FOREST LIGHT AND STRUCTURE IN RELATION TO DISTURBANCES: COMPARING MOUNTAIN PINE BEETLE, WILDFIRE AND SALVAGE LOGGING

by

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ABSTRACT

In this research I characterize the early post-disturbance forest light environment and structure of lodgepole pine forests in the southern interior of British Columbia after mountain pine beetle attack, wildfire and salvage logging. These different, and at times sequential, disturbances influence structural complexity, overstory composition and the heterogeneity of light transmission in different ways. Beetle disturbance left complex patterns of gap light in the mixed-species canopy, which accelerated the growth release of surviving trees. After wildfire, there were predominantly dead structural legacies and high variability of light and residual structural elements. Salvage logging after fire or beetles significantly reduced the amount and diversity of biological legacies and led to a more homogeneous, bright light environment than after only the natural disturbances. The resulting homogeneity of post-salvaged stands and variability of light and structure in unsalvaged stands will influence patterns of forest development and have implications for management.

Keywords: lodgepole pine forests; natural disturbances; salvage logging; light transmission; residual structure; biological legacies

For John Jules
1954 to 2010

John exuded joy, laughter, and a strong heart every time I saw him. He inspired and supported my graduate studies research and every time I encountered him I walked away with a new perspective and some of his pithy words and thoughts to ponder

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GLOSSARY

Biological legacy	An organism, a reproductive portion of an organism, or a biologically derived structure or pattern inherited from a previous ecosystem.
Residual structure	Trees left standing after harvesting. Sometimes used in relation to structure remaining in a forest ecosystem after a major natural disturbance. For the latter case it is also termed “secondary“, particularly in British Columbia.
Advanced regeneration	Trees that have become established naturally under a mature forest canopy and are capable of becoming the next crop after the mature crop is removed.
Hemispherical photography	Also known as fisheye or canopy photography, is a technique to estimate solar radiation and characterize plant canopy geometry using photographs taken looking upward through an extreme wide-angle lens.
PAR	Photosynthetically Active Radiation with spectral range of 380 – 710 nm. Often used synonymously with visible light (380 – 770nm) because of the overlap. Other spectral bands may be important for the thermal environment in the understory but the methods used in this study do not capture these and are not the focus of this research.
LAI	Leaf Area Index is defined as the one sided green leaf area per unit ground area in broadleaf canopies, or as the projected needleleaf area per unit ground area in needle canopies.

INTRODUCTION

Disturbances are important catalysts in population and community dynamics, they drive ecological processes and are key regulators in patterns of development in forest ecosystems (White 1979, White & Jentsch 2001). Disturbance events vary broadly in size, frequency and intensity, and forested landscapes around the world are increasingly affected by novel disturbances, often at the extremes of more than one of these gradients (i.e. Turner et al. 1998, Bergeron et al. 2006, Lindenmayer et al. 2008). The appearance of unprecedented or new combinations of disturbances poses challenges to researchers and practitioners alike in developing appropriate policy, management and planning for disturbance-prone forests. The complexity of managing disturbance-prone forest ecosystems is challenged by factors such as major gaps in ecological and management knowledge (Lindenmayer et al. 2008), high variability of disturbances and the ecological responses to disturbance (DeLong & Kessler 2000, Lertzman et al. 1998), differing land-use histories, strong socio-economic concerns and polarised views in relation to them (Burton 2006, DellaSala et al. 2006), and altered disturbance regimes and future uncertainties as a result of climate change (Bentz et al. 2010, Bergeron et al. 2006). Disturbance *severity* refers to the effects a disturbance event has on organisms, communities or ecosystems (White 1979). Other factors acting together to vary the disturbance and its effects include the cause or agent (i.e. type), timing, heterogeneity (i.e. variation in intensity) and duration. Disturbances may be discrete events that are completed over a relatively short period of time, such as many fires, or may exert their influence over a prolonged period of time (such as some insects and disease) (Lindenmayer et al. 2008, Lertzman & Fall 1998, Lertzman et al. 1997, Shore et al. 2004). Important areas of disturbance research in forests include understanding the effects on organisms, on ecosystem processes, on the interactions between organisms and processes, and determining what conditions promote cumulative and/or a magnification of effects (Lindenmayer et al. 2008).

Early post-disturbance environments reflect the initial effects of a disturbance well. By characterising the elements of a forest that persist through a disturbance, one can get a measure of severity (Turner et al. 1998). These forest attributes, also known as biological legacies, include organisms, organically-derived structures, and organically-produced patterns that survive from the pre-disturbance system (Franklin et al. 2000, Franklin et al. 2002). Biological legacies vary in composition, spatial arrangements and functional form and are a consequence of the interaction between the pre-disturbance environment and the nature of the disturbance itself (Franklin et al. 2000, Franklin et al. 2007, Lindenmayer & Noss 2006, Turner et al. 1999). They are critical to the response to and recovery of the forest ecosystem post-disturbance (Foster & Orwig 2006, Turner et al. 1999, Franklin et al. 2000), are integral to the distinctive conditions of early-successional ecosystems (Swanson et al. 2011), create habitat for surviving and colonising organisms (DeLong & Kessler 2000, Klutsch et al. 2009) and have been shown to be linked to the conservation of biological diversity and to ecosystem function (Swanson et al. 2011, Franklin et al. 2007). Early post-disturbance systems are dynamic environments. Thus, management activities during this stage can strongly influence the duration of and patterns in early successional pathways and future stand development (DellaSalla et al. 2006, Franklin et al. 2002, Collins et al. 2011, Franklin et al. 2007).

A number of interacting factors will influence future development pathways in post-disturbance environments (Astrup et al. 2008, Coates et al. 2006, Nigh et al. 2008, Lochhead & Comeau 2011). However, the abundance, distribution and composition of residual structure, and the changes to the availability of resources such as light, moisture and nutrients are, in general, determined by the type and severity of the disturbance (Franklin et al. 2002, Franklin et al. 2007, Turner et al. 1999). High severity disturbances, such as crown wildfire, will more completely remove or kill the canopy, providing greater opportunity for the establishment of new individuals either through regeneration and colonisation (Turner et al. 1999, Axelson et al. 2009). A less severe disturbance is more likely to leave larger amounts of residual structure and there will be more emphasis on the reorganisation of surviving trees and advanced regeneration in the dynamics of forest development (Diskin et al. 2011, Safranyik & Wilson 2006, Vyse et al. 2009, Rocca & Romme 2009). The relative importance of these two different processes (establishment of new individuals versus reorganisation of the existing community) in stands shaped by different types and severities of disturbance is a primary focus of my research.

Salvage logging is practiced widely around the world (Lindenmayer et al. 2008). Salvage is logging after a natural disturbance event, such as wildfire or insect attack, which typically targets the removal of dead, dying or damaged trees as a way to recoup economic gains before they are lost. Although there can be various justifications for salvage logging (e.g. Foster & Orwig 2006, Shore et al. 2004, B.C. MoFR 2007), the economic rationale is the most obvious. However, the trade-offs between economic opportunity and ecological issues are often overlooked, and this can lead to unexpected ecological consequences (Lindenmayer & Noss 2006, DellaSalla et al. 2006). For example, in practice, many healthy trees are often taken in the harvest as well as damaged trees, particularly in larger disturbance patches where clear-cut logging prescriptions are used (Foster & Orwig 2006, Safranyik & Wilson 2006, Burton 2006, Franklin et al. 2007).

There is abundant evidence that salvage logging interferes with the natural recovery of stands (Donato et al. 2006, Rocca & Romme 2009) and alters a variety of ecosystem processes (Lindenmayer et al. 2008), population dynamics, and community composition (Kurulok & Macdonald 2007). Lindenmayer and Noss (2006) summarise three main but interrelated consequences of salvage logging: 1) reduced stand structural complexity; 2) altered ecosystem processes and functions; and 3) changes to the distinctive characteristics of biodiversity of the recovering ecosystem. Furthermore, active management (ie harvesting and/or restoration) is often unnecessary following disturbance events in order to achieve desired future conditions (i.e. Kayes & Tinker 2012, Coates et al. 2006, Burton 2006, Turner et al. 1998).

The amount of residual structure in the overstory and the light transmitted through the remaining canopy and into the understory can be considered as indicators of disturbance severity. Photosynthetically active radiation (PAR) is essential for growth and survival in the understory and the way light intercepts the understory largely depends on the structural architecture and spatial arrangement of these biological legacies within the canopy (Canham et al. 1994, Messier et al. 1998). Light and overstory structure are therefore key variables driving regeneration, species and community level stand responses and early successional patterns (Bartemucci et al. 2006). There is a large body of literature on light dynamics in forest stands primarily represented by intact canopies and/or partial-cut silvicultural systems (i.e. Leiffers et al. 1999, Canham et al. 1990, Drever & Lertzman 2003, Lochhead & Comeau 2012, Van

Pelt & Franklin 2000). Other studies have explored post-disturbance regeneration in a variety of forests finding growth and survival to be influenced and constrained by several factors (Antos & Parish 2002, Astrup et al. 2008, Nigh et al. 2008, Vyse et al. 2009, Turner et al. 1999). However, these light and canopy structure studies haven't examined concatenating disturbances, such as fire or insects followed by salvage logging, and there is still little information characterising light regimes and canopy structure across a wide range of disturbance scenarios.

The lodgepole pine (*Pinus contorta* Dougl.) forests of the interior of British Columbia (B.C.), Canada, provide a good case study of multiple interacting disturbances. Forests across western North America have experienced the largest and longest outbreak of the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins on record, beginning in the mid-1990s (NRC, Canadian Forest Service and USDA Forest Service, Forest Health Protection). Lodgepole pine is the most susceptible host, resulting in widespread mortality and heavy economic impacts in pine dominated forests in the last decade or so (B.C. MoFR 2007, Shore et al. 2004, Westfall & Ebata 2009). In addition, large, high intensity wildfires have burnt extensive areas of forest across the province of British Columbia since the early 2000s, with major "firestorm" events occurring in 2003, 2004, 2009 and 2010 (B.C. Wildfire Management Branch). Widespread and intense salvage logging has been undertaken across B.C. since 2001 (Westfall & Ebata 2009), however, not all naturally disturbed stands should and can be salvaged (Burton 2006, Coates et al. 2006). To make better decisions about the post-disturbance management of these forests, we need a better understanding of the ecological trade-offs between post-disturbance harvesting and other forms of management.

My goal in this research was to study the early post-disturbance environment of three categories of disturbance, insect epidemic, fire, and salvage logging, within the same type of forest. Specific objectives were to (i) characterise overstory light transmission and understory light availability under different disturbance scenarios using hemispherical photographs, (ii) quantify how different disturbances affects the structural and compositional attributes of the overstory, and (iii) examine the light and structural patterns over a short period of time in the early stages of post-mountain pine beetle attack.

