory communities in their association with the overstory. On exposed 'Lithic' sites, the *Cladina* community was negatively associated with total canopy cover, while other groups such as *Dicranum* spp./liverwort and *Pleurozium schreberi* communities were positively associated with overstory cover. Our results indicate that the *Cladina* community was common on exposed 'Lithic' sites and not associated with canopy trees.

Both non-spatial and spatial analyses indicate that understory composition on 'Fluvial' sites was associated with different overstory species. Given the potential role of interspecific interactions or tree-environment relationships driving overstory change on these sites, we expect that the canopy will continue to change under ongoing disturbance to whitebark pine, and over time overstory-understory relationships will lead to a shift in the understory. Without the limiting physical environment found on the exposed 'Lithic' sites, Fluvial' sites may transition to a canopy dominated by *Tsuga mertensiana* (as seen in Ch.2 and Ch. 3). In turn, this could result in decreased total understory cover but increased abundance of certain understory communities such as the *Dicranum* spp./liverwort community. This suggests that 'Fluvial' sites may be vulnerable to ecosystem change.

The 'Moderately dry/poor' ecosystem may be the most vulnerable to regime shift due to less regenerating *P. albicaulis*, greater stand density and increasing dominance of *Tsuga mertensiana*. Ongoing disturbance to whitebark pine will continue to decrease the abundance of *Pinus albicaulis*, and increase *Tsuga mertensiana* and *Abies lasiocarpa* in the overstory. This will likely alter the understory due to the strong association between understory communities and different overstory trees.

5.3 Restoration applications

Planting rust-resistant *Pinus albicaulis* seedlings to restore whitebark pine ecosystems in NW BC would be best applied in the 'Dry/poor' ecosystem. These stands have continued to house regenerating *P. albicaulis* due to the presence of suitable microsites and the lack of competition from other tree species. Rust-resistant seedlings would enable recruitment of *P. albicaulis* to the canopy, slowing or reversing the shift in the canopy towards shade tolerant conifers. Exposed 'Lithic' sites are the most limited by harsh environmental conditions, so are not likely to see increased canopy density with the presence of shade tolerant conifers such as *Abies lasiocarpa*. Simply planting rust-resistant seedlings could potentially be enough to facilitate the return to the original ecosystem state. Planting rust-resistant *P. albicaulis* seedlings on 'Fluvial' sites in the 'Dry/poor' ecosystem may not necessarily ensure whitebark pine will re-establish in the canopy as biotic factors between trees and their environment appear to be important in shaping the canopy. Other restoration techniques, such as use of prescribed fire, may be needed to restore 'Fluvial' sites as this would reduce the abundance of shade tolerant conifers such as *Tsuga mertensiana*. The 'Moderately dry/poor' ecosystem would also likely require fire as a restoration technique to open up the dense canopy and create suitable seed caching sites for Clark's nutcrackers (Tomback 1982). These stands could also be planted with rust-resistant *P. albicaulis* to ensure that some are able to recruit to the canopy.

5.4 Future Research

This thesis indicates that site type is important in determining the impact of disturbance on ecosystems and how forests may change in the future. Whitebark pine research would benefit from ongoing monitoring of the sites surveyed in the 1970/80's and in 2007/09 to continue assessment of forest change. A greater number of transects across 'Fluvial' and 'Lithic' sites in the 'Dry/poor' ecosystem for spatial analysis may also help clarify trends and make inference into process more feasible. I would recommend that future research on whitebark pine ecosystems of BC include dendrochronological work to determine exactly how these stands have developed over time throughout succession. For instance, when did *Tsuga mertensiana* and *Abies lasiocarpa* establish and begin to increase in abundance on these sites? I would also recommend expanding the areas surveyed to determine whether whitebark pine ecosystems across the Coastal and Rocky Mountains have changed over time in similar ways (albeit towards different shade tolerant conifers depending on location). I would recommend more research on canopy-understory interactions across site types within the Coastal and Rocky Mountain Ranges. Finally, research on the effects of climate and climate change on the direction of change within these systems would greatly inform restoration of whitebark pine ecosystems across its range.

