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**Characteristics of forest legacies following two mountain pine beetle outbreaks in
British Columbia, Canada.**

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Abstract

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), a native insect of North America, periodically reaches population sizes that cause serious economic impact to the forest industry in western North America. The most recent outbreak in British Columbia (BC), Canada, which began in the late 1990s, is only now (2015) abating, after causing unprecedented tree mortality in lodgepole pine (*Pinus contorta* Douglas ex. Loudon) forests. In this paper we make use of permanent research plots to report on the condition of lodgepole pine forests in the Chilcotin Plateau of central BC, which underwent two fully documented mountain pine beetle outbreaks. In this region the first outbreak started in the late 1970s and lasted until the mid-1980s; the second outbreak began in the early 2000s and ended in 2010. We measured the impacts of these outbreaks in terms of tree mortality, and describe the characteristics of the legacies that remain following these outbreaks, including survivors in various canopy layers and levels of existing and new regeneration. We provide evidence in support of the existence of post disturbance legacies that classify into five distinct stand structures. Abundant regeneration and surviving intermediate canopy layers in most stands indicate that management actions to restock pine stands in this area will not likely be necessary. The information provided by this study is important for estimating future forest development and timber supply, and for forest planning and management.

Keywords: mountain pine beetle, forest disturbance, forest dynamics

Introduction

During the last decade, the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), a native insect of North America, has had an unprecedented impact on pine forests of western North America, causing tree mortality in close to 20 million hectares (ha) of pine forests in Canada and the United States (Natural Resources Canada 2014; United States Department of Agriculture 2014). All pine species in western North America are suitable hosts for this beetle (Furniss and Carolin 1977), however, lodgepole pine, *Pinus contorta* Douglas ex. Loudon, is one of the most susceptible and most widely distributed species. This species is a significant component of the commercial forests of British Columbia (BC) and, in the central regions of this province, it is a critical component of the timber supply (BC Ministry of Forests 1995).

MPB and wildfire are the main natural disturbances affecting lodgepole pine forests in BC, impacting forests at varying scales depending on intensity of the disturbance. Tree mortality, changes in the physical environment and resource availability disrupt successional development of the forest by influencing population structure and the processes of regeneration and recovery (Attiwill 1994, and references there in). Natural disturbances leave biological legacies (hereafter referred to as legacies), which are defined as the organisms, organic matter, and biologically created patterns that persist from the pre-disturbance ecosystem and influence recovery processes in the post-disturbance ecosystem (Franklin *et al.* 2000). Legacies play important roles in ecosystem resilience (the capacity of a system to retain its function, structure, identity and feedbacks following disturbance (Walker *et al.* 2004)), by impacting reorganization and recovery

63 following disturbance. Surviving forest patches serve as reservoirs of biodiversity,
64 regeneration propagules, habitat and nutrients, and provide landscape connectivity
65 (Franklin *et al.* 2007). Consequently, the amount and spatial distribution of legacies
66 (spatial heterogeneity) play a pivotal role in determining succession and recovery
67 following disturbance (Turner *et al.* 2013). Remnant patches of surviving trees (also
68 referred to as secondary structure) are an important element of MPB outbreak legacies.
69 They have the potential to: act as a seed source for regeneration, increase structural
70 complexity of canopies, speed up successional development and ecological recovery and
71 enhance the recovery of ecosystem carbon stocks after disturbance.

72
73 The Chilcotin Forest District in the interior of BC is one of the areas of this province
74 most heavily impacted by MPB in the recent outbreak (Westfall and Ebata 2010). On the
75 Chilcotin Plateau, in the IDF (interior Douglas-fir) biogeoclimatic zone, uneven-aged,
76 lodgepole pine-dominated stands have been historically created and maintained by the
77 combined impacts of a mixed-severity fire regime and MPB outbreaks (Daniels and
78 Watson 2003; Axelson *et al.* 2010). In dry forests such as these, stands are commonly a
79 mosaic of uneven-aged individual trees, tree clumps, and openings, creating a complex
80 pattern across the landscape (Larson and Churchill 2012). MPB outbreaks, varying in
81 intensity from small gap-creating events to large stand-replacing events, have played an
82 increasingly important role in maintaining this mosaic since fire suppression began in the
83 early 20th century (Axelson *et al.* 2010). During the endemic stage of outbreaks, MPB
84 typically exists at low population levels, feeding and reproducing in weakened trees,
85 however, when conditions are favourable, outbreaks occur at landscape scales, killing

mainly large diameter trees until the host has been depleted and only small diameter pines and other species unsuitable as hosts for MPB remain (Safranyik and Carroll 2006). Overstory mortality creates canopy gaps and favours the release of existing suppressed and understory trees (e.g., Heath and Alfaro 1990, Axelson *et al.* 2009). The ability of lodgepole pine to regenerate under its own canopy (Hawkes *et al.* 2004), in combination with multiple MPB disturbances has resulted in mosaics of multi-age lodgepole pine stands across the Chilcotin landscape (Axelson *et al.* 2010). Outbreaks re-occur when stands recover through natural regeneration and have accumulated sufficient quantities of large diameter trees to again maintain growing MPB populations, a process that may take 30 to 40 years (Alfaro *et al.* 2009; Axelson *et al.* 2009).