METHODS

Study Area

I conducted this research in the plateau region of the southern interior of British Columbia, near the city of Kamloops (Fig. 1). In B.C., ecosystems are classified according to similar ecological, physiographical and climatic features using the BEC system (Meidinger and Pojar 1991). I conducted the research within the Montane Spruce biogeoclimatic zone and restricted sites to the dry mild subzone and North Thompson Uplands variant (MSdm3; previously classified as MSdm2; Lloyd et al. 1990, Lloyd 2005). The MSdm3 occurs at mid elevations on the plateau downcut by the North Thompson River valley north of Kamloops. The MSdm3 is dominated by mixed, mature seral stands represented by lodgepole pine *Pinus contorta* Dougl. Ex Loud. and the more shade-tolerant conifers interior (hybrid) spruce *Picea engelmannii* Parry ex Engelm. x *Picea glauca* (Moench) Voss and sub-alpine fir *Abies lasiocarpa* (Hook.) Nutt. Smaller amounts of Douglas-fir *Pseudotsuga menziesii* (Mirb.)Franco as well as trembling aspen *Populus tremuloides* Michx are also found in the MSdm3 landscape. Lodgepole pine (LPP), which is a species typical of early seral and young stands, often dominates stands across the landscape which have been subject to stand-replacing fires. LPP dominated forests in the MSdm3 are not only commercially desirable and suitable to clear-clearcutting silvicultural systems but also very susceptible to mountain pine beetle (Lloyd et al. 1990, Shore et al. 2004). I selected two sites that were between 1220 – 1520m in elevation on either side of the North Thompson River: Community Lake, 33km to the northeast from Kamloops (50º 57’4’’N; 120 5’40’’W); and Parky Mountain, 53km to the north of Kamloops (51º 9’40”N; 120 19’18”W; Fig. 1).

The climate in the MS zone is generally cool and dry with a mean annual precipitation estimated between 525-650mm (Lloyd et al. 1990). The growing season begins around May and runs through to the end of August with a mean warmest month temperature of 13.4º Celsius. Given the location of the study area the solar angles are expected to be characterised by relatively low maximum solar elevations through the summers and the longer winters with very low solar elevations (Leiffers et al. 1999).

Reference conditions

Comparable, undisturbed Montane spruce zone forests close to the study area in which baseline conditions could be measured were not available because of widespread disturbances by mountain pine beetle, wildfire, and logging. Thus I could not make direct comparisons of stands before and after natural disturbances. However, I queried other studies in both similar and different forest types and with silvicultural treatments representing varying levels of retention to provide some reference conditions for pre-disturbance conditions and for putting the values obtained in this study in context (Table 1). Pre-disturbance conditions in the MSdm3 stands I studied were probably variable, but most likely similar to mature Engelmann spruce-subalpine fir temperate forest (Wright et al. 1998), Montane spruce-fir forest (Canham et al. 1990) and uncut second-growth Douglas-fir stands (Drever & Lertzman 2003).

Experimental treatments

Sampling in the study area occurred within 5 years of disturbance in areas burnt by the 2003 Firestorm (Fire Protection Program 2004) and in areas which had experienced beetle outbreak. The current mountain pine beetle epidemic began in the mid 1990's in B.C., spreading through the Kamloops Timber Supply Area from around 2001 (BCMoFR 2007). According to local inventory records for the Community Lake site, by 2005 60% of lodgepole pine had been attacked and in various stages after mortality (TFDC 2006). The Parky Mountain site occurs on the western edge of the 26,420 hectare McClure wildfire that was ignited on July 30, 2003 and contained after 48 days (Protection Branch 2003).

I selected stands following a mixed-effect design structure of plots within replicated blocks nested within four disturbance scenarios or "treatments" (Fig. 2). These treatments were selected to compare the combinations of fire, beetles, and forest salvage logging:

Mountain pine beetle, unsalvaged treatment (MPBU), with a mountain pine beetle outbreak peaking in 2005 and subsiding after that. No management has occurred since the disturbance.

Mountain pine beetle, salvaged treatment (MPBS). These blocks were logged with a clear-cut harvesting prescription from January to May 2007, and then planted in the spring 2007.

Wildfire burnt, unsalvaged treatment (BU), meaning a wildfire went through the forest for several weeks in 2003 and there has been no further management intervention since the disturbance.

Wildfire burnt, salvaged treatment (BS). After the wildfire, blocks were logged May to Sep 2004 and planted the following spring 2005.

Harvesting in both scenarios 2 and 4 was a result of the increase in the Annual Allowable Cut (AAC) effective from January 1st 2003 to allow explicitly for fire and beetle salvaging (Pederson 2003). The harvesting units I selected for this study ranged in size from 11.8 ha to 150.8 ha, although sampling occurred in a smaller area within the largest blocks (Table 2).

Sampling design

There were three replicate blocks for each of the treatments, except for the beetle, unsalvaged, which had two, making this an unbalanced design (Table 2, Fig. 2). I only included stands where the dominant cohort of pine was between 80 and 100 years in age. I attempted to select for stands where the dominant (more than 50%) species was lodgepole pine, but this was not possible in the unsalvaged burnt scenario since many of these stands in the study area were targeted for salvage after the 2003 fire. Also, I attempted to sample in blocks that were at least 20 ha in size. Two of the salvaged block options did not meet the size criterion but were suitable because of general slope and aspect (ie one burnt replicate was 11.8 ha, and a beetle replicate was 14.5 ha; Table 2). I reconstructed the pre-disturbance species composition and some structural parameters for canopy trees in the salvaged blocks from Cruise Compilation Project and Stand Summary Reports (MOF 2006; SEDC 2004; Table 3) to assess their comparability to the unsalvaged stands. The stands for which I examined this were generally comparable to the unsalvaged stands I studied.

Within each block, a randomized systematic grid with minimum 50 m spacing between grid points was established. The grid point, or “plot” in this case, is also the plot centre in which a fixed area sample unit of 4 X 4 m (16 m^2) was established for collecting a selection of metrics. Only plots characterized as within the mesic range of the edatopic grid (Meidinger and Pojar 1991) for the MSdm3 were selected. Plot sites with piles to be burnt or recently burnt were avoided and edge influences were minimized by establishing plots at least 25 m from openings or the cut-block boundaries. Sixty plots were sampled for all treatments except MPBU (N=59 plots; Table 2).

Light and structure measurements

I used hemispheric photographs of the forest canopy (see Fig. 3 for an example) to obtain estimates of understory light availability, overstory light transmission and leaf area index. Hemispheric photography provides a record of the overstory geometry relative to a position in the understory (Leiffers et al 1999) and is an indirect optical technique that provides a good estimation of the mean seasonal light availability reaching any location in the understory (Fiala et al. 2006, Frazer et al. 2000b; Gendron et al. 1998, Bartemucci et al. 2006).

At each plot centre I levelled a Canon EOS 5D digital camera with Sigma 8mm F3.5 fisheye lens on a tripod at a minimum height of 1.5 m from the ground surface, with an LED oriented north. During September 2007, between September and October 2008 and in October 2009 I took photographs under overcast sky conditions or at dawn and dusk to avoid sun glare distortions and to reduce the spatial and temporal variation in light within the forest. I analysed the images with the software Gap Light Analyzer 2.0 (GLA: Frazer et al. 2000a) using a custom-built lens calibration from data provided by the Sigma Corporation. I used the default settings except for the Universal Overcast (UOC) Sky region brightness model configuration, and the Clear-sky coefficient, which was adjusted to 0.65 to reflect regional conditions.

Using the latitude, slope and aspect, GLA computes a number of attributes of canopy structure and transmitted gap light, which integrate daily and seasonal measures for that location for a specified growing season. I used relative estimates (measured in percentages) versus absolute estimates (measured as mol m^{-2} day^{-1}) for light transmission because not all locally specific climate parameters could be easily obtained. Thus, for each photograph the percentage of total incident light or photosynthetic active radiation (PAR) is transmitted direct (TrDir) and transmitted diffuse (TrDif) radiation. I inferred dates for the growing season from a combination of expert opinion and derived variables generated from the ClimateBC v3.2 model (Wang et al.

2006), which uses annual climate normal data for the reference period 1961-1990. Thus, I specified early June to late August for Community Lake and late May to early September for Parky Mountain.

Additional measures more directly related to overstory structure that GLA provided each plot included the percentage canopy openness (or full sunlight) and effective leaf area index (LAI: Frazer et al. 2000a). Percentage canopy openness is essentially a measure of overstory cover that calculates all the unobscured areas in the sky hemisphere directly above each photo point (Canham et al. 1994). It is also referred to as overstory light transmission. The openness measure can be distinguished from the understory light availability or transmission, which are estimates based on that structural measure plus a variety of other site inputs and assumptions (Frazer et al. 2000a). The foliage captured in the photos includes the main overstory trees species, the intermediate layer of sub-canopy trees, and advanced regeneration of tree species and taller shrubs that are functionally part of the understory. However, because of the minimal amount of understory foliage above the camera height of 1.5 m, all vegetation in this study is considered part of the “overstory”. The LAI 5 ring index used here is defined as the ratio of leaf surface and/or needle area per unit ground area integrated over the zenith angle 0 to 75 degrees (foliage m^2/ground m^2).

I collected other quantitative descriptors of the overstory stratum at each sampling plot. Measurements included for the live or dead tree stem nearest to the plot centre in each of the canopy (A2) and sub-canopy (A3) size classes: height (m), the diameter at breast height (DBH; in cm, taken at a height of 1.3 m), species, and distance (cm) to plot centre. Using criteria derived from Provincial guidelines, canopy trees are specified as having a DBH larger than 15 cm, and sub-canopy trees as having a DBH 7.5 cm to 14.9 cm (Province of B.C. 1998). The main tree species sampled were lodgepole pine, sub-alpine fir, interior spruce and Douglas-fir with Western redcedar *Thuja plicata* and black cottonwood *Populus trichocarpa* present only in very small numbers.

For the lower overstory stratum (B1, height > 2m), within each of the 16 m^2 plots I identified and counted all individual saplings (with a DBH less than 7.5 cm) present to assess density (the number of stems within each plot) and frequency (the percentage of plots where a taxa was found). I visually estimated the percent cover of all individuals rooted within the plot for each coniferous species and other upper shrub plant species, including alder *Alnus* sp. and poplar *Populus tremuloides*, and as a summed total percentage cover value for that stratum.

Data analysis

I derived estimates of canopy and sub-canopy densities and basal areas using a plotless density estimator method (Cottam and Curtis 1956). I estimated the average density of trees (number/ha) for each block, a plot-based predictor for the basal area or cover (cm^2) of the tree measured, which when multiplied by density gives the block total basal area (m^2/ha). The formula for the unbiased estimate of density using the method outlined from Mitchell (2007) is:

$$\lambda = \frac{n-1}{\pi \sum_{i=1}^{n} R_i^2}$$

Where n is the number of sample plots in that block, i is a particular plot, where i = 1,..., n, and R_i is the distance from plot centre to the nearest tree for plot i. I calculated the estimates of confidence intervals for average block density through normal approximation at the ($1-\alpha$) 100% level. I estimated heights of individual trees using a distance scope and trigonometry. I measured tree species composition as the relative basal area (percentage basal area of the total basal area calculated for all individuals of that species) and relative frequency (percentage of the total number of observations for that species) of the overstory trees for the canopy and sub-canopy stratum.

I used both univariate statistical analyses and mixed-effect models developed in R (R Development Core Team 2010). I used an analysis of variance (ANOVA) to characterise and compare the four disturbance scenarios, the effect of treatment on the means of various light and overstory structural variables. I modelled treatment differences with linear mixed-effects models (lme procedure in R) and fit by the restricted maximum likelihood (REML) method following steps described in Zuur et al. (2009). All linear models accounted for random variation due to nesting of blocks within treatment units. I compared various models using corrected Akaike Information Criteria (AIC_C) and visually examined residual plots to evaluate model fit, normality and homogeneity of variance. I used log or arcsine transformations when necessary to homogenize the variance or satisfy assumptions of normality. With the p-value adjusted, I judged treatment differences to be significant at α=0.05. For canopy and sub-canopy tree measures I used only pairwise unsalvaged treatments in comparative analysis. When there were comparisons between all treatments, i.e. as for GLA generated variables and slope, I used a Tukey post-hoc test to determine which treatments were different.

