Differentiating mixed- and high-severity fire regimes in mixed-conifer forests of the Canadian Cordillera

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Mixed-severity fire regimes are important drivers of forest dynamics, stand structural attributes, and regional and local landscape heterogeneity, but they remain poorly understood. We reconstructed site-level fire histories using fire scars and even-aged cohorts at 20 sites in two contiguous watersheds in southeastern British Columbia, Canada, a region that is particularly understudied. We compared stand composition and structural attributes (i.e., snag and veteran tree densities, tree size variability, and maximum tree size) at sites found to be mixed-severity, as well as those found to be high-severity after recent (<150 years) and older (>150 years) stand-replacing fires. We developed two forest indices capturing age-structure complexity and continuity to refine these comparisons.

Eleven of 20 sites displayed mixed-severity fire histories and were located at elevations 600 m higher than previously described for this landscape. Tree species composition varied with disturbance history. Mixed-severity sites were dominated by Douglas-fir and western larch that regenerated after frequent low- to moderate-intensity fires, which created fire scars. Periodic moderate-severity fires generated some even-aged cohorts with surviving veteran trees. At higher-elevations, intense fires generated cohorts dominated by lodgepole pine. Subalpine fir dominated high-severity sites that last burned >250 years ago.

Age structures at mixed- and older high-severity sites were of similar complexity, but could be differentiated using our index of age structure continuity. We found western larch to be a strong indicator of historical mixed-severity fire regimes. Western larch trees and stumps were only found at mixed-severity sites, and 84% of these individuals established within 15 years of antecedent fire scars. Snag densities were greatest at high-severity sites that burned >150 years ago, in contrast to expectations that mixed-severity sites would be more structurally complex. Tree size attributes were indistinguishable between mixed- and high-severity sites, although subcanopy densities were particularly high (upwards of 5600 ha−1) having persisted since the last fire at most sites. Selective harvesting and fire suppression during the 20th century have homogenized contemporary forest structures in mid-elevation forests. An improved understanding of mixed-severity fire regimes is vital to determining whether forest resilience is compromised and where ecological restoration is warranted.

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1. Introduction

Wildland fires are a keystone disturbance shaping forested landscapes in western North America (Agee, 1993; Hessburg and Agee, 2003). Increasing recognition of the historical prevalence of mixed-severity fire regimes has ushered in a new paradigm of fire ecology and management (Hessburg et al., 2007; Halofsky et al., 2011; Perry et al., 2011). Until the last decade, most fire history research focused on quantifying the frequency of low-severity and high-severity fire regimes, with less attention paid to variations in fire severity (Amoroso et al., 2011; Perry et al., 2011). Although the prevalence and importance of mixed-severity fire regimes in many mixed-conifer forests is increasingly recognized, many aspects of these fire regimes remain poorly understood (Halofsky et al., 2011; Perry et al., 2011). For example, the relative importance of low- versus high-severity fires and their spatio-temporal variation is a vital component of mixed-severity fire regimes...
(Agee, 1998). Understanding variation within and among forest types is key to identifying fire regimes that have been significantly altered by fire exclusion and suppression during the 20th century. Knowledge of fire regime variability is also critical for determining where forest resilience is compromised and ecological restoration is justified (Stephens et al., 2013; Odion et al., 2014; Stine et al., 2014). Knowledge gaps related to fire regime variability pose substantial challenges to managers who are responsible for sustainable harvest planning and biodiversity conservation. Hence, new research approaches are needed to better understand the spatio-temporal complexities of mixed-severity fire regimes and their influences on forest dynamics.

A fire regime describes the spatial and temporal dimensions of many fires for a defined area and time period (Agee, 1993, 1998; Turner, 2010). In forest ecosystems, low-severity fire regimes are characterized by frequent, low-intensity surface fires that burn at short intervals, consume surface fuels and understory vegetation, and kill a minority of the overstory trees (Agee, 1993; Schoennagel et al., 2004). Thick-barked trees mostly survive surface fires, often forming cambial scars, and resulting in open-canopied stands with few subcanopy trees. Traditionally, the resulting fire scars were used to quantify historical fire frequency of individual stands, or of larger areas (Swetnam et al., 1999). In contrast, high-severity fire regimes are characterized by infrequent, high-intensity active or passive crown fires that kill understory vegetation and most overstory trees (Agee, 1993), initiating new even-aged cohorts dominated by early-successional tree species (Kipfmueller and Baker, 1998). Fire frequency in these forests has been reconstructed using landscape-level time-since-fire maps combined with age-class modeling, a method that requires assigning a single age to each patch of forest and does not account for variation in historical fire severity (Johnson and Gutsell, 1994; Van Wagner et al., 2006). It is now recognized that classifying fire regimes as solely high- or low-severity oversimplifies variability inherent of many forest ecosystems (Perry et al., 2011).