The characteristics of disturbance legacies are also key factors determining the recurrence and severity of future disturbances (Fleming *et al.* 2002; Kulakowski *et al.* 2003). In the case of MPB, the probability of trees and stands being attacked by MPB is affected by the characteristics of structures left by previous disturbances, particularly the age class structure of a stand and its density. Based on this, Shore and Safranyik (1992) developed a MPB susceptibility index, which integrates factors intrinsic to stand structure, including stand age and proportion of the basal area in large diameter trees and stand density, and geographic location (a surrogate for climatic suitability for MPB).

In this paper we report on the long-term impacts of MPB on lodgepole pine forests of the Chilcotin Plateau of central BC, based on re-measurements of research plots located in areas which sustained heavy MPB impacts, during the two most recent outbreaks in our

study area: the 1980s and the 2000s outbreak (Figure 1). We present tree mortality data for each outbreak and describe the structure of the legacies that remain today. We provide evidence in support of the existence of five distinct forest legacy types that remain in lodgepole pine forests of the Chilcotin Plateau. As the current MPB population declines in BC, forest managers need to develop strategies to manage the large areas left unsalvaged following the outbreaks. Therefore, the classification of post MPB legacies provides a means of describing current stand heterogeneity across the landscape and could inform forest management practices that focus on ecosystem resilience. This information will also aid in post-beetle timber supply planning.

Methods

Study area

The Chilcotin Plateau (also known as the Fraser Plateau), in the BC interior, is located between the Coast and Columbia Mountains, with the town of Alexis Creek at its centre (Figure 2). The Plateau is characterized by a cold, dry climate and is dominated by the Sub-Boreal Pine Spruce (SBPS) and Interior Douglas-fir (IFD) biogeoclimatic zones (Steen and Coupé 1997). Forests in this area are predominantly lodgepole pine, with occasional trembling aspen (*Populus tremuloides* Michx.), or white birch (*Betula papyrifera* Marsh.), and with a small component of white spruce (*Picea glauca* (Moench) Voss) occurring on moist sites. The study stands are located in the SBPSxc (very dry cold) and the IDFdk3 (dry cool) biogeoclimatic subzones.

In our study area, the Chilcotin Plateau, the first reports of the 1980s MPB outbreak date to 1975 (Figure 1). The infestation, as measured by the geographic area in which newly beetle killed trees (red trees) were detected, began gradually, but increased rapidly starting in 1982, and then it collapsed suddenly in 1986 (Figure 1). The 2000s outbreak began abruptly in the Chilcotin area in 2002, peaked in 2008 and collapsed in 2010, most likely due to exhaustion of suitable hosts.

We used data from permanent sample plots established in the Chilcotin Plateau in the fall of 1987, one year following the collapse of the 1980s outbreak (Figure 2). The plots were first re-measured in August 2001, prior to the 2000s outbreak spreading into the Chilcotin Plateau and in September of 2013, three years following the collapse of the 2000s outbreak in the study area (Figure 1).

Initial plot establishment.

In 1987, 30 stands in the Chilcotin Plateau area were randomly selected from a larger population of beetle infested stands in the area, and measured for tree mortality and stand characteristics as described below. However, due to salvage harvesting or fire, by 2013 only 11 stands were available for re-measurement (Figure 2). The analysis in this paper is based on these surviving stands. Within each stand, ten plots were established on two parallel transects, with approximately 100 m between plots. By 2013 the number of plots remaining within each of the surviving stands varied from 5 to 10, for a total of 87 plots. Plot centres were marked with a painted wooden stake. Live and dead overstory plot trees (trees greater than or equal to 7.0 cm dbh) were selected using a wedge prism.

Depending on average tree size and stand density at a given sampling point, a wedge prism with imperial basal area factor (BAF) 10 ft²/ac, or BAF 20 ft²/ac (metric BAF 2.296 or 4.591 m²/ha) was selected to provide a tally of at least 8 trees per plot. Plot trees were marked and numbered with spray paint. Diameter, species and tree status (live or dead), was noted. In addition, a fixed area plot (3.10 m radius) was established at each plot centre and all live tree regeneration (less than 1.5 m tall) was tallied by species and height class. Trees less than 0.5 m tall were tallied as small regeneration and trees greater than or equal to 0.5 m but less than 1.5 m were tallied as large regeneration.