I also examined the understory light and overstory structural patterns within the mountain pine beetle unsalvaged stands between years 2007 and 2009. I calculated the difference between years (D) for each plot for each of the four GLA derived variables (TrDif, TrDir, Open, LAI). Using the D value, the effect of time on each of the GLA variables was modelled with the following random intercept linear mixed-effects model:

$$D_{jk} = \beta_0 + \beta_{1j} + \varepsilon_{jk} \quad j = 1,2, k = 1,...29,30$$
$$\beta_{1j} \sim N(0,\sigma_a^2) \quad \varepsilon_{jk} \sim N(0,\sigma_b^2)$$

where *D* is the between year difference value for each of the GLA variables for *k*th sampled plot, β_0 is the intercept (fixed), β_1 is the *j*th block (random effects), ε is the residual error term (sampled plots within block) assumed to be normally distributed and with constant variance (*a* for random effects and *b* for residuals). Plots of the residuals were examined to evaluate model fit, normality and homoscedasticity.

RESULTS

Canopy openness and leaf area index under all treatments

The canopy openness environments created from the various disturbance scenarios examined were widely variable (Fig. 3) with the average % openness differing between each of the treatments (Table 3, ANOVA, $p<0.0001$). Salvage logging resulted in a relatively narrow range of high percentages of canopy openness in stands previously subject to beetle outbreaks (72.8% to 94.4%) and after wildfire (81.6% to 94%; Fig. 3). Wildfire alone created moderate to high levels of % openness (31.5% to 73.5%), whereas beetle-mortality four years after the peak of the attack resulted in relatively low levels of % openness (6% to 35.8%; Fig. 3). Leaf area index (LAI) was very low for all treatments except for unsalvaged beetle stands where it was between 0.84 to 3.63 foliage m^2/ground m^2, indicating that substantial live residual structure was retained in these stands (Table 3).

Understory light availability under all treatments

Understory light availability was highly variable in the unsalvaged stands examined (after both beetle and wildfire; Table 4). The % diffuse transmitted radiation ranged between 7.5% and 87.6% and % direct transmitted radiation ranged between 1.9% and 93.9% across the unsalvaged treatments (Fig. 4). Salvage logging affected the range of both diffuse and direct transmitted light, where the understory light availability was at its highest levels (90% or above) in most parts of the salvaged stands (Fig. 4). The average diffuse and direct transmitted radiation values differed statistically between all treatments (ANOVA, p-value <0.0001).

Comparing canopy openness and light transmission between treatments

Salvage logging tends to homogenize variable post-disturbance environments. Canopy openness and light transmission in both of the salvaged scenarios (after wildfire and after beetles) were generally more similar to each other than to any of the unsalvaged conditions (Table 3). For example, the difference in mean canopy openness between the unsalvaged treatments is 39.1% compared to a difference between salvaged treatments of 4%. There was also more similarity between salvaged stands when comparing the averages for transmitted radiation, where the difference between the means in the salvaged treatments was 1.7% and 0.4% for diffuse and direct transmitted light respectively.

Because MPB stands had more residual structure, salvage logging had more impact on them than it did after fire. The differences between salvaged and unsalvaged MPB stands in the mean diffuse and direct light was 74% and 76%, versus 30% and 28% for differences in mean values of diffuse and direct light for wildfire treatments (Table 3). Salvaging was thus a more substantial incremental disturbance to light environments after beetle-attack than after wildfire.

The treatments had varied effects on the relative amounts of diffuse and direct radiation received in the understory. Diffuse and direct transmitted radiation values in MPB unsalvaged stands were essentially the same, whereas direct understory light was higher than diffuse light in all other treatments (Table 3). In general, as severity of overstory disturbance increased from MPBU to BU to MPBS to BS there was a partitioning between mean values of diffuse and direct understory light (Table 3). The amount of direct light reaching the understory was higher than diffuse light because the direct beam pathway of transmitted radiation was less obstructed by overstory cover in the more severe disturbances (i.e. salvaged).

The range of light transmission variability is more similar in salvaged stands than in unsalvaged stands, after beetle and fire (Table 4). The coefficient of variation in all three light transmission variables was relatively low (less than 6%) in both salvaged treatments, compared to the coefficients for the unsalvaged treatments (over 12% and 31% after fire and beetle respectively). This reinforces the idea that salvaging leads to a homogenisation of the variability of canopy cover and understory light environments in stands disturbed by beetles and fire.

Density, basal area and other characteristics of overstory structure

The differences between salvaged and unsalvaged treatments in the average density, basal area, DBH, tree heights, and % cover characterising the overstory structure were major, given all canopy and sub-canopy structure was removed by salvage (Fig.5). However, when comparing the unsalvaged treatments to each other, only the average tree height (in both canopy and sub-canopy strata), and the canopy basal area were statistically different (Table 3; Fig. 5). The average value for sapling density in the MPB, unsalvaged treatment was 667 stems/ha, compared to 156 stems/ha for burnt, unsalvaged treatment and 42 stems/ha for beetle-salvaged stands. Almost half of the beetle-attacked, unsalvaged plots (N=27 of 59) had saplings versus only 16% of the plots (N=10) in the burnt, unsalvaged stands and 5% (N=3) in the beetle-salvaged stands. Treatment differences for the density of saplings and % cover of overstory shrubs and saplings were significant (ANOVA p-value >0.0001).

Composition of overstory trees, saplings and shrubs

The species composition of the overstory after disturbance differs between the unsalvaged treatments after beetle and fire (Table 5a). Notably, while in the beetle-attacked stands, lodgepole pine accounted for the largest portion of the basal area of canopy trees (53.8%), in the burnt stands pine had nearly the smallest basal area (6.1%) (ANOVA p-value <0.0001; Table 5b; Fig. 6). The amount of lodgepole pine in the sub-canopy was 27.4% in the beetle stands, and 17.1% in the burnt stands, but the difference between the natural disturbances was not significant (ANOVA p-value 0.436, Table 5b). Sub-alpine fir was the dominant species in the canopy of the burnt stands as well as in the sub-canopy and sapling layers in stands for both unsalvaged treatments in terms of both relative density and relative basal area (or % cover for saplings) (Table 5a; Fig. 6). Interior spruce and Douglas-fir also occur in the canopy of unsalvaged stands after MPB and fire, however were absent from the sub-canopy and the sapling strata in the post-wildfire stands (Table 5a; Fig. 6).

Sub-alpine fir and alder are the main species in the lower overstory stratum in all treatments except for salvaged post-fire stands, which were devoid of all vegetation above a height of 2 m (Table 5a). There were also a few live lodgepole pine saplings present in all treatments except burnt, salvaged stands, interior spruce in both salvaged and unsalvaged beetle treatments and poplar within the burnt, unsalvaged treatment.

Overstory mortality after natural disturbance

Natural disturbances affected the patterns of mortality among species in different ways. In MPB-attacked stands, all lodgepole pine trees within the canopy layer and almost all sub-canopy lodgepole pine trees were dead. Only occasional individuals of other species (e.g. interior spruce and sub-alpine fir) were also dead. In these stands, approximately 45% and 60% of the total canopy and sub-canopy basal area respectively was still healthy four years after the peak of beetle-induced mortality. In contrast, all tree stems within the post-wildfire stands, except for a few surviving large Douglas-fir and interior spruce trees within the canopy, were dead. Therefore, only 18% of the overall basal area in the canopy in burnt, unsalvaged stands was in live trees.

Light and structure patterns between years after beetle-mortality

In the MPB stands, which hadn't been salvaged forest structure changed over time, reflecting both the ongoing process of canopy loss in beetle-killed trees and the growth and reorganisation of residual live structure. Over the two-year period of time examined since beetle attack, there was an overall progression towards a denser foliage and thus a darker understory, as demonstrated by the openness and leaf area index attributes in Fig. 7. Conditions across the plots were heterogeneous whereby 61% (N=36) of the plots with an average openness of 17.9% in 2007 became on average darker between 2007 and 2009. Only the remaining 39% of the plots, which had an average openness of 14.9% in 2007, were brighter in 2009. For the leaf area index, the difference between the average LAI values in 59% (N=35) of the plots increased between the two years and decreased in the other 41% of the plots. Thus overall there was a foliage growth response in more than half of the plots.

Between 2007 and 2009 the overall changes to the averages for the GLA derived light and structure measures included decreases in % openness, % diffuse and direct transmitted radiation and increases for the leaf area index (Table 3). The "difference between years" effect was significant for all GLA variables except the direct light transmission measure (with p-value 0.069; Table 6). I did not detect a change in direct transmitted radiation presumably due to the smaller sized gaps within the early post-disturbance beetle-attacked canopy hindering the transmission of direct radiation.

DISCUSSION

The consequences of salvage logging after natural disturbances in forests have been a subject of substantial controversy and research interest (Lindenmayer et al. 2008, Donato et al. 2006, DellaSala et al. 2006). Lindenmayer & Noss 2006 identified three broad classes of impacts from salvage logging after natural disturbances. Of these, I can address two of them: altered stand structural complexity and altered populations of species and community composition. This discussion has focused on three key themes: 1) the impacts from salvage logging to forest light and structure; 2) the differential effects of natural disturbances after beetle-attack and after wildfire on stand structure and composition; and, 3) the implications and recommendations for management. In my work, I have provided evidence that salvage after both MPB and fire substantially reduces the residual structure and diversity in the stands (Table 3), leads to the homogenisation of light environments, and alters the range of variability and complexity of light and structure compared to unsalvaged stands (Fig. 3). Repeated hemispheric canopy photography shows the ability of the residual forest structure in post-beetle stands to reorganize and respond to the patchy light environment created as individual trees succumb to beetle attack. This underlines the importance of post-disturbance legacies in shaping the adaptive response of forest communities to disturbance, and the role successive disturbances in eroding that adaptive capacity.

Cumulative impacts of salvage logging

The cumulative impact of sequential disturbances, such as salvage logging following wildfire or beetle outbreaks, reduces the heterogeneity and diversity of forest light and structure. Not only did salvage logging decrease canopy cover, with a consequent increase in light, but variability in canopy cover decreased as well (Fig. 3). Salvage also reduced the amount, availability and diversity of biological legacies (Table 3). In general, the light and structural attributes in both post-salvage treatments were more similar to each other than to either pre-salvage condition, after beetle and after fire. Stands subject only to either of the natural disturbances, without subsequent management, exhibited a broader range of ecological conditions. Thus, concatenating disturbances homogenize ecosystem structure through the removal of and damage to biological legacies (Franklin et al. 2000, Lindenmeyer et al. 2008). As a result, at least in the short-term, options for forest successional pathways are also likely to be limited (DellaSalla et al. 2006, Collins et al. 2011).

Cumulative impacts result in greater homogeneity in structure and consequently light, especially when the severity of the sequential disturbances is high or if they occur in quick succession (Lindenmayer et al. 2008). For example, with both the salvaged scenarios, although there was a dramatic shift toward much brighter light environments, only in salvaged stands after high severity wildfire was no overstory structure at all left. The MPB, unsalvaged treatment was the least severe disturbance scenario in this study and these stands showed the greatest variability of the amount and spatial arrangement of overstory structure.