By definition, mixed-severity fire regimes are inherently complex and vary at multiple scales (Agee, 1998; Lertzman et al., 1998; Falk et al., 2007; Perry et al., 2011). Across a landscape, different fires can burn at different severities (Halofsky et al., 2011). Within an individual fire, effects can be variable resulting in patches with low, moderate or high levels of tree mortality within the perimeter of a single fire (Lentile et al., 2006; Collins and Stephens, 2010; Turner, 2010). Over time, consecutive fires at a given location can burn at different severities leaving a range of compositional and structural legacies persisting for decades to centuries (Hessburg et al., 2007; Collins and Stephens, 2010; Heyerdahl et al., 2012). Moreover, this spatio-temporal variation in fire severity is influenced by topography, vegetation, climate and fire weather, past natural and anthropogenic disturbances, as well as their interactions and feedbacks (McKenzie and Kennedy, 2011; Moritz et al., 2011; Turner, 2010; Perry et al., 2011).

Wide variability in fire severity within and among regions has prompted re-evaluation of many fire histories, including understudied forest types. The re-evaluation of some ponderosa pine (Pinus ponderosa Dougl. ex Laws.) Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forests previously described as having a low-severity fire regime has yielded evidence of mixed-severity fire histories in the western US (e.g. Sherriff and Veblen, 2006; Sherriff et al., 2014; Odion et al., 2014) and British Columbia (e.g. Heyerdahl et al., 2012). Historical mixed-severity fires were also reconstructed at high latitudes in the foothills of the Rocky Mountains in west-central Alberta, Canada (Amoroso et al., 2011). In mountainous terrain, fire regimes vary along elevational gradients, with mixed-severity fire regimes commonly associated with montane forests growing in the ecotone between low-elevation woodlands and high-elevation subalpine forests (Schoennagel et al., 2004; Sherriff and Veblen, 2006; Sherriff et al., 2014). In the Canadian Cordillera, montane forests (elevations from 1200 to 1800 m.a.s.l) have received little attention and represent a significant knowledge gap in our understanding of the prevalence of mixed-severity fire regimes (Marcoux et al., 2013).

The use of multiple lines of evidence has helped bolster inferences of historical fire severity and regimes (Swetnam et al., 1999; Hessburg et al., 2007). While severity of modern fires can be measured directly by examining fire perimeters and variations in tree mortality using aerial photography (Anderson, 2012), remote sensing (Lentile et al., 2006; Soverel et al., 2011; Arnett et al., 2015) or postfire field-work (Halofsky et al., 2011), inferring severity for historical fires that burned prior to the 20th century requires paleoecological methods because direct measurements are impossible. One dendrochronology approach reconstructs the occurrence and severity of past fires using fire scars on surviving trees in combination with tree age data to identify even-aged cohorts (Sherriff and Veblen, 2006; Amoroso et al., 2011; Heyerdahl et al., 2012). Fire scars and an abundance of veteran trees can provide evidence of low- or mixed-severity fire whereas the presence of even-aged cohorts often indicates mixed- or high-severity fire (Brown et al., 1999; Heyerdahl et al., 2012). A second approach uses variations in age structure to differentiate regeneration dynamics (after Veblen, 1992) associated with fires of different magnitudes (Sherriff and Veblen, 2006). Stands burned by high-severity fires regenerate forming even-aged cohorts as trees simultaneously colonize available growing space (Agee, 1993; Kipfmueller and Baker, 1998; Taylor and Skinner, 2003). Low-severity fires generate multiple regeneration opportunities through time yielding uneven-aged forests (Agee, 1993; Covington and Moore, 1994). Fires of intermediate severity (e.g., moderate-severity) or a mixture of low- and high-severity (e.g. mixed-severity) fires generate multi-aged stands including veteran trees and cohorts that establish on areas that burned at higher severity (Heyerdahl et al., 2012). Thus, a combination of fire scar, cohort, and age structure analyses could help strengthen severity inferences in forest types historically shaped by mixed-severity fire regimes.