Plot re-measurements

In 2001 and 2013 all overstory and regeneration plots were re-measured using the same plot centers and methodology, and all trees sampled in 1987 were re-examined. Changes in tree status (alive or dead) were noted and trees which had grown large enough to be included in the overstory were measured. In addition, understory density (trees greater than 1.5 m tall but less than 7.0 cm dbh) was also measured in the 2001 survey by establishing a fixed area plot at each plot centre, with a radius of either 5.64m or 7.98m (total area of 100 m² or 200 m² respectively). All understory trees were tallied by species. Measurements in 2013 followed the same methodology, including the understory re-measurement.

Analysis

The analysis was conducted in two phases. At the stand level we calculated means in terms of volume and stems per hectare of live and dead trees, by measurement year.

Because of the high variability observed among plots within stands, observations at the plot level were used to study the characteristics of surviving legacies, including their susceptibility to MPB.

Overstory stand density at the beginning of the 1980s outbreak was estimated by assuming that all trees killed by the MPB as of 1987 were alive at the start of this outbreak (in the late 1970s, Figure 1). This assumption is reasonable since the annual rate of tree mortality due to causes other than MPB is normally very low. To calculate per hectare values for each plot we used the prism plot sampling methodology described by Marshall and LeMay (2005). In a small number of cases, it was difficult to distinguish between mortality caused by MPB and mortality due to other bark beetles (e.g., *Ips* spp), therefore, the percent of pine dead due to beetle included a small amount of trees killed by secondary beetles.

For each re-measurement year, the percent of *new* trees killed by beetle was calculated by taking the total number of trees dead due to beetle (i.e., not including dead trees that had been counted in the previous survey) divided by the total number of live and dead trees (again not including trees that had been previously recorded as dead). Stand means were calculated by averaging plots within stands. Repeated measures ANOVA was performed using STATISTICA (v. 7.1, StatSoft) to identify changes over time in volume-based diameter class distribution of overstory pine.

Characterizing the living forest legacies remaining after two outbreaks

The remaining analyses were conducted at the plot level. Cluster analysis was used to characterize the living stand structures that remained (legacies) following the two outbreaks. Hierarchical agglomerative cluster analysis (McCune and Grace 2002), using Bray-Curtis dissimilarities and the flexible-beta linkage method ($\beta = -0.25$), was performed to group plots ($n=87$) into legacy types based on post-outbreak stand structure, using the following variables: density of overstory lodgepole pine, density of understory conifers (trees less than 7.0 cm dbh but taller than 150 cm), density of small conifer regeneration (< 50 cm tall), density of large conifer regeneration ($150 \text{ cm} < \text{height} \leq 50 \text{ cm}$), density of all aspen taller or equal to 150 cm, and density of aspen smaller than 150 cm. Before the analysis, data were relativized to give equal weight to all variables in the analysis.

Multiresponse permutation procedures (MRPP) were used to test for differences among the legacy types identified in the cluster analysis, and nonmetric multidimensional scaling (NMS) was used to confirm the clustering and to visualize patterns of stand structure (McCune and Grace 2002). Both MRPP and NMS were based on Bray-Curtis dissimilarities (McCune and Grace 2002). Two ordination axes were extracted and Pearson's correlations were calculated between these axes and stand structure variables. The above analyses were performed using R (v3.0.2 R Core Team 2013) and the vegan package (Oksanen *et al.* 2013). Correlations were calculated using STATISTICA (v. 7.1, StatSoft).

In order to determine if the initial conditions in the forest and level of tree mortality caused by MPB, could be used to predict the types of forest legacy that were found in 2013, we employed discriminant analysis (McCune and Grace 2002). Using the plot data we related present-day structures to the following six variables:

- Initial number of pine trees per hectare alive prior to the start of the 1980s outbreak (PineDensityPre)
- Mean DBH of pine prior to the start of the 1980s outbreak (PineDBHpre)
- Amount of conifer regeneration (stems per ha) as measured in 1987, at the end of the 1980s outbreak. We assumed that this variable approximated the regeneration present in the plots prior to the start of the 1980s outbreak (RegenDensity1987)
- Number of new trees found dead at each measurement date (1987, 2001 and 2013) (DeadPineDensity1987, etc)

Multiple regression (forward stepwise, F to enter = 4) was used to calculate linear equations that related the groups identified in the discriminant analysis to the initial conditions as described by the measured variables. This analysis was also run using the software STATISTICA (v.12, StatSoft, 2013). A square root transformation ($\sqrt{x+0.5}$) was applied to all variables except mean DBH of pine (PineDBHpre), in order to satisfy the requirements for normality.

Measurement of present and past susceptibility in the living legacies

A susceptibility index value (S) was calculated for each legacy type found in 2013, based on the Shore and Safranyik (1992) susceptibility-rating system. In order to determine the

changes in susceptibility over time, this analysis was done on the present day structures and retrospectively at each measurement time, for the plots in each legacy type.