Light and structural patterns across the treatments showed gradients in disturbance severity that was tied to the type and severity of the original large natural disturbance and subsequent disturbance from salvage. For example, as the level of overstory disturbance increased the ratio of direct transmitted radiation increased over % diffuse transmitted radiation. As canopy cover was removed there were fewer obstructions for transmitted gap light and a larger proportion of the path of the sun was revealed, where more of the understory received direct solar radiation (Canham et al 1994, Leiffers et al. 1999). The trends, in general, were consistent with other studies showing increased light levels with increasing levels of disturbance in the overstory (Bartemucci et al. 2006, Beaudet et al. 2004, Drever & Lertzman 2003, Canham et al. 1994, Heithecker & Halpern 2006).

Consequences of different natural disturbances: comparing the impacts of fire and beetles

Though naturally disturbed stands were more similar to each other than they were to the post-salvage stands, there were ecologically significant differences in the kind of filter that each disturbance type imposed on the stand. For example, compared to post-beetle stands, post-wildfire stands had more canopy openness, lower average tree height at the canopy and sub-canopy levels, reduced basal area, lower density of sub-canopy trees and saplings and lower cover of shrubs and saplings (Table 3). The wildfire these stands experience was a higher severity disturbance than the beetle outbreak, though elsewhere in the province, the beetle outbreak was as severe, at least in its impact on forest canopy mortality, as the wildfires (Astrup et al. 2008, Coates et al. 2006, Safranyik & Wilson 2006). The range of openness from the burnt unsalvaged stands in this study is most similar to the gap light after the treatment removing 95% of merchantable timber (green-tree retention) in second growth Douglas-fir stands on Vancouver Island (Drever & Lertzman 2003; see Table 1). Treatments removing 75% of the timber (shelterwood) overlap with the light range in MPB disturbed stands (Table 1). The range of density, basal area, and DBH of trees and advanced regeneration obtained in post-beetle stands are comparable to findings by Nigh et al. (2008) and Vyse et al. (2009) on regeneration and structure in MSdm forests attacked by mountain pine beetle.

Stands that had experienced disturbance by mountain pine beetle and wildfire but were not salvaged both exhibited complex patterns of residual structure and understory light, however, the mechanisms of canopy mortality distinguish each disturbance type. The McClure fire (Fire Protection Program 2004), as is common among high severity crown fires (Agee 1996, Turner et al. 1999, Lertzman et al. 1998), occurred as a discrete disturbance event in time and burned through forest relatively indiscriminately with regard to composition or structure. Many individuals of all species and strata were killed over a short period of time. In contrast, while the MPB epidemic peaked locally in 2005, (Axelson et al. 2009, Coates et al. 2006, this study), unlike a high severity wildfire where tree death typically occurs within a couple of years from the event (Antos & Parish 2002, Turner et al. 1998), MPB discriminates among tree species. The mortality process affects some stands before the peak and often progresses through a stand over a period of years, with post-beetle structural and compositional changes extending for years to decades (Safranyik & Wilson 2006, Shore et al. 2004). The beetle mortality in mixed stands is thus patchy in space and time and results in light gaps ranging in size and shape, largely depending on the mix of tree species in a stand (Rocca & Romme 2009, Axelson et al. 2009, Diskin et al. 2011). In the kind of mixed stands I studied, more trees across all strata survived the mountain pine beetle than did the high severity fire (see also Axelson et al. 2008).

Response to natural disturbances: reorganisation versus re-establishment

Where there is a paucity of live trees in all strata, as observed in the post-fire stands in this study, then seedling germination and establishment will be an important process shaping the composition of future stands (Axelson et al. 2009, Turner et al. 1999, DeLong & Kessler 2000). The few scattered live mature trees remaining in these fire-initiated stands are likely to act as seed sources, and the abundant amount of residual structure, although mostly dead, will continue to contribute to a wide range of variation in light growth environments over the decades of forest development to come. Here, in unsalvaged post-fire stands, these structural legacies are the anchor points around which recovering ecological communities organise. In salvaged stands, however, planting programs are necessary to produce the next cohort of trees.

When there are abundant and diverse surviving trees and advanced regeneration, as in the beetle-attacked stands I studied (Fig. 5), the most important mechanism for the initial stages of forest recovery is a release of surviving trees, particularly the shade-tolerant sub-alpine fir. Sub-alpine fir is likely to survive and dominate future stands (Antos & Parish 2002, Nigh et al. 2008). Accelerated growth of individuals present before the disturbance, along with canopy mortality, prolonged periods of community reorganisation and the occasional window where seedlings of shade-intolerant species could establish characterise forest development after an MPB epidemic (Astrup et al. 2008, Hawkes et al. 2003, Shore et al. 2004, Diskin et al. 2011). These processes will promote uneven aged, mixed-species, multilayered forest stands (Axelson et al. 2009, Safranyik & Wilson 2006).

Hemispheric photography is an effective method for characterizing the light environment in different forests and under different management prescriptions (Canham et al 1990, Drever & Lertzman 2003) and when used in repeat sampling, as for this study, is also a useful tool for looking at subtle changes over time. Very little published work has been done with canopy photographs after disturbances of this magnitude and repeated hemispheric photography is a tool that should be applied more often in research and monitoring programs.

Management implications and recommendations

In British Columbia, forest management is regulated under the *Forest & Range Practices Act* (FRPA; 2004), which mandates goals for a variety of values including timber, such as biodiversity, cultural heritage, recreation, soils, water, wildlife etc. For example, the goal statement for biodiversity is: *Harvesting activities will retain old forest and other age classes consistent with land use objectives established by government*. Although goals for forest management won't be site specific, the objectives may be, and all of these values should be considered when making decisions about salvage and post-disturbance management actions.

More options are available within the unsalvaged scenarios for meeting multiple and diverse management objectives, including ecological ones. The primary consideration for planning and management after disturbances should be to make better use of existing, multi-functional resources (i.e. those legacies and residual structure within unsalvaged stands; Burton 2006, Franklin et al. 2007, Kayes & Tinker 2012, Rocca & Romme 2009). In this context, five management recommendations emerge from this study. Three focus on minimizing effects in post-disturbance forest stands and two are related to monitoring.

1. If managers wish to provide structurally complex patches and thereby increase landscape diversity, they should retain a portion of the naturally disturbed landscape as **unsalvaged**. These patches provide variability in forest structure, light environment, and plant communities that is lost through the salvage process. One short-term management implication of leaving patches alone is that active management i.e. tree planting, may not be necessary in the unsalvaged part of the landscape (Diskin et al. 2011, Vyse et al. 2009). Also, in the mixed stands I studied and other lodgepole pine forests attacked by beetle there was a substantial amount of live residual structure (e.g. Coates et al. 2006, Burton 2006, Collins et al. 2011). If left unsalvaged, these stands may be available to contribute to a future timber supply.

2. To minimise the effect of cumulative disturbances to residual structure, then, if salvage occurs, managers should consider using lower impact alternatives to clear-cut logging in a substantial portion of the landscape where salvage does occur. For example, alternative silvicultural systems could be used, such as variable retention forestry (Gustaffson et al. 2012). For MPB stands particularly, there are opportunities

to manipulate the residual canopy to deliver a variety of desired light and growth environments while avoiding the light extremes found in the open and homogeneous clear-cut salvaged environment. If seed-bearing adult trees remain in the stand, another alternative that has been suggested is a low severity prescribed burn to stimulate regeneration of species such as lodgepole pine (Wayman & North 2007).

3. To address values related to soils and water, salvage operations should not be carried out with a lower standard of environmental protection/management than is prescribed for conventional (green-tree) logging (e.g. road standards, riparian protection, etc.). Salvage logging is often undertaken in an ad-hoc and crisis-mode manner and management issues such as sediment control, site preparation, and the building and maintenance of roads are not considered with the preceding natural disturbance in mind (DellaSalla et al. 2006, Lindenmayer et al. 2008). In this context, salvaging practices, particularly when clear-cutting in larger blocks, often magnify or compound impacts on essential processes such as hydrological regimes, soil profile development and nutrient cycling (Foster & Orwig 2006, Beschta et al. 2004).

4. It is important to monitor all three categories of post-disturbance stands (after MPB attack, after wildfire and after salvage logging), so we can better understand the consequences of management choices on structural complexity and the compositional diversity of developing stands.

5. Repeat hemispherical photography should be used as a tool in monitoring and research. When applied in this way, canopy photographs may provide measures of subtle changes in forest canopies over time. This information may be important to better understanding the post-disturbance mechanisms of recovery and development within forest ecosystems and may assist managers to plan for forests that meet multiple and diverse objectives.

REFERENCE LIST

Agee, J. (1996). *Fire ecology of Pacific Northwest forests*: Island Press.

Antos, J. A., & Parish, R. (2002). Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: tree size, age, and spatial structure. *Canadian Journal of Forest Research*, 32, 1935-1946.

Astrup, R., Coates, K. D., & Hall, E. (2008). Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. *Forest Ecology and Management*, 256(10), 1743-1750.

Axelson, J. N., Alfaro, R. I., & Hawkes, B. C. (2009). Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management*, 257(9), 1874-1882.

Bartemucci, P., Messier, C., & Canham, C. D. (2006). Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research*, 36, 2065-2079.

Beaudet, M., Messier, C., & Leduc, A. (2004). Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. *Journal of Ecology*, 92, 328-338.

Bentz, B. J., Regniere, J., Fettig, C. J., Hansen, E. M., Hayes, J. L., Hicke, J. A., et al. (2010). Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience, 60*(8), 602-613.

Beschta, R. L., Rhodes, J. J., Kauffman, J. B., Griesswell, R. E., Minshall, G. W., Karr, J. R., et al. (2004). Post-fire management on forested public lands of the western United States. *Conservation Biology, 18*(4), 957-967.

British Columbia Ministry of Forests and Range (2007). *Timber supply review for the Kamloops timber supply area, public discussion paper*. Forest Analysis and Inventory Branch, Victoria, B.C., October, 19 p.

Burton, P. J. (2006). Restoration of forests attacked by mountain pine beetle: Misnomer, misdirected or must-do? *British Columbia Journal of Ecosystems and Management, 7*(2), 1-10.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., & White, P. S. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, 20(5), 620-631.

Canham, C. D., Finzi, A. C., Pacala, S. W., & Burbank, D. H. (1994). Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24(2), 337-349.

Coates, K.D., DeLong, C., Burton, P. J., & Sachs, D. L. (2006). *Abundance of Secondary Structure in Lodgepole Pine Stands: Affected by the Mountain Pine Beetle*. Report to the Chief Forester, May. 17pp.

Collins, B. J., Rhoades, C. C., Hubbard, R. M., & Battaglia, M. A. (2011). Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *Forest Ecology and Management*, 261(11), 2168-2175.

Cottam, G. & Curtis, J.T. (1956). The use of distance measures in phytosociological sampling. *Ecology,* 37, 451-460.

DellaSala, D. A., Karr, J. R., Schoennagel, T., Perry, D., Noss, R. F., Lindenmayer, D., et al. (2006). Post-fire logging debate ignores many issues. *Science, 314*(5796), 51-52.

DeLong, S. C., & Kessler, W. B. (2000). Ecological characteristics of mature forest remnants left by wildfire. *Forest Ecology and Management*, 131(1-3), 93-106.

Diskin, M., Rocca, M. E., Nelson, K. N., Aoki, C. F., & Romme, W. H. (2011). Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research*, 41(4), 782-792.

Drever, C. R., & Lertzman, K. P. (2003). Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. *Canadian Journal of Forest Research*, 33(1), 137-146.

Drever, C. R., & Lertzman, K. P. (2001). Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. *Canadian Journal of Forest Research*, 31, 2124-2133.

Fiala, A. C. S., Garman, S. L., & Gray, A. N. (2006). Comparison of five canopy cover estimation techniques in the western Oregon Cascades. *Forest Ecology and Management, 232*(1-3), 188-197.