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APPENDIX 1

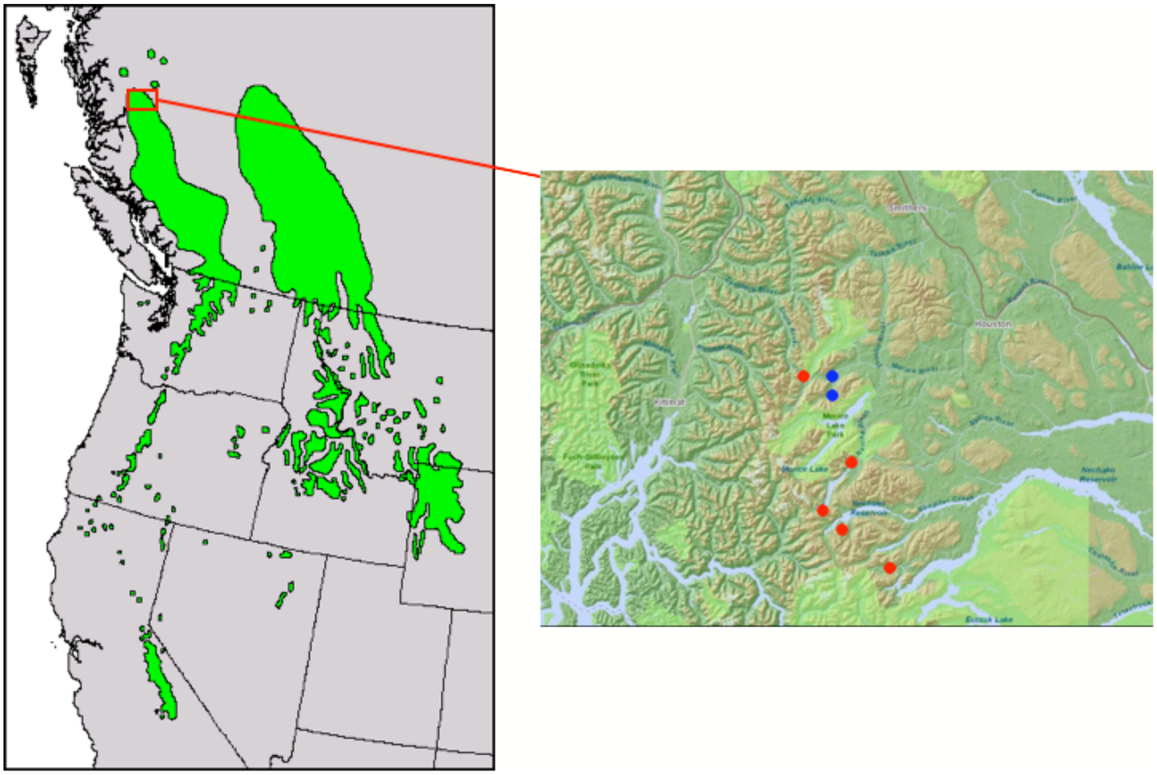

Figure 1 - Map of study area. The left box indicates the range of *Pinus albicaulis* (Little 1999) and the right box indicates the study area south of Smithers, BC. Blue dots represent sites only surveyed for Ch.4 spatial analyses and red dots represent re-surveyed sites as well as sites surveyed for spatial analyses.