The susceptibility index (S) was calculated as the product of 3 variables:

$$S = P \times D \times L$$

where P is the percentage of the stand basal area composed of susceptible pine, i.e. the basal area of pine greater than or equal to 15 cm DBH (Safranyik *et al.* 1974), expressed as a percentage of the basal area of all species in the stand greater than or equal to 7.5 cm DBH; D is a density factor for the number of stems per hectare of all trees greater than or equal to 7.5 cm DBH (<250 stems = 0.1, 251-750 stems = 0.5, 751-1500 stems = 1.0, 1501-2000 stems = 0.8, 2001-2500 stems = 0.5, >2500 stems = 0.1); and L is a geographic location factor, a proxy variable for climatic suitability, determined by calculating the variable Y:

$$Y = (24.4 \times \text{longitude (degrees)}) - (121.9 \times \text{latitude (degrees)}) - (\text{elevation (m)}) + 4545.1$$

which is then used to determine L (Y>0, then L=1.0; 0>Y>-500, then L = 0.7; Y < -500, then L = 0.3). Shore and Safranyik (1992) also included in their index a factor pertaining to the average age of co-dominant and dominant pine. We did not measure stand ages in these multi-aged stands, but consider P to be a surrogate variable for age.

Results

Initial stand conditions and MPB mortality

Pre-outbreak overstory

Before the onset of the 1980s outbreak, the surveyed stands were dominated by pure lodgepole pine. We estimated that prior to the first survey only one stand (and only 2 plots within this stand) contained other species in the overstory. In this stand, trembling aspen made up 8% of the overstory density on average. Overstory canopies were well stocked with lodgepole pine, having an average density of 1139 stems per hectare (sph) and average volume of 119 m³/ha (Table 1). Mean overstory diameter was 16.1 cm (Table 1), however larger diameter trees (up to 57.3 cm) were present in some plots (Figure 3).

Overstory mortality (1975 to present)

The 1980s outbreak caused, on average, a 25% decrease in live overstory pine density, to 855 stems/ha by 1987 (ranging from 5 to 50% among stands) (Table 1). The outbreak killed the largest trees in the stands, however many trees large enough to be suitable hosts (>15 cm dbh) for MPB remained as susceptible host for the 2000s outbreak. Additional mortality occurred between the two outbreaks (from 1987 until 2001) and was assumed to be due to low level MPB activity, secondary bark beetles, competition and drought. The pine engraver, *Ips pini* (Say), often causes mortality following an MPB outbreak (Safranyik and Linton 1991), and was likely responsible for the mortality observed in the smaller diameter classes (Table 2).

The 2000s MPB outbreak caused mortality in our stands from 2002 until 2010 (BC Ministry of Forests, Lands and Natural Resource Operations aerial survey data) and ground surveys in 2013 indicated a further 22% decrease in overstory pine density on average (ranging from a 28% increase (due to recruitment), to a 56% decrease among stands), to a mean of 510 sph (Table 1).

Stand structure changes following two outbreaks

Overstory changes

In all years, the volume-based diameter class distribution of overstory pine was heavily weighted to the small diameter classes (Figure 3). Classes 15 and 20 cm contributed the most to stand volume in all years except 2013. In addition to the death of all trees in the larger diameter classes (30-55 cm), the two outbreaks caused significant mortality, by volume, in the 15 and 20 cm classes. By 2013, a downward shift in the diameter class distribution resulted in stand volume being dominated by trees in the 10 and 15 cm classes (Figure 3). Repeated measures ANOVA indicated that the volume present in each DBH class (dclass) varied significantly depending on the measurement year (yr) (yr*dclass interaction: $F=8.03$, $p<0.001$, $df=27$). These results highlight our observations of additional tree mortality in the smaller diameter classes occurring between the two outbreaks (2001) and of higher mortality in the smaller diameter classes during the 2000s outbreak than in the 1980s outbreak.

Overstory species composition shifted slightly over the 26 year study period due to pine mortality and an increase in the frequency of species other than lodgepole pine. By 2013,

three stands now had trembling aspen in the overstory (at densities ranging from 50 to 212 sph), which contributed between 7 and 45% of the stem density, and one stand (1 out of 87 plots) had interior spruce (*Picea glauca x engelmannii* Engelm.) (77 sph and 7% of the stem density).

Changes in the understory

Understory species composition and density did not change significantly between 2001 and 2013 (no understory data was collected at earlier dates). By 2013, this layer contained a minimum of 650 trees per ha (1265 sph on average, to a maximum of 2804 sph) and was dominated by lodgepole pine, with small components of trembling aspen (12% on average), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) (<2%), interior spruce (<2%) and rocky mountain juniper (*Juniperus scopulorum* Sarg.) (<2%) also present. There was a small decline (11%) in understory conifer density between 2001 and 2013, likely due to secondary beetles and diameter growth, which caused understory stems to become large enough to be counted as overstory. In 2013, understory conifers contributed 1094 sph (ranging from 650 to 2546 sph) on average, to the overall stem density.