Forest Protection Program (2004). Ministry of Forests Report to the 2003 Firestorm Provincial Review. January 2004. http://bcwildfire.ca/History/ReportsAndReviews/2003/ (Accessed 27 January 2010)

Foster, D. R., & Orwig, D. A. (2006). Preemptive and salvage harvesting of New England forests: When doing nothing is a viable alternative. *Conservation Biology, 20*(4), 959-970.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, et al. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155, 399-423.

Franklin, J. F., R. J., Mitchell, and B. J. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. USDA Forest Service General Technical Report NRS-19.

Franklin, J. F., Lindenmayer, D., MacMahon, J. A., McKee, A., Magnuson, J., Perry, D. A., et al. (2000). Threads of Continuity. *Conservation in Practice,* 1(1), 8-17.

Frazer, G. W., C.D. Canham and K.P. Lertzman (2000a). Gap light analyzer (GLA), version 2.0 edition. *Bulletin of the Ecological Society of America,* 81,191-197.

Frazer, G. W., Trofymow, J. A., & Lertzman, K. P. (2000b). Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Canadian Journal of Forest Research,* 30(2), 239-256.

Gendron, F., Messier, C., & Comeau, P. G. (1998). Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agricultural and Forest Meteorology*, 92(1), 55-70.

Gustafsson, L., Baker, S. C., Bauhus, J. U., Beese, W. J., Brodie, A., Kouki, J., et al. (2012). Retention forestry to maintain multifunctional forests: a world perspective. *Bioscience,* 62(7), 633-645.

Heithecker, T. D., & Halpern, C. B. (2006). Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. *Forest Ecology and Management*, 226, 60-71.

Jennings, S., Brown, N., & Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, 72(1), 59-74.

Kayes, L. J., & Tinker, D. B. (2012). Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management*, 263, 57-66.

Klutsch, J. G., Negrun, J. F., Costello, S. L., Rhoades, C. C., West, D. R., Popp, J., et al. (2009). Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management, 258*(5), 641-649.

Krasowski, M. J., & Wang, J. R. (2003). Aboveground growth responses of understory Abies lasiocarpa saplings to different release cuts. *Canadian Journal of Forest Research*, 33(9), 1593-1601.

Kurulok, S. E., & Macdonald, S. E. (2007). Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. *Canadian Journal of Forest Research*, 37, 2637-2651.

Leiffers, V. J., Messier, C., Gendron, F., & Comeau, P. G. (1999). Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research*, 29, 796-811.

Lertzman, K., & Fall, J. (1998). From forest stands to landscapes: spatial scales and the roles of disturbances. *Ecological scale: theory and applications. Columbia University Press, New York, New York, USA*, 339-367.

Lertzman, K., Fall, J., & Dorner, B. (1998). Three kinds of heterogeneity in fire regimes: At the crossroads of fire history and landscape ecology. *Northwest Science, 72*, 4-23.

Lertzman, K., Spies, T., & Swanson, F. (1997). 14. From Ecosystem Dynamics to Ecosystem Management. *The rain forests of home: profile of a North American bioregion*, 361.

Lindenmayer, D. B., Burton, P. J., & Franklin, J. F. (2008). *Salvage logging and its ecological consequences*: Island Press.

Lindenmayer, D. B., & Noss, R. F. (2006). Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology, 20*(4), 949-958.

Lloyd, D., Angrove, K., Hope, G., & Thompson, C. (1990). *A guide to site identification and interpretation for the Kamloops Forest Region*. Land Management Handbook No. 23.

Lochhead, K. D., & Comeau, P. G. (2012). Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. *Forest Ecology and Management*, 284(0), 12-22.

Meidinger, D., & Pojar, J. (1991). *Ecosystems of British Columbia*. Research Branch, British Columbia Ministry of Forest, Victoria, B.C. Special Report Series 6.

Messier, C., Parent, S., & Bergeron, Y. (1998). Effects of overstory and understory vegetation on the understory light environment in mixed Boreal forests. *Journal of Vegetation Science*, 9(4), 511-520.

Ministry of Forests (2006) Stand Summary Report, Kamloops Indian Band – A73555. Ministry of Forests Appraisal Information. 27 September 2006.

Mitchell, K (2007) Quantitative analysis by the point-centered quarter method, Version 2.15. http://people.hws.edu/mitchell/PCQM.pdf (Accessed 12 May 2008)

Newsome, T. A., Heineman, J. L., Nemec, A. F. L., Comeau, P. G., Arsenault, A., & Waterhouse, M. (2010). Ten-year regeneration responses to varying levels of overstory retention in two productive southern British Columbia ecosystems. *Forest Ecology and Management*, 260(1), 132-145.

Nigh, G. D., Antos, J. A., & Parish, R. (2008). Density and distribution of advance regeneration in mountain pine beetle killed lodgepole pine stands of the Montane Spruce zone of southern British Columbia. *Canadian Journal of Forest Research*, 38(11), 2826-2836.

Pederson, L. (2003) Rationale for Allowable Annual Cut (AAC) Determination, Kamloops Timber Supply Area. British Columbia Ministry of Forests. (Accessed 16 May 2011)

Protection Branch (2003). Fire Review Summary for the McLure Fire (K20272). Ministry of Forests, B.C. Summer 2003. 8pp. http://www.bcwildfire.ca/History/ReportsAndReviews/2003 (Accessed 27 January 2010)

Province of British Columbia (1998). *Field manual for describing terrestrial ecosystems: Land Management Handbook Number 25*. B.C. Ministry of Environment, Lands and Parks and B.C. Ministry of Forests, Victoria, B.C..

R Development Core Team (2010). R: A language and environment for statistical computing, reference index version 2.11.2010-07-27. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-08-09, URL http://www.R-project.org.

Rocca, M. E., & Romme, W. H. (2009). Beetle-infested forests are not "destroyed". *Frontiers in Ecology and the Environment, 7*(2), 71-72.

Safranyik, L., Wilson, B. (Eds.) (2006). *The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Ottawa, p. 304.

Secwepemc Economic Development Corporation (2004). Cruise Compilation Project Report. 30 January 2004

Shore, T.L., Brooks, J.E. & Stone, J.E. (Eds.) (2004). *Mountain Pine Beetle Symposium: Challenges and Solutions*. October 30-31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 p.

Tk'emlupsemc Forestry Development Corporation (2006) Site Plan, Licence No: A73555, Community Lake, September 2006.

Turner, M. G., Romme, W. H., & Gardner, R. H. (1999). Pre-fire heterogeneity, fire severity, and early post-fire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire, 9*(1), 21-36.

Turner, M. G., Baker, W. L., Peterson, C. J., & Peet, R. K. (1998). Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems*, 1(6), 511-523.

Van Pelt, R., & Franklin, J. F. (2000). Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Canadian Journal of Forest Research, 30, 1231-1245.

Vyse, A., Ferguson, C., Huggard, D. J., Roach, J., & Zimonick, B. (2009). Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. *Forest Ecology and Management*, 258(Supplement 1), S36-S43.

Wang, T., Hamann, A., Spittlehouse, D. L., & Aitken, S. N. (2006). Development of scale-free climate data for Western Canada for use in resource management. *International Journal of Climatology, 26*(3), 383-397.

Wayman, R. B., & North, M. (2007). Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecology and Management, 239*(1-3), 32-44.

Westfall, J. & Ebata, T. (2009) 2009 Summary of forest health condition in British Columbia. Pest Management Report Number 15.

Whelan, R. J. (1995). *The ecology of fire*: Cambridge University Press.

White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *The Botanical Review*, 45(3), 229-299.

Wright, E. F., Coates, K. D., Canham, C. D., & Bartemucci, P. (1998). Species variability in growth response to light across climatic regions in northwestern British Columbia. *Canadian Journal of Forest Research*, 28, 871-886.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer. Pp. 5

TABLES AND FIGURES

Table 1: Range of the percentage of sunlight through the canopy in different types of forests and at various locations

Stand type, location, silvicultural treatment (if applicable)	Percentage light transmitted through canopy	Reference
Mature interior cedar-hemlock, intermontane boreal and sub-alpine forest, northwestern British Columbia	rarely below 5%	Wright et al. (1998)
Old-growth Douglas-fir - Hemlock forest, northwestern US	0.1-1.7% (range)	Canham et al. (1990)
Montane red spruce - balsam fir forest, northeastern US	1.6-9.7% (range)	Canham et al. (1990)
Tropical rainforest, Costa Rica	1-2% (range)	Canham et al. (1990)
Old-growth cedar-dominated stands, northwestern Quebec	27% (mean)	Bartemucci et al. (2006)
Aspen stands and mixed deciduous-coniferous forests, northwestern Quebec	18-19% (mean)	Bartemucci et al. (2006)
Second-growth Douglas-fir stands, Vancouver Island	3-22% (range)	Drever & Lertzman (2003)
Clear-cut	95% (approx mean)	
Green-tree retention	26-88%(range)	
Shelterwood	45% (approx mean)	
Commercial thinning	32% (approx mean)	
Thinning from above	25% (approx mean)	
Individual-tree selection	2-22% (range)	
Douglas-fir stands, Southern cascade range, Washington	9-11% (averages)	Heithecker & Halpern (2006)
40% dispersed retention	17-29% (averages)	
15% dispersed retention	36-49% (averages)	
0%: all merchantable timber removed	53-61% (averages)	

Table 2: General conditions within all four disturbance scenarios at Community Lake and Parky Mountain, and for both sampling years in the mountain pine beetle unsalvaged treatment

	Community Lake			***Parky Mountain***	
	MPB Unsalvaged 2007	*MPB Unsalvaged 2009*	*MPB Salvaged*	*Burnt Unsalvaged*	*Burnt Salvaged*
Number of plots (N)	same as '09	59	60	60	60
Number of blocks (n)	same as '09	2	3	3	3
Total sample area (ha)	same as '09	46.7	87.8	75.4	68.1
Elevation (m) range	same as '09	1415 to 1516	1277 to 1456	1230 to 1414	1286 to 1386
% Slope range (mean)	same as '09	2 to 105 (20.8)	2 to 55 (17)	2 to 28 (11.6)	2 to 36 (13)
Aspect (mode)	same as '09	SSW	WSW	SSW	NNW
Time since natural disturbance (years)	2	4	3	5	5
Time since logging (years)	-	-	1.4	-	4

Note: The slope variable was tested in a mixed-effect ANOVA with no significant differences between treatments (p-value 0.224). Years are approximate where the peak of the mountain pine beetle disturbance occurred in 2005 (TFDC 2006), and the McClure wildfire burned

Table 3: Summary table for light and overstory structure variables

Mean value for overstory structure and understory light variables calculated across all four treatments at Community Lake and Parky Mountain, and for both sampling years in mountain pine beetle unsalvaged treatments. Overstory structural attributes were measured for all treatments by stratum and the main coniferous tree species lodgepole pine, sub-alpine fir, interior spruce and Douglas-fir. Values are means with standard deviation provided in parentheses except for density variables where the confidence interval in [ ] is presented. Selected data * from salvaged treatments have been reconstructed from cruise compilation and appraisal reports (SEDC 2004, MOF 2006) and are not used in the mixed-effect ANOVA. The p-value results from mixed-effect ANOVA are also provided (MPB 2007 data not used in comparative analysis).