Improving our knowledge of forests with mixed-severity fire regimes is a research and management imperative (Spies et al., 2006; Perry et al., 2011) and is essential to emulating natural disturbance regimes and the diverse patterns and habitats they help create (Landres et al., 1999; Cissel et al., 1999). For managers, knowledge of stand attributes produced by successive fires of a range of severities is quite limited. As a result, forest management can be influenced by a variety of untested assumptions. One assumption is that high-severity fires lead to simple age and size structures within individual stands, while mixed-severity fires result in age complexity and structural diversity (Agee, 1993; Taylor and Skinner, 2003). It has also been proposed that some forests frequently burned by low- and mixed-severity fires may harbor stand structural attributes similar to late successional stands that develop over long periods following stand-replacing disturbances (Spies et al., 2006; Perry et al., 2011). Comparisons of stand-level attributes generated by mixed- and high-severity fire regimes within the same landscape are rare; our research addresses this critical knowledge gap.

We reconstructed site-level fire histories using annually resolved fire scars and high-resolution forest age structures to address three questions: (1) What is the prevalence of mixed-severity fire in two mid-elevation, mixed-conifer watersheds? (2) How do forest composition and structure differ between sites with mixed- and high-severity fire histories? (3) How do fire and topography influence forest composition, structure and dynamics? To answer these questions, we sampled 20 sites for fire history, forest age, and size structure, including snag and veteran tree densities, and developed...
two new indices to quantify stand age-structure complexity and continuity. To address questions regarding stand-level attributes produced by different fire regimes, we contrasted mixed-severity sites, as well as high-severity sites after recent (<150 years) and older (>150 years) stand-replacing fires. Given that forests and fire regimes vary with topography (Heyerdahl et al., 2001; Taylor and Skinner, 2003), we also sampled site-level topographic characteristics and tested for interactions between topography and fire regimes and their combined influence on forest dynamics.

2. Methods and materials

2.1. Study area

This study included 20 research sites in the contiguous Joseph and Gold Creek (JGC) watersheds (49°25′25″N 115°40′00″W, Fig. 1) that encompass 15,400 ha south of the City of Cranbrook in southeastern British Columbia. Climate is continental with a strong rain shadow effect created by the Purcell Mountains, which block the prevailing westerly air masses (Meidinger and Pojar, 1991). At the Cranbrook meteorological station (940 m above sea level (m.a.s.l.)), winters are cold with daily average temperatures of −7.5 °C in January (Environment Canada, 2011). July and August are warmest with daily averages of 18 °C and daily maximums of 26 °C. Annual precipitation averages 383 mm, with 70% as rain between May and September when monthly averages are 275 mm. The largest number of lightning-ignited fires in the last 30 years occurred from July through August (B.C. Wildfire Management Branch, unpublished data).

The JGC watersheds extend from approximately 1000 to 2000 m.a.s.l. Dominant soils are Eutric Brunisols at low- to mid-elevations on fluvo-glacial gravel and morainal till deposits and Humo-Ferric Podzols at high elevation on coarse-grained colluvium and till (Valentine et al., 1978). The dominant tree species along this elevational gradient are: P. menziesii var. glauca (Mirb.) Franco (Douglas-fir), Larix occidentalis Nutt. (western larch), Pinus contorta var. latifolia Douglas ex Loudon Engelm. Ex S. Watson (lodgepole pine), Picea engelmannii Parry ex Engelm. (Engelmann spruce) and Abies lasiocarpa (Hook.) Nutt. (subalpine fir).

Two existing classification systems provide contrasting interpretations of fire regimes in the study watersheds (Marcoux et al., 2013). According to the natural disturbance type classification (B.C. Ministry of Forests, 1995), which currently guides forest management, 94% of the watersheds have a high-severity fire regime with mean fire intervals of 150 years and low-severity fires burn only in the valley bottoms. Alternatively, the historical natural fire regime system (sensu Hardy et al., 2001; Blackwell et al., 2003) classifies 87% of the watersheds as a mixed-severity fire regime with mean fire intervals of 35 years and 35–100 years at low and middle elevations, respectively. The high-elevation subalpine forests (13%) are classified as a high-severity fire regime (Blackwell et al., 2003).