Changes in the regeneration layer

Our surveys indicated that there was little change in density and species composition in the regeneration layer over the study period. In 2013, on average, conifer regeneration contributed 3427 sph (ranging from 199 to 10694 sph among stands) to the overall stem density. Lodgepole pine was the dominant conifer regeneration species, while Douglas-fir

and interior spruce were occasionally found in small proportions (<3%). Trembling aspen was found in 45% of the stands at densities ranging from 710 to 1730 sph. The spatial distribution of regeneration within stands was patchy; for example, one stand contained a plot with no regeneration at all, while another plot within the same stand had a pine regeneration density of over 27 000 sph.

Current (2013) state of lodgepole pine forests impacted by two mountain pine beetle outbreaks

By 2013, after two documented outbreaks, and considering all forest layers (overstory, understory and regeneration), there was an average of 5 032 sph of conifers surviving (min = 1714, max = 12 093). However, there was a large amount of variation within stands (between plots) in the abundance of surviving trees among the forest layers, particularly in the regeneration layer.

Considering all forest layers, by 2013, species composition varied from 100% lodgepole pine (four stands) to >25% trembling aspen in most layers (three stands). The remaining four stands had smaller percentages (<2%) of other conifer species (white spruce, Douglas-fir, and Rocky Mountain juniper) mainly in the regeneration and understory layers.

Legacies: Classification of the remaining living structures

Cluster analysis of plots using present-day stand structure variables identified five distinct living legacy types that remained following the two outbreaks in our study area (Figures 4, 5; Table 3). These types were significantly different ($p < 0.001$) and had high within-type homogeneity ($A = 0.33$). The number of plots representing each legacy type ranged from 14 to 22. Also, the legacy types defined in this study were dispersed throughout the stands so that different types occurred within the initial eleven stands. In 2013 the number of legacy types per stand ranged from 2 to 4.

Distances between the points in the two-dimensional ordination corresponded well with the original distance measures (linear fit $r^2 = 0.82$). Correlation analyses indicated that axis 1 (NDMS1) represented a gradient in the proportion of aspen in a legacy type relative to pine, which varied from high densities of aspen (all layers) and low densities of pine overstory, to relatively high densities of pine overstory and little aspen (Figure 5). The segregation of the groups identified in the cluster analysis also reflected this trend. Axis 2 represented a gradient of legacies with relatively high densities of conifer regeneration and understory ($r = -0.53$ and -0.69 for small and large regeneration respectively, $r = -0.69$ for understory) and low densities of aspen regeneration ($r = 0.32$), to high densities of aspen and low densities of conifer understory and regeneration.

The surviving legacies are described as follows (Figures 4, 5; Table 3):

Type 1. Abundant small lodgepole pine regeneration with sparse pine overstory (Short name: Small Pl regen): Small (< 50 cm tall) regeneration density in these plots was greater

(almost two times) than that in any of the other legacy types. There was no aspen present in the regeneration layer in any of these plots. There was below average density of overstory pine, the majority of which was distributed equally between the 10 and 15 cm dbh classes, with very few trees in the 20 and 25 cm classes.

Type 2. Abundant overstory aspen with sparse pine overstory (Short name: Aspen): This legacy type was defined by relatively high density aspen in all canopy layers. Overstory lodgepole pine in these plots was sparse and mostly in the 10 cm dbh class. Average densities of conifer understory and regeneration were also present.

Type 3. Abundant lodgepole pine understory and large regeneration (Short name: Advance regen): Characterized by high densities of large conifer regeneration and understory. Pine overstory is relatively abundant (560 sph) and mainly in the 10 cm dbh class.

Type 4. Low density overstory, understory and regeneration (Short name: Sparse): Both conifer and aspen densities, in all canopy layers were relatively low in this type. Overstory pine was distributed equally between the 10 and 15 cm dbh classes.

Type 5. Remnant lodgepole pine overstory (Short name: Remnant PI): Lodgepole pine overstory density was greatest in this type and was dominated by trees in the 10cm dbh class. This type also had the most trees from the higher dbh classes. Densities of all other conifer and aspen layers were lower than the overall average.

405
406 Discriminant analysis indicated that, overall, the six variables selected (representing
407 initial stand conditions and mortality at subsequent measurement dates) (Table 4)
408 influenced the type of legacy present in 2013 (Wilk's Lambda 0.298, $F(24,269) = 4.66$,
409 $p < 0.01$). Canonical analysis indicated that two roots (significant functions) described the
410 relationship between initial forest conditions and the type of legacy found in the plots in
411 2013 (Table 4). Root 1 was positively influenced (loaded) by the amount of live pine
412 overstory at the start of the outbreak, and negatively influenced by the mean diameter of
413 the initial overstory, amount of conifer regeneration present in 1987 and the density of
414 dead overstory pine in 1987, whereas Root 2 was significantly loaded (positively) only by
415 the amount of regeneration present in 1987 (Table 4). Recent tree mortality (2001 and
416 2013) had only a small influence on the discriminatory power of the two discriminant
417 functions (Table 4).