		Community Lake			***Parky Mountain***		
Variable		*Unsalvaged 2007*	*MPB Unsalvaged 2009*	*MPB Salvaged*	*Burnt Unsalvaged*	*Burnt Salvaged*	p-value
Overstory structure (canopy photos)							
% Canopy Openness		16.8 (4.3)	15.2 (5.5)	85.6 (5.0)	54.3 (8.7)	89.6 (2.4)	0.0001
Leaf Area Index (foliage m^2/ground m^2)		1.97 (0.39)	2.17 (0.55)	0.03 (0.05)	0.47 (0.19)	0.004 (0.008)	0.0001
Understory light transmission							
% Diffuse Transmitted Radiation		25.1 (5.7)	22.8 (7.2)	96.5 (2.5)	68.6 (8.9)	98.1 (0.7)	0.0001
% Direct Transmitted Radiation		25.1 (9.3)	22.9 (11.3)	99.3 (0.9)	71.8 (10)	99.7 (0.7)	0.0001
Overstory structure	**Stratum**						
DBH (cm)	*Canopy*	-	27.5 (9.7)	24*	30.1 (13.4)	33*	0.6296
	Sub-canopy	-	11.1 (2.0)		11.3 (2.1)		0.5694
Height (m)	*Canopy*	-	18 (4.2)	27.3*	16.2 (4.5)	28.6*	0.0252
	Sub-canopy	-	10.7 (2.3)		8.9 (2.5)		0.0001
Density (stems/ha)	*Canopy*	-	899 [681, 1139]	1219*	501 [379, 631]	369*	0.3046
	Sub-canopy	-	283 [212, 354]	-	186 [125, 209]	-	0.0468
	Saplings	-	667 (1100)	42 (195)	156 (392)	0	0.0001
Basal Area (m^2/ha)	*Canopy*	-	57.6 (39.8)	-	40.3 (41.3)	-	0.0005
	Sub-canopy	-	2.8 (1.2)	-	2 (1.3)	-	0.5072
Sum of the cover (%) of all saplings and overstory shrubs above 2m		-	6.4 (8.4)	0.2 (1.0)	0.4 (1.4)	0	0.0001

Table 4: Coefficient of variation (CV; %) of various structure and light variables by treatment

Variable (from canopy photos)		MPB unsalvaged	MPB salvaged	Burnt unsalvaged	Burnt salvaged
% Canopy Openness	Open	36.3	5.8	16.1	2.6
% Diffuse Transmitted Radiation	TrDif	31.6	2.6	12.9	0.7
% Direct Transmitted Radiation	TrDir	49.4	0.9	13.9	0.6

Table 5: Summary of composition in the overstory

a) Tree and advanced regeneration composition in the overstory by treatment. Where Pl, lodgepole pine; Bl, sub-alpine fir; Sx, interior spruce; Fd, Douglas-fir; other species, A2 and A3 include red cedar and black cottonwood; other species, B1 alder and poplar, n/a applies when only stems of conifer species counted. Structural layers are defined as canopy (A2) where DBH >15 cm, sub-canopy (A3): 15 cm> DBH >7.5 cm; saplings and upper shrubs (B1) DBH <7.5 cm, height >2 m.

				Composition (%)				
Treatment	Stratum	Basis of measure	Total stems	Pl	Bl	Sx	Fd	Other spp.
MPB Unsalvaged	*Canopy*	Frequency (N)	59	62.7	15.2	13.6	6.8	1.7
		Basal area (m^2/ha)		53.8	9.2	19.1	12.6	5.3
	Sub-canopy	Frequency (N)	59	23.7	69.5	5.1	1.7	0
		Basal area (m^2/ha)		27.4	65.2	4.4	3	0
	Saplings	Frequency (N)	61	3.7	92.6	3.7	0	n/a
		% cover		2.9	71.1	2.9	0	23.1
MPB Salvaged	*Saplings*	Frequency (N)	61	3.7	92.6	3.7	0	n/a
		% cover		2.9	71.1	2.9	0	23.1
Burnt Unsalvaged	*Canopy*	Frequency (N)	60	13.3	66.7	11.7	5	3.3
		Basal area (m^2/ha)		6.1	57.0	22.0	11.8	3.1
	Sub-canopy	Frequency (N)	59	16.9	81.4	0	0	1.7
		Basal area (m^2/ha)		17.1	80.2	0	0	2.7
	Saplings	Frequency (N)	14	10	90	0	0	n/a
		% cover		9.1	67.8	0	0	23.1
Burnt Salvaged	*Saplings*	Frequency (N)	0	0	0	0	0	n/a
		% cover		0	0	0	0	0

b) Relative basal area calculated for the four main coniferous tree species in the unsalvaged treatments, after beetle and after fire, with results of the mixed-effect ANOVA.

Variable	Stratum		MPB unsalvaged	Burnt unsalvaged	p-value
Relative basal area of lodgepole pine (%)	*Canopy*	A2Pl	53.8	6.1	<0.0001
	Sub-canopy	A3Pl	27.4	17.1	0.4363
Relative basal area of sub-alpine fir (%)	*Canopy*	A2Bl	9.2	57	<0.0001
	Sub-canopy	A3Bl	65.2	82.2	0.1054
Relative basal area of interior spruce (%)	*Canopy*	A2Sx	19.1	22	0.4068
	Sub-canopy	A3Sx	4.4	0	<0.0001
Relative basal area of Douglas-fir (%)	*Canopy*	A2Fd	12.6	11.8	0.0258
	Sub-canopy	A3Fd	3	0	<0.0001

Table 6: Differences to GLA derived variables between 2007 & 2009 in beetle, unsalvaged stands

Differences to GLA variables between 2007 and 2009 in mountain pine beetle unsalvaged blocks at Community Lake. To assess the overall (D) differences, the effect of time on each of the GLA variables was modelled with a random intercept linear mixed-effect model with block as random effect. The mean difference between 2007 and 2009 (D value) is significant for all variables except direct light.

GLA variable (from hemispheric photos)	Total mean difference (D = 2009 - 2007)	p-value
Canopy Openness (%)	-1.50	0.040
Leaf Area Index (foliage m^2/ground m^2)	0.202	0.024
Diffuse transmitted radiation (%)	-2.18	0.025
Direct transmitted radiation (%)	-2.10	0.069

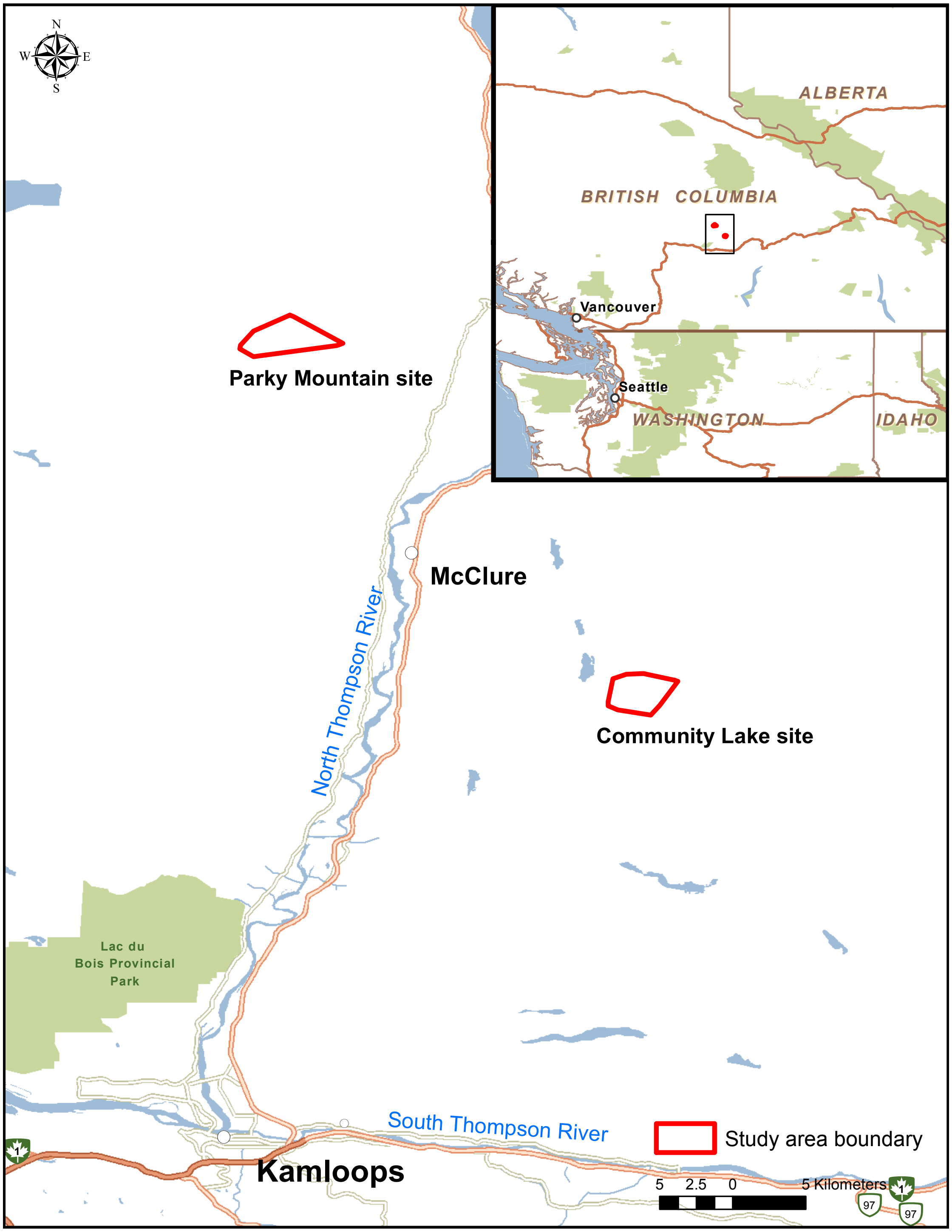

Figure 1: Location of the two study sites on both sides of the North Thompson River, within the Kamloops region of south-central British Columbia, Canada.