The study area has a diverse land use history. It lies within the Ktunaxa Nation traditional territory. Although fire was used by the Ktunaxa people to enhance the growth of important plant species (e.g., bitterroot (Lewisia rediviva) (Mah, 2000)), to improve hunting, and maintain open stands for campsites and travel (Barrett and Arno, 1982), its use was likely limited to lower elevation ponderosa
pine – Douglas-fir dry forests. European settlement began in the late 1800s, concurrent with the gold rush, followed by railway development. Timber harvesting, cattle grazing and forest management have been predominant in the watershed since the early 20th century. Today, the JGC watersheds provide the drinking water source for Cranbrook, B.C., and represent the wildland-urban interface for this community.

2.2. Site selection

We used a stratified-random sampling approach to locate 20 study sites. In a geographical information system (GIS), we stratified the study area according to fire regime classification, forest composition and accessibility. Potential study sites included forests classified as a mixed-severity fire regime (Blackwell et al., 2003). We used the provincial forest cover inventory (B.C. Forest Analysis and Inventory, 2012) to identify stands that were >3 ha in size, dominated by conifers, and for ease of access, within 600 m of a traversable road. From the subset of potential study sites, we randomly selected 10 sites with mean fire intervals of 35 years and 35–100 years at low and middle elevations, respectively based on the historical natural fire regime classification (Blackwell et al., 2003). After an initial site visit, sites with evidence of historical partial harvesting were included if fire history and age structure could be reconstructed from intact stumps and remnant trees. At each selected study site, fire history and forest structure plots were located at the center of the stand using predetermined GPS coordinates. Three topographic characteristics, elevation (m.a.s.l.), aspect and slope were measured in the field at the center of each plot. Aspect was converted into a linear index representing warm (0 = southwest) to cool (180 = northeast) aspects for subsequent analyses (Beaty and Taylor, 2007).

2.3. Site-level fire history

At each site, we constrained our sampling of fire-scarred trees to a 1-ha fire-history plot allowing direct comparison among sites (Da Silva, 2009; Marcoux et al., 2013). We selected the oldest trees, including charred remnant logs or snags, and those with multiple scars to provide the most complete representation of plot-level fire history. Full or partial cross-sectional disks that included the tip of each fire scar were sampled using chainsaws (Cochrane and Daniels, 2008). Fire disks were sanded with progressively finer paper (up to 600 grit), measured using WinDendro Software (Ver 2004) and visually and statistically cross-dated to an annual resolution using the program COFECHA (Holmes, 1983) to yield plot-level composite fire-scar chronologies (Dietrich, 1980).

We sampled canopy and subcanopy trees at the center of each fire-history plot. For canopy trees (dbh ≥ 25 cm), an N-tree distance sampling scheme was used to select the 30 live trees, snags or stumps closest to plot center (Jonsson et al., 1992). For each site, we used the distance to the furthest tree and applied a Poisson distribution correction to scale each observation to a density per hectare in subsequent analyses (Lessard et al., 2002; Jonsson et al., 1992). Live subcanopy (dbh ≤ 25 cm) trees were tallied in a 10 × 10 m quad at breast height (dbh) were recorded for all trees, snags or stumps. All canopy trees and 10 randomly selected subcanopy trees were sampled to assess tree ages. Increment cores were extracted as close to the base of trees as possible (30 ± 21 cm; mean ± standard deviation); multiple cores were taken to increase the likelihood of pith intersection. Partial sections were taken from stumps and logs. We noted evidence of mountain pine beetle (Dendroctonus ponderosae Hopkins) on P. contorta snags, including entrance holes in the bark, pitch tubes, blue stain fungus in the sapwood and vertically oriented J-shaped egg galleries engraved in the cambium and secondary xylem tissue (Axelson et al., 2009).