418
419 The discriminatory power of the variables used to describe the initial forest conditions,
420 was not strong enough to distinguish between individual legacy types (Figure 6). Instead,
421 the legacy types could be split into broader groups:

422 Root 1 (R_1) discriminated between types that currently have high densities of understory
423 and regeneration (named *high regeneration* group: types 1-3) and those that do not (*low*
424 *regeneration* group: types 4 and 5) and Root 2 (R_2) discriminated between groups based
425 on current overstory density (*low overstory* group: types 1,3,5 and *high overstory* group:
426 types 2 and 4). The levels of regeneration or overstory associated with the high or low
427 categories are given in Table 3.

Multiple regression to predict the groups identified in the discriminant analysis yielded two significant linear equations.

$$R_1 = 0.653 + 0.006(\text{RegenDensity1987}) + 0.029(\text{PineDBHpre}) + 0.011(\text{DeadPineDensity1987})$$

where an R_1 value of 1 indicates the type falls in the *low regeneration* legacy group and 2 indicates the *high regeneration* group ($r^2 = 0.40$, $p < 0.001$). The positive coefficients indicate that plots with initial conditions containing high densities of conifer regeneration, high levels of live pine and which sustained high pine mortality, had a high probability of being transformed into legacies characterized by dense understory and regeneration.

And

$$R_2 = 1.902 - 0.004(\text{RegenDensity1987}) - 0.019(\text{PineDensityPre}) + 0.014(\text{DeadPineDensity1987}) + 0.013(\text{DeadPineDensity2013})$$

where an R_2 value of 1 indicates that the legacy type falls into the *high overstory* group and a value of 2 indicates a *low overstory* type ($r^2 = 0.30$, $p < 0.001$). The coefficients of this equation indicate plots with high initial levels of conifer regeneration, high density of live pine and which sustained relatively low pine mortality in 1987 and 2013, would be transformed into legacies of the *high overstory* type.

Changes in forest susceptibility

The forests in this study were in a high state of susceptibility prior to the 1980s outbreak: the surveyed stands consisted of mainly pure lodgepole pine, with many trees of large diameter (Figure 3) and had susceptibility indices (S) that ranged from 34 to 57 among the legacy types (Figure 7). Susceptibility index values declined following the 1980s outbreak, however the magnitude of the decline varied among the types. During the period between outbreaks, S remained relatively stable and declined again in all types except Remnant PI following the 2000s outbreak. Susceptibility index values as of 2013 ranged from 5 to 20 among the five types, which were significantly lower (non-overlapping confidence intervals) than the pre-1980s level (Figure 7).

Discussion

Development of legacy types

Over the period of this study, each of the original eleven stands were fragmented into patches which were characterized as one of five legacy types, and which occurred in different frequencies among the stands. This increase in structural heterogeneity in response to bark beetle outbreaks has been reported in other forest systems (Winter *et al.* 2015) and in our study can be attributed to variability in MPB disturbance severity which created legacies at different successional stages within the original stands.

Our study indicates that single species, fire origin lodgepole pine stands in the Chilcotin were fragmented by MPB into a mosaic of patches that varied in species composition and

conifer and aspen density. But, undoubtedly, future wildfires, if uncontrolled, will re-set this mosaic back to larger patches of single-species lodgepole pine forests. This interaction between disturbances contributes to maintenance of structural and compositional diversity at all scales, from the stand to the landscape scale.

Predicting the type of legacy following MPB outbreaks

The Discriminant analysis was significant, i.e., it indicated a significant relationship between the variables that measured the stand conditions before the two outbreaks, and mortality caused by each outbreak, and the legacy types found in 2013, more than 30 years after the 1980's outbreak. However, the discriminatory power of the two significant roots (Table 4) was not strong enough to separate the five individual legacy types based on the variables measured (Fig. 6), i.e., the variables used, do not discriminate the legacies into single, "clean cut" groups, but into broad groups, which separated legacies that, in 2013, contained high or low levels of regeneration or overstory. The lack of precision in the prediction may be attributed to the fact that no measures of beetle population (beetle pressure in Shore and Safranyik 1992) were incorporated into the initial study.

Resiliency of the Chilcotin forest and susceptibility to MPB

In the landscapes of the Chilcotin, resiliency implies a dynamic mosaic of pine and aspen in various stages of succession, which undergoes constant re-organization following disturbance (Amoroso *et al.*, 2013). We found that, despite repeated MPB outbreaks and

recurrent fire over the previous century (Alfaro *et al.* 2004; Axelson *et al.* 2010), lodgepole pine remains the most common regeneration and understory tree species in legacies found these pine forests, with a lesser component of other species (see also Coates *et al.* 2009). Disturbance legacies including abundant pine regeneration and spatial heterogeneity of legacy types increase the resiliency of these forests (Seidl *et al.* 2014) and ensure the continuity of this complex lodgepole pine/fire/beetle system (Alfaro *et al.* 2008) at the landscape level, over decades. This enduring cycle, is an example of a stable and resilient system.