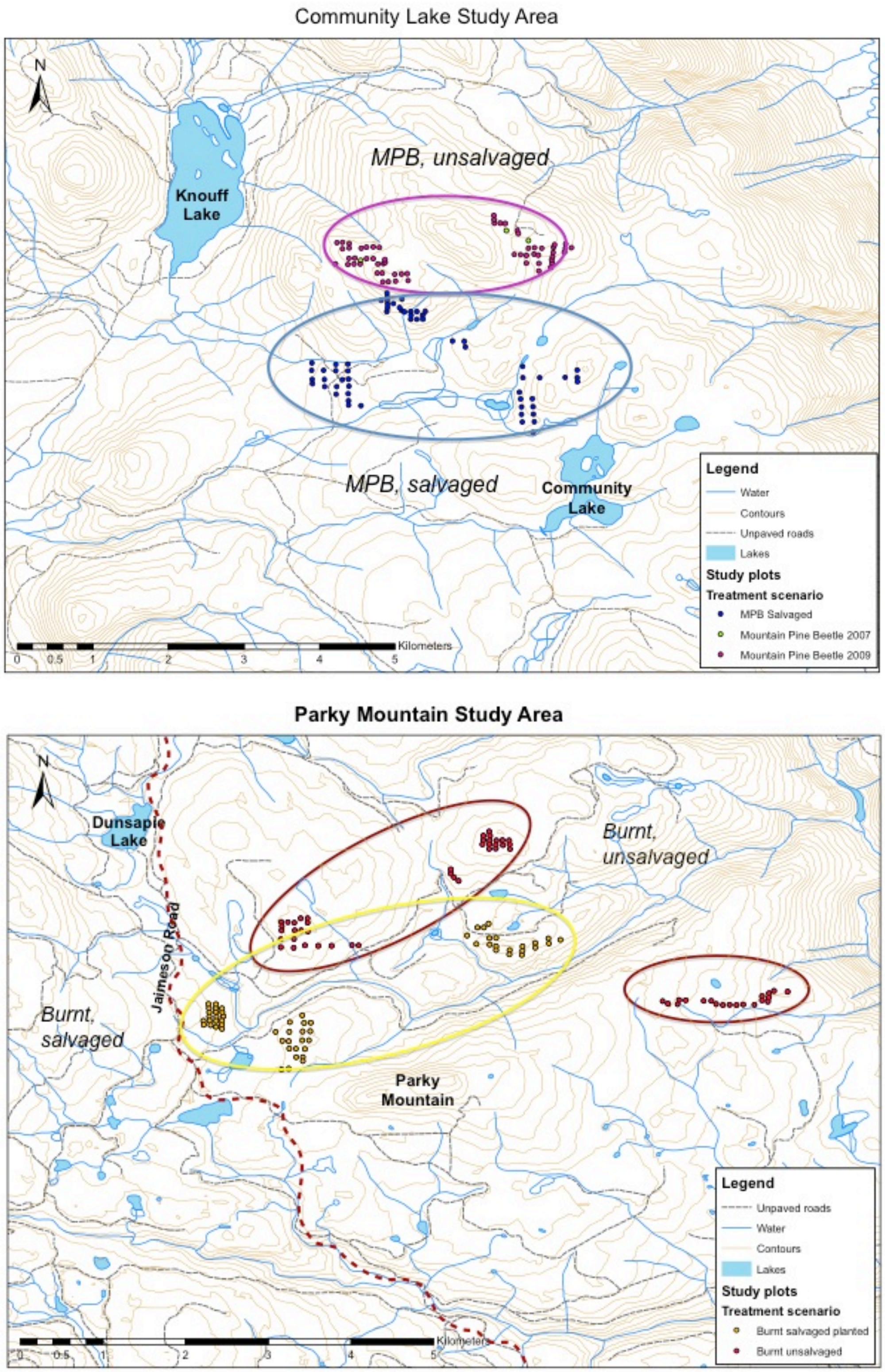

Figure 2: Location of the plots and blocks sampled within the salvaged and unsalvaged treatments at the mountain pine beetle disturbed Community Lake site and wildfire disturbed Parky Mountain site north of Kamloops, British Columbia

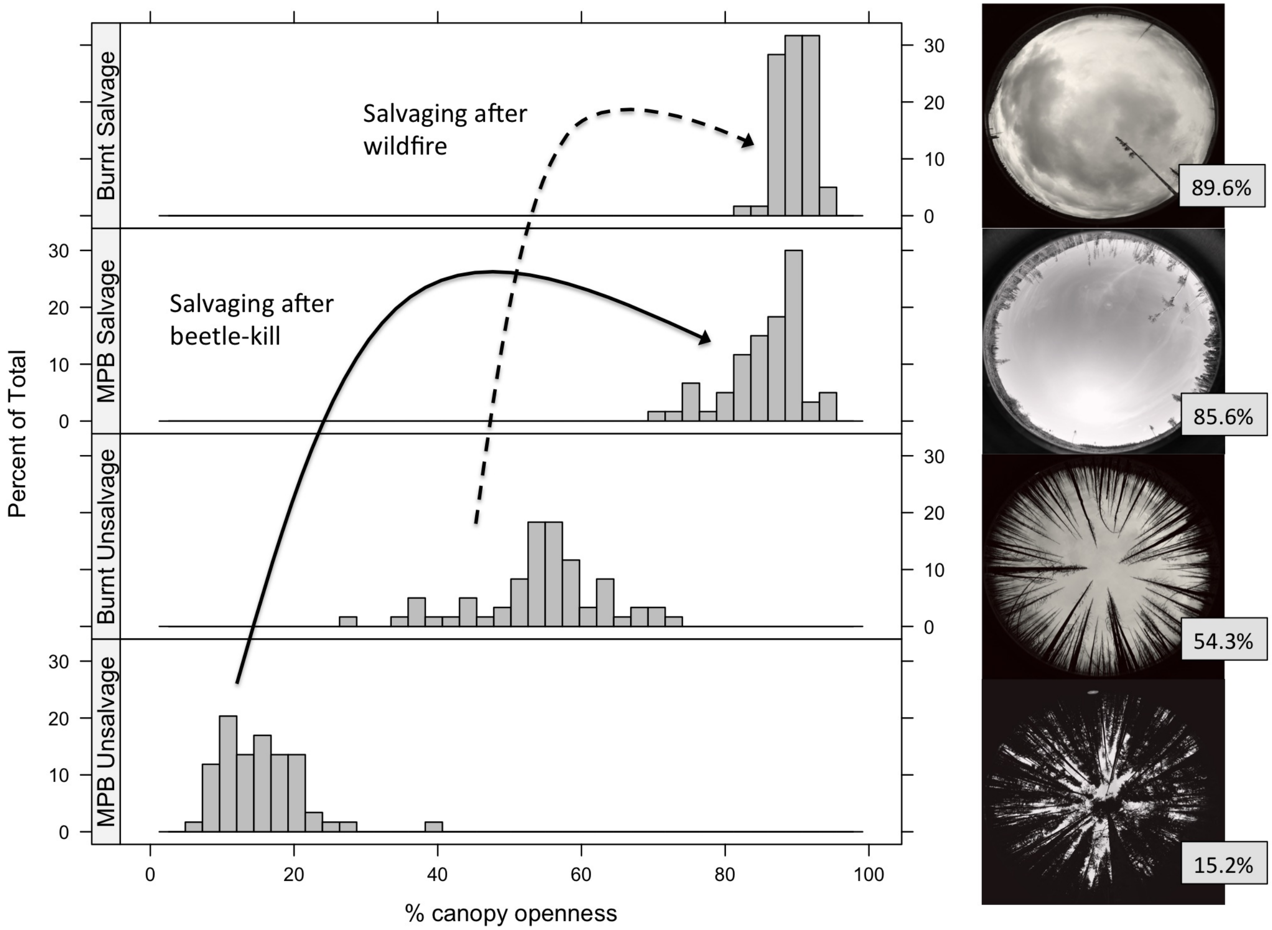

Figure 3: Distribution of canopy openness across treatments and the effect of salvage
The main figure shows the frequency distributions of canopy openness across each of the four treatments. The arrows indicate the change in this distribution from unsalvaged to salvaged in each of the disturbance cases. Photographs on the right are representative of the mean value of canopy openness for each treatment.

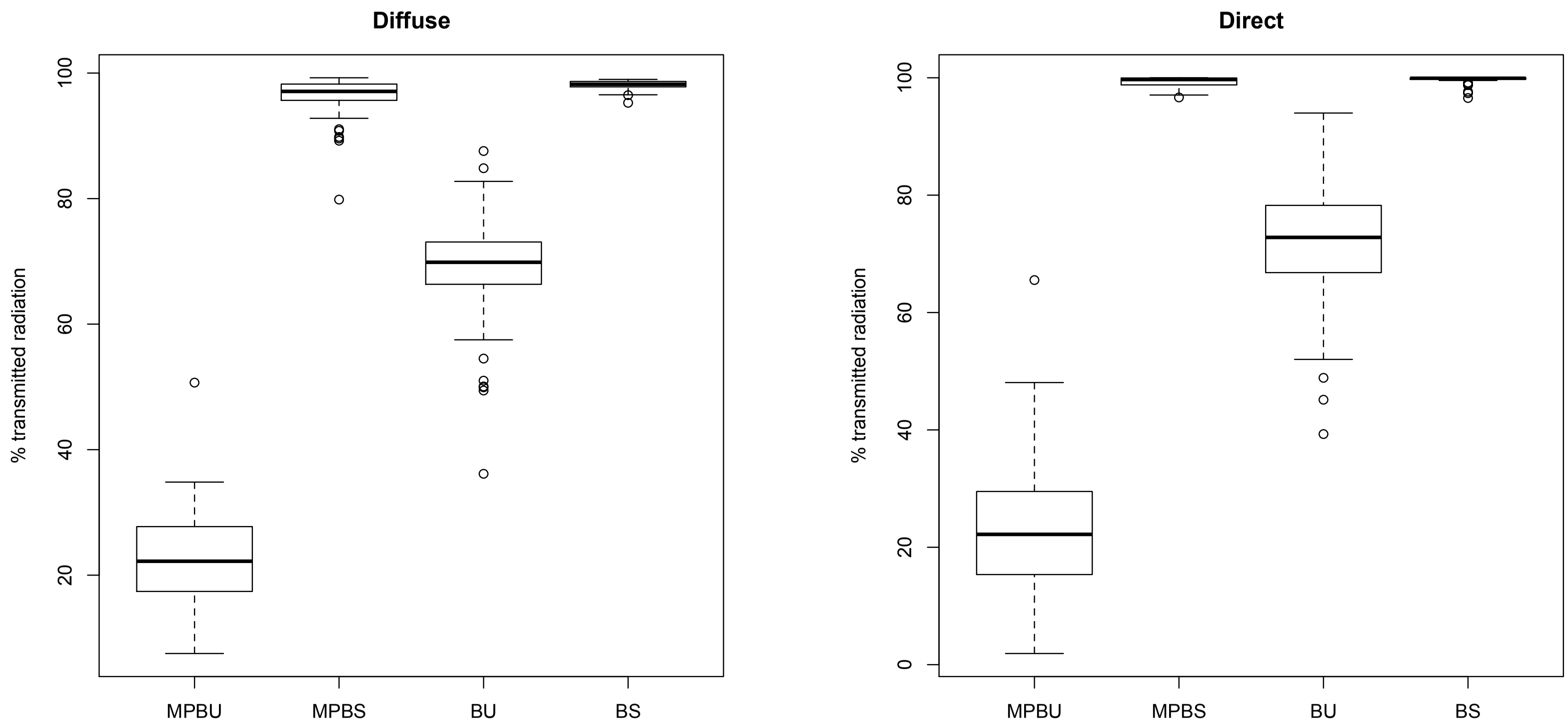

Figure 4: Understory light transmission in salvaged and unsalvaged stands within the study area

The range of understory light transmission varied across the different disturbances and when salvage logging was added. Both diffuse and direct transmitted radiation is closest to 100% in both the salvaged treatments. Treatment types are MPBU, mountain pine beetle unsalvaged; MPBS, mountain pine beetle salvaged; BU, burnt unsalvaged; BS, burnt salvaged. The darker centre line of the box plot indicates the median with the boundaries of the boxes to either side indicating the 25^{th} and 75^{th} percentiles. Error bars represent the 10^{th} and 90^{th} percentiles.