Increment cores and partial sections from stumps and logs were mounted and glued to grooved wooden blocks and sanded with progressively finer paper (from 80 to 400 grit). Ring-width series of each sample were measured using a VelMex bench interfaced with a computer and statistically cross-dated using the program COFECHA (Holmes, 1983) to determine inner-ring dates of all samples and outer-ring dates of samples from dead trees. For cores that did not intercept the pith (37%), we estimated the number of missing rings using a geometric correction (Duncan, 1989). The number of years for trees to grow to core height was estimated using species-specific height-age regressions developed by counting the rings on disks cut from seedlings at the root collar and up the stem at 10 cm intervals. Combined, 87% of the pith and height corrections were <15 years; therefore, 15-year age classes were considered a suitable representation of stand age structures and used for subsequent analyses.

To address the prevalence of mixed-severity fire regimes, site-level fire demography diagrams were developed and fire history was reconstructed using fire-scar evidence of low-severity fires and even-aged cohorts (hereafter ‘cohorts’) as evidence of higher-severity fires that produce conditions conducive to tree establishment (Sherriff and Veblen, 2006; Heyerdahl et al., 2012). Cohorts were identified at each site by analyzing the number of trees per hectare (tph, scaled based on the N-tree sampling design) establishing in 15-year periods that started from the pith date of the oldest tree, shifted one year at a time, and ended with the pith date of the youngest tree per site. Cohorts were detected when (a) >50 tph established within 15 years after 1800 or (b) >30 tph established within 15 years before 1800. We modified the criterion for cohorts through time after determining only 29% of sampled trees established before 1800. Because the number of living trees decreases through time due to tree death, decay of coarse wood and subsequent fires (Ehle and Baker, 2003), 40% of plots included <10 trees, reducing the chance of detecting a cohort with the conservative (>50 tph) criterion. To evaluate the sensitivity of our cohort identification, we repeated our analysis using a 20-year period; however, no additional cohorts were detected. For cohorts that established within 15 years of a fire scar at the same site (n = 15) or fires that scarred trees at ≥2 adjacent sites (n = 4), we inferred that they originated from fire and assigned the same calendar year as the fire scars. The remaining cohorts (n = 10) were assigned the calendar year prior to the pith date of their oldest tree, and we assessed whether they originated after fire, using four lines of evidence (after Marcoux et al., 2013). (1) Fire scars occurred at elevations up to 1871 m.a.s.l. (2) Most cohorts included the oldest trees at each site (e.g. there were few or no veteran trees). (3) Many cohorts were comprised of shade-intolerant lodgepole pine, which regenerates after fire. (4) The cohorts did not correspond with years of death of logs or snags, which may have indicated regeneration after windthrow or insect outbreaks rather than fire.

The site-level fire reconstructions were used to identify veteran trees and calculate time since last fire (TSLF). Veteran trees are defined here as those that survived at least one fire and had a dbh ≥ 25 cm at the time of sampling. TSLF was calculated as the number of years between the most recent fire scar or cohort date and 2009, the year of sampling.

2.4. Inferring fire severity

The presence of fire scars, cohorts, and TSLF determined from the fire history reconstructions were used to classify each site into one of three mutually exclusive fire history groups (after Heyerdahl et al., 2012): (I) mixed-severity fire; (II) high-severity fire; young forest; and (III) high-severity fire, old forest. Sites
with ≥ 2 different fire years indicated by scars and ≥ 1 cohort were classified as a mixed-severity fire history (Heyerdahl et al., 2012). Sites with cohorts including the oldest trees and < 1 fire year indicated by scars were classified as a high-severity fire history (Antos and Parish, 2002; Heyerdahl et al., 2012). For the high-severity sites, TSLF was used to differentiate young (TSLF ≤ 150 years) and old (TSLF > 150 years) forests (B.C. Ministry of Forests, 1995).

2.5. Forest composition and structure

To address the effects of mixed- and high-severity fire histories on stand composition and structure, we derived several site-level metrics. For each site, we calculated density and basal area m² ha⁻¹ of the canopy trees of each species. To calculate the basal area of stumps, we estimated diameter at breast height using appropriate regression models for trees for this region in British Columbia (Demarschalk and Omule, 1982). Using the data from all live canopy and subcanopy trees and stumps with dbh ≥ 5 cm, we calculated modified species-specific importance values for each site as the sum of relative basal area and relative density (after Curtis and McIntosh, 1951). To assess site structure, we calculated site-level densities of living trees in each of three dbh-classes (5–24.9 cm, 25–44.9 cm, ≥ 45 cm) and of large snags (≥ 25 cm). Because we were interested specifically in the effects of fire on stand structure, we excluded 25 lodgepole pine snags at 3 sites that were killed by mountain pine beetle in the 1980s and 2000s. Tree size variability was represented by the maximum dbh at each site and the coefficient of variation of trees with dbh ≥ 25 cm.