Because each legacy type identified in this study currently has a different susceptibility index (Figure 7) the present distribution and abundance of these legacies will determine the future susceptibility of the Chilcotin landscapes to MPB outbreaks. Current pine stands in the Chilcotin Plateau are presently not susceptible to mountain pine beetle (low susceptibility indices), however, as surviving overstory and understory trees respond to reduced competition with increased growth rates (Axelson *et al.* 2009), the legacies will become susceptible again. The length of time required for a legacy type to become susceptible again will vary according to its intrinsic characteristics. Long term studies are needed to determine how the present day mosaic will evolve over time and determine future likelihood of fire and beetle disturbance.

Management implications

520 Analysis of the impacts of the two recent MPB outbreaks reported in this paper indicates
521 that Chilcotin pine forests remain well stocked with conifers. Target stocking standards
522 for stands in the SBPSxc and IDFdk fall between 800 and 1200 well-spaced stems/ha
523 (BC MoF 2002), well below the average total stem density present in each of the legacy
524 types identified in this paper following two documented outbreaks (Table 3). Considering
525 only the remaining overstory pine and understory conifers, and making the conservative
526 assumption that half the understory will be lost to attrition, mistletoe or drought, densities
527 (in 2013) for three of the legacy types (Advance regen, Remnant Pl and Aspen types)
528 were still greater than the target standards following the two outbreaks, while densities of
529 the other two types (Sparse and Pl regen types) met the minimum stocking standards.
530 However, a key factor not measured in this study, and which is critical for assessing the
531 potential contribution of existing regeneration to future crops, is the spatial distribution of
532 the regeneration (stocking standards measure well-spaced trees). For this reason, it is
533 possible that the low density stand structures (Small Pl regen, Aspen and Sparse types)
534 may remain understocked for some years. Over time, this shortage may be mitigated as
535 we expect that regeneration density will increase in these structures as a consequence of
536 the regeneration opportunities created by canopy openings caused by the 2000s outbreak.
537 In the absence of fire, a delay in regeneration establishment of up to 10-15 years
538 (Axelson *et al.* 2010) is common following MPB outbreak, as canopy gaps are gradually
539 created as MPB killed trees fall. Where wood production is not the main objective, a
540 strategy of no intervention following bark beetle outbreaks is an effective approach to
541 maintaining diverse forest structures on a large scale, supporting ecosystem biodiversity
542 and resilience (Winter *et al.* 2015).

Forest ecosystems are shaped by processes that unfold over centuries. For this reason, predictions of forest ecosystem responses to disturbances, climate change and forest management need to be based on long-term observations. Permanent research plots such as those described in this study, contribute to our understanding of forest dynamics, and are crucial to the development and validation of forest process models, and in testing predictions of ecological models and theories. The knowledge gained from long-term observations facilitates the development of long-term strategies of conservation and sustainable forest management. In addition, such studies will provide an invaluable reference and resource for future generations that will be critical for understanding the impacts of global change and carbon dynamics.

Conclusions

Disturbances are key drivers of forest ecosystem dynamics, and forests are well adapted to their natural disturbance regimes. The Chilcotin pine forests remain well stocked with conifers. Barring quick ecosystem transformation due to climate change, it appears that, for the next decades, forests impacted by beetle and fire, in the Chilcotin Plateau, will continue to deliver most, if not all of the ecosystem services they have for the last 100 years. However, from an economic perspective, after two documented MPB outbreaks, live lodgepole pine density and volume was reduced to 510 sph and 35 m3/ha respectively, and is now dominated by trees in the 10 and 15 cm DBH classes. Unless dead lodgepole pine could still be utilized as wood products, the remaining live stand volume would not be enough to sustain a commercial harvest in the immediate future.

566

567 There is an increasing requirement to manage forests for ecological objectives along with
568 wood production and to incorporate legacy management into harvesting prescriptions. A
569 useful framework for assessing how well ecological objectives are being met is to
570 compare stands to reference conditions. The legacy types we describe here could be used
571 to define a natural range of reference conditions to guide silviculture methods that
572 emulate natural heterogeneity.

573

574

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Table 1. Average live conifer overstory (trees greater than or equal to 7 cm dbh) measurements in lodgepole pine stands in the Chilcotin Plateau, British Columbia. These stands sustained two mountain pine outbreaks: the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2012).