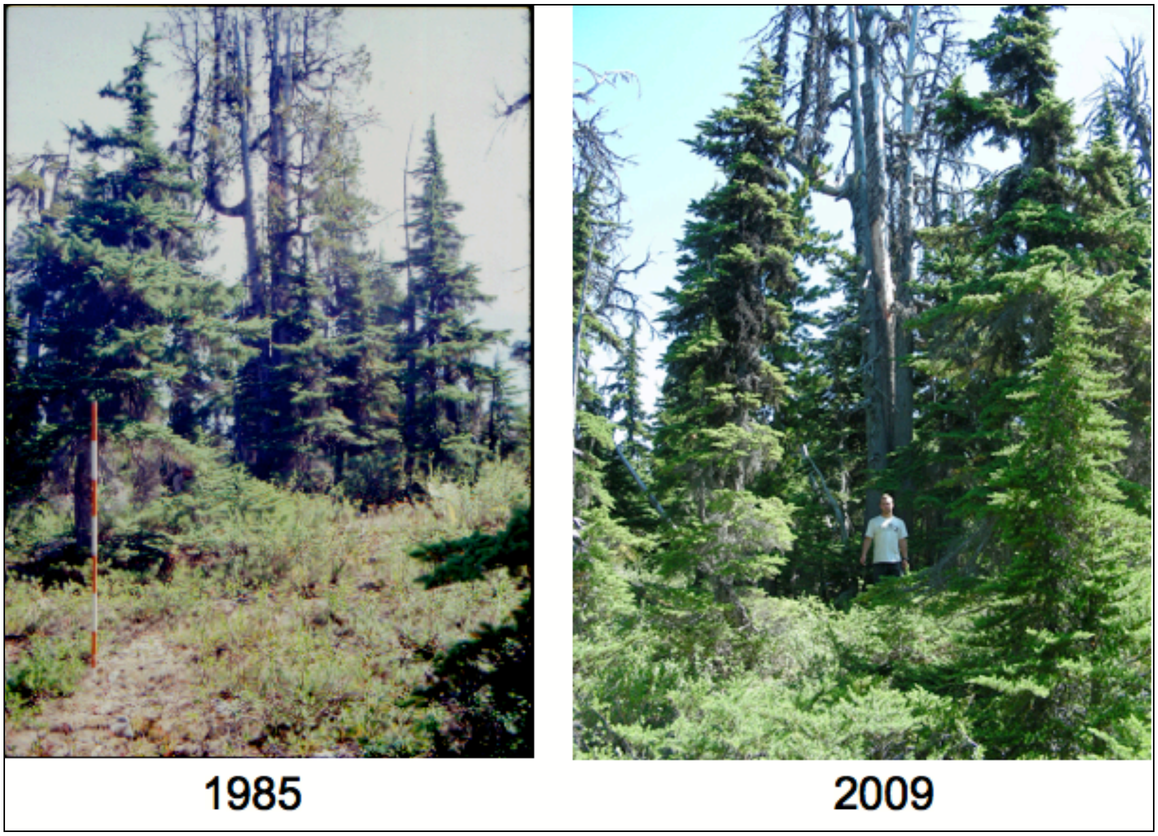

Figure 2 – Photos from the two survey periods (Plot 922) taken from the same location on Coles Lake, BC.

Table 1 – Detailed study site descriptions for re-surveyed sites

Stand	Site	Ecosystem Type	Survey period	Latitude	Longitude	UTM	Elevation	Date surveyed	Age†	Disturbance intensity (snags/ha)
TL041	41	*Mesic/medium*	First	53°29'15	127°16'30"		1070	8/26/85	.	.
AC41	41	*Mesic/medium*	Second			0614478 5927888	.	7/24/09	56-443	163.54
TL043	43	*Mesic/medium*	First	53°29'50"	127°13'15"		980	8/27/85	.	.
AC43	43	*Mesic/medium*	Second			0617765 5929089	966	7/26/09	168-204	29.03
TL046R	46	*Mesic/medium*	First	53°30	127°12'20"		1020	8/27/85	.	.
AC46	46	*Mesic/medium*	Second			0617847 5929789	1008	7/26/09	69-126	271.49
P925	925	*Mesic/medium*	First	53°29'45"20	127°14'10"20		1030	8/27/85	230-280 [1]	166.03
AC925	925	*Mesic/medium*	Second			0616842 5929044	925	7/25/09	112-164	200.65
P928	928	*Mesic/medium*	First	53°28'	127°15'		1010	8/28/89	78-207 [1]	0.00
AC928	928	*Mesic/medium*	Second			0615337 5926218	980	7/29/09	60-250	0.00
TL044	44	*Moderately dry/poor*	First	53°29'50"	127°11'25"		1010	8/27/85	.	.
AC44	44	*Moderately dry/poor*	Second			0618845 5928933	951	7/28/09	95-355	311.10
P67	67	*Moderately dry/poor*	First	54°49'0"	127°33'30"		990	8/11/78	182-244 [1]	300.00
SH67	67	*Moderately dry/poor*	Second	53°48'57"	127°31'55"		1017	9/6/07	69-306	332.30
P493	493	*Moderately dry/poor*	First	53°36'55"	127°31'35"		1020	7/14/80	100-286 [1]	334.29
SH493	493	*Moderately dry/poor*	Second	53°37'06"	127°31'34"		1026	9/6/07	153-190	73.10
P923	923	*Moderately dry/poor*	First	53°29'	127°14'		1080	8/26/85	170-265 [1]	176.26
AC923	923	*Moderately dry/poor*	Second			0617213 5928104	1055	7/27/09	175-415	133.99
TL042	42	*Dry/poor*	First	53°29'	127°16'30"		1380	8/26/85	.	.
AC42	42	*Dry/poor*	Second			0615332 5927714	1130	8/1/09	112-240	38.10
P65	65	*Dry/poor*	First	54°93'0"	127°49'30"		861	8/11/78	160-330 [1]	681.82
SH65	65	*Dry/poor*	Second			0577549 6002545	831	8/31/07	10-590 [2]	750.00
P922	922	*Dry/poor*	First	53°29'	127°14'		1095	8/26/85	115-247 [1]	133.92
AC922	922	*Dry/poor*	Second			0617138 5928415	1062	7/27/09	171-301	151.78
P924	924	*Dry/poor*	First	53°29'50"20	127°14'20"20		1150	8/27/85	142-180 [1]	0.00
AC924	924	*Dry/poor*	Second			0616692 5929121	1073	7/25/09	160-200	254.30
TL067R	67R	*Dry/poor*	First	53°54'45"	127°29'10"		970	9/2/85	.	.
SH67R	67R	*Dry/poor*	Second	53°54'44"	127°29'35"		987	9/6/07	44-419	281.33

†Age range estimated from tree cores of different species from each stand. This does not represent absolute stand age.

[1] Ages approximated to account for location on stem where core was taken (i.e from the base vs. breast height).

[2] Age range calculated from stand reconstruction data

Appendix Literature Cited:

Little Jr., E.L., 1999. U.S. Geological Survey, Digital representation of "Atlas of United States Trees"