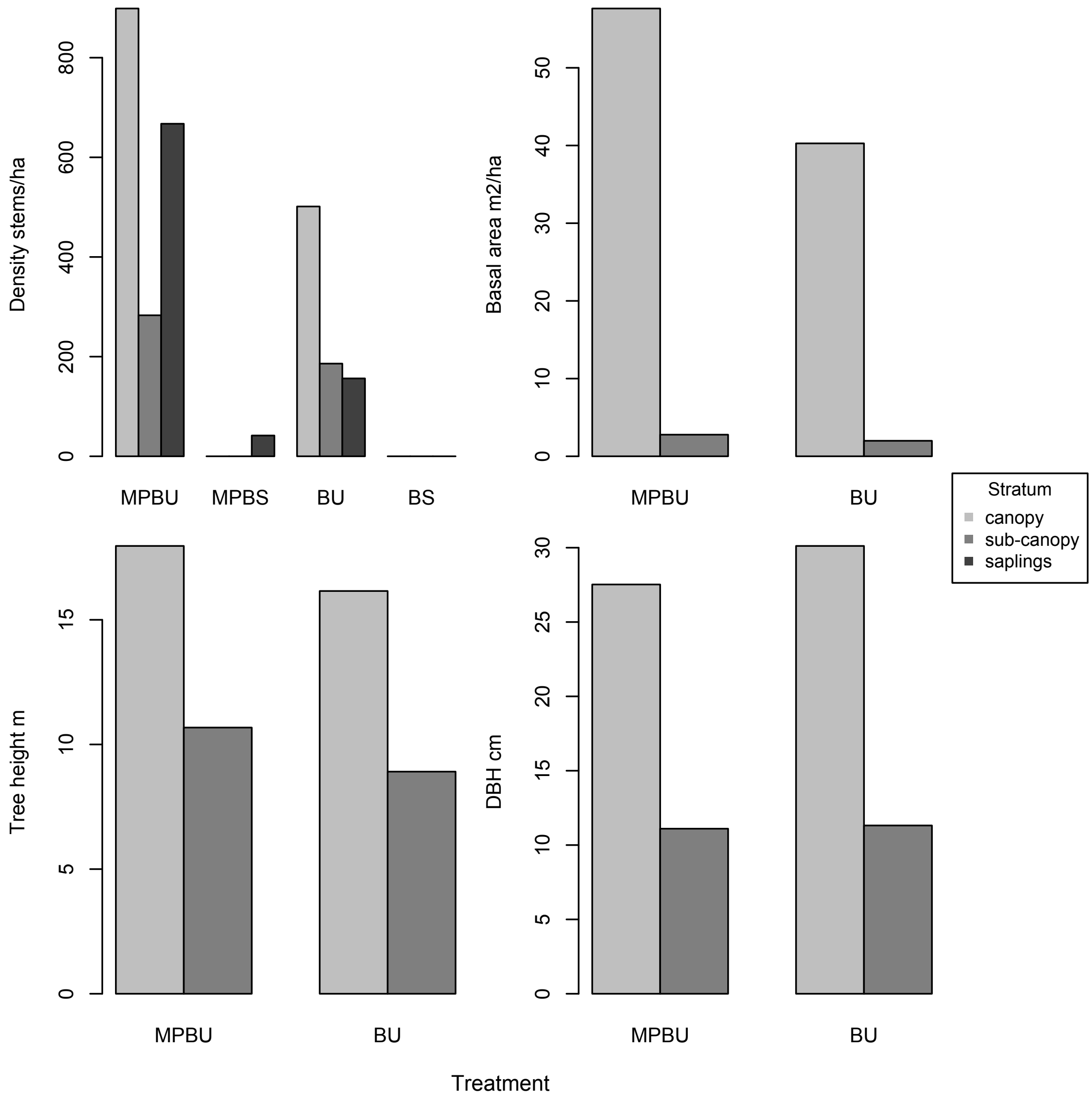

Figure 5: Mean value of various overstory structural variables by treatment and stratum

Means of various overstory structural variables by stratum in unsalvaged stands after beetle-attack and after wildfire. The mean density (stems/ha) of saplings is also presented for both salvaged treatments. See Fig. 4 for definition of treatments. Structural layers are defined as canopy (A2) where DBH >15 cm, sub-canopy (A3): 15 cm> DBH >7.5 cm; saplings and upper shrubs (B1) DBH <7.5 cm, height >2 m.

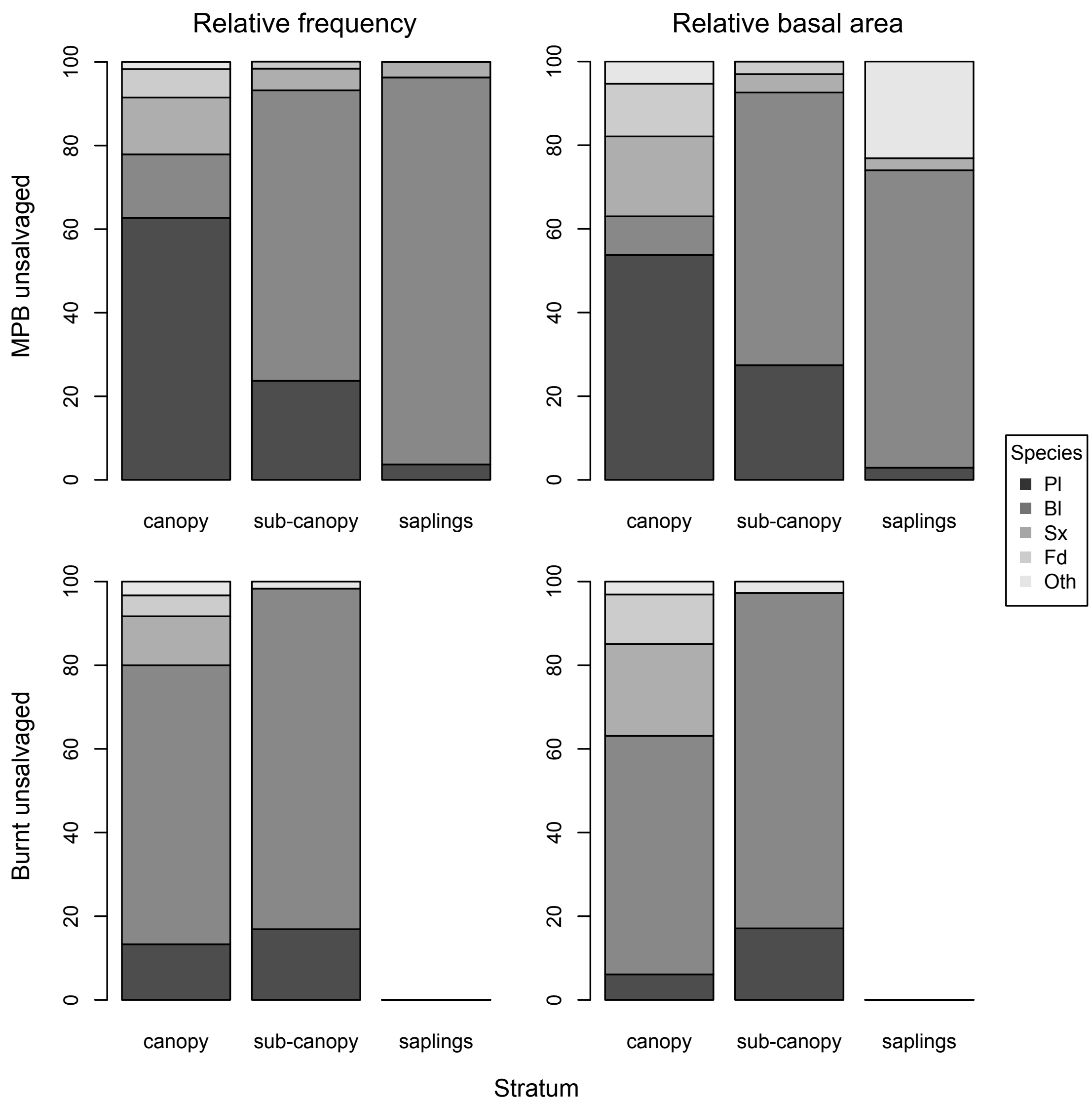

Figure 6: Composition in the overstory layers for unsalvaged treatments

Composition of overstory trees in unsalvaged stands disturbed by mountain pine beetle and wildfire. Values are the percentage of individuals that belong to a given species among all individuals sampled within a structural layer within all blocks. Trees in the canopy (A2) have DBH>15 cm, sub-canopy (A3): 15 cm> DBH>7.5 cm, and regenerating as saplings (B1) DBH <7.5 cm, height >2 m. Where tree species Pl, lodgepole pine; Bl, sub-alpine fir; Sx, interior spruce; Fd, Douglas-fir; Oth, other species, A2 and A3 include red cedar and black cottonwood, B1 alder and poplar.

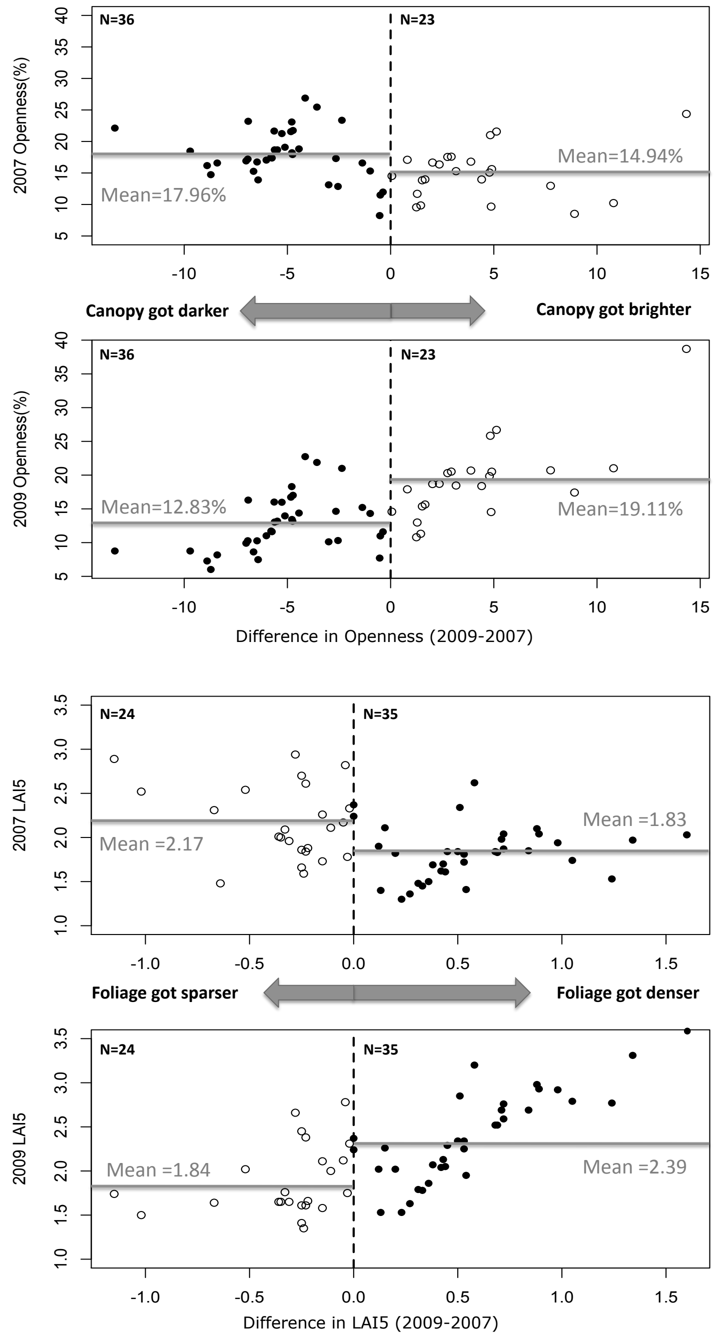

Figure 7: Changes to canopy openness and leaf area index over 2-years across the unsalvaged mountain pine beetle stands

The figures depict the relationship between sampling undertaken in 2007 and in 2009 and the corresponding differences to canopy and foliage structure. The overall trend in the 2-year period was a progression towards a darker canopy (N=36 is 61% of the plots for % openness) and denser foliage (N=35 is 59% of the plots for LAI). Across the plots conditions were very heterogeneous, with most plots getting on average darker in 2009 and some plots that were less open than average getting brighter in 2009.