Year	Density (stems/ha)				Volume (m ³ /ha)				Diameter (cm)			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
pre-1987	1139	406	638	2008	119	37	85	208	16.1	2.6	11.6	19.6
1987	855	464	418	1900	66	24	30	96	14.9	2.1	10.8	17.6
2001	651	323	301	1286	64	23	36	107	16.2	2.0	13.3	19.3
2013	510	242	226	1051	35	22	9	83	13.3	1.4	11.0	15.8

Table 2. Percent overstory lodgepole pine stems killed by mountain pine and secondary beetles in each diameter class and for each survey year, in lodgepole pine forests impacted by mountain pine beetle in the Chilcotin Plateau of British Columbia. These stands sustained two mountain pine outbreaks: the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2012).

Diameter class (cm)	% Stems killed		
	Post 1980's outbreak (1987)	Interim (2001)	Post 2000's outbreak (2013)
10	13	22	19
15	25	16	42
20	49	20	76
25	77	16	84
30	75	51	100
35	88	50	100
40	100		
45	100		
50	100		
55	100		

Table 3. Initial (1980’s) and present (2013) characteristics of five legacy types in lodgepole pine forests impacted by two mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. These stands sustained two mountain pine beetle outbreaks: the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2010). Legacy types are illustrated in Figure 4.

	Legacy type					
Variable	1. Small PI regen ^{ac}	2. Aspen ^{ad}	3. Advance Regen ^{ac}	4. Sparse ^{bd}	5. Remnant PI ^{bc}	Mean
Initial density (sph)						
Overstory pine	1173	688	933	1097	1730	1099
Understory conifers	~	~	N/A	~	~	~
Small conifer regen	7248	2815	4330	460	1511	3198
Large conifer regen	1208	1084	3005	202	518	1131
Present density (sph)						
Overstory pine	339	277	560	202	1182	468
Understory conifers	886	1063	2779	539	655	1121
Small conifer regen	5962	964	1017	304	642	1753
Large conifer regen	2611	1656	3525	193	186	1571
Aspen regen	0	2364	47	18	0	609
Aspen (>1.5 m tall)	12	672	74	11	77	201
Initial overstory PI dbh (cm)	14.9	19.1	18.7	15.7	12.9	16.4
Present overstory PI dbh (cm)	15.5	13.1	11.3	15.5	12.0	13.5
Number of plots	17	22	14	18	16	87

Superscripts indicate additional classification based on present density as per discriminant analysis

^a *high regeneration* group

^b *low regeneration* group

^c *low overstory* group

^d *high overstory* group

Table 4. Factor structure matrix resulting from discriminant function analysis used to determine the discriminatory power of six variables in predicting the type of legacy found following two mountain pine beetle outbreaks (in the 1980s and 2000s) in the Chilcotin Plateau of British Columbia. *denotes a variable with significant discriminatory power in Root 1 or 2. (Eigenvalues <0.15).

Variable	Pooled-within-groups correlations	
	Root 1	Root 2
SQRT Initial overstory PI density (sph)	0.419138*	0.262645
Initial overstory PI dbh (cm)	-0.512948*	-0.275565
SQRT Initial conifer regen density (sph)	-0.584147*	0.747382*
SQRT Dead PI overstory density 1987 (sph)	-0.378138*	-0.134343
SQRT Dead PI overstory density 2001 (sph)	-0.025043	0.122185
SQRT Dead PI overstory density 2013 (sph)	0.167044	-0.270446

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Figure 1. Annual number of hectares of pine forests impacted by mountain pine beetle in our study area on the Chilcotin Plateau of British Columbia (data from Ministry of Forests, Lands and Natural Resource Operations. Resource Practices Branch. Aerial Overview Surveys. <http://www.for.gov.bc.ca/hfp/health/overview/overview.htm>.)

Figure 2. Location of eleven stands in the Chilcotin Region of British Columbia used to measure the impacts of two mountain pine beetle outbreaks.

Figure 3. Changes in volume-based diameter class distribution over time, in Chilcotin region lodgepole pine forests impacted by mountain pine beetle. These stands sustained two mountain pine outbreaks: the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2010).

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Figure 7. Mean susceptibility index (S) values over time, for five lodgepole pine stand structure types. These forests were impacted by two mountain pine beetle outbreaks that occurred on the Chilcotin Plateau of British Columbia; the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2010). Structure types are described in Figure 4.

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69x55mm (300 x 300 DPI)

Figure 2. Location of eleven stands in the Chilcotin Region of British Columbia used to measure the impacts of two mountain pine beetle outbreaks.
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Figure 5. Two-dimensional ordination showing the segregation of lodgepole pine plots by cluster (each point is a plot and symbols represent clusters) and gradients of stand structure. Scores for each stand structure variable are indicated by lines from the origin. These stands sustained two mountain pine outbreaks: the 1980s outbreak (1975-1985) and the 2000s outbreak (2002-2010). Structure types are described in Figure 4.

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Figure 6. Results of canonical analysis representing the discriminatory power of two discriminant functions (Root 1 vs Root 2) to separate between living legacy types present in the Chilcotin Plateau of British Columbia following two mountain pine beetle outbreaks.
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86x62mm (300 x 300 DPI)