We developed two indices to characterize the variability in stand age structures resulting from different fire histories. For each site, we determined the frequency of trees that established in 15-year age classes using all live and dead trees sampled for age. The first index, age-structure complexity (hereafter ‘complexity’), represented instances where age structures were either simple or complex by counting the number of 15-year classes occupied by at least one tree. Simple age structures have few classes; complex age structures have many classes and a wide range of tree ages. The second index, age-structure continuity (hereafter ‘continuity’), represented whether age-structures were relatively continuous or discontinuous by counting the number of unoccupied (or empty) 15-year classes within the range of occupied classes. Continuous age structures have fewer unoccupied classes than discontinuous sites.

At the tree level, we assessed lags between fire and establishment. We identified the fire scar or post-fire cohort preceding the establishment of each tree. Lags were calculated in one of two ways, depending on the type of fire evidence: (1) the difference between the fire-scar year and tree pith date or (2) the difference between the pith dates of the oldest tree in the post-fire cohort and individual tree. We determined if each tree established as part of an even-aged cohort within 15 years of fire. Frequency histograms of lag times relative to scars and post-fire cohorts were compared among species.

2.6. Comparison of fire history groups

We stratified sites by the three fire history groups and tested for differences in topographical site characteristics using ANOVA and a post hoc Tukey–Kramer test for unequal sample sizes (Kutner et al., 2005) in R software using the DTK package (Lau, 2013). We compared species importance values to test for compositional differences (Taylor and Skinner, 2003) using a Kruskal–Wallis H-Test and pairwise comparisons with Bonferroni correction (Kutner et al., 2005) in R software using the asbio package (Aho, 2011). We tested for differences in forest structure (size classes, snags, tree-size variability) among the fire history groups using the same approach as importance values.

To examine concordance among approaches used to infer severity of past fires, we compared the two age-structure indices, complexity and continuity, among the three fire history groups using ANOVA and a post hoc Tukey test (using Systat software 2008). Continuity values were square root transformed to meet normality assumptions of ANOVA.

Principal components analysis (PCA) was used to relate variation in species importance values to topography and forest structure (Beaty and Taylor, 2007) (using R software, vegan package; Oksanen et al., 2011). Compositional gradients were then identified by correlating the original species importance values (i.e., component loadings) with the three PCA axis scores (Peres-Neto et al., 2003). Topographic characteristics and structural attributes were correlated with PCA axis scores to identify underlying trends. Correlation significance was determined using a cut-off value of [0.5] (Richman, 1988; Peres-Neto et al., 2003).

3. Results

3.1. Fire history

At all 20 sites, fire scars or cohorts provided evidence of past fires (Table 1, Fig. 2). In total, 155 fire scars between 1578 and 1953 were cross-dated on 74 trees from 12 sites (Table 1). Tree ages were determined for 590 live trees, 45 snags and 19 stumps (Fig. 2). Trees established between 1270 and 1953. Tree deaths were between 1885 and 2007, with 55% of snags dying from mountain pine beetle in the late-20th century and the stumps resulting from harvesting in the early- and mid-20th century. On average, 33 ± 5 trees (mean ± standard deviation) were aged at each site and all sites included at least one cohort. A total of 29 cohorts were identified, including 11 cohorts that established prior to 1800 (326 sampled trees per cohort), and 18 cohorts that established after 1800 (538 sampled trees per cohort). Of all the cohorts, 27 likely originated after fire: 19 cohorts were associated with fire scars at the same site or an adjacent site; another seven were dominated by P. contorta or L. occidentalis; and, one was comprised of P. menziesii only. Of the remaining two cohorts, one originated after early 20th century logging (site 7) and the origin of the last could not be determined (a mid-1800s cohort at site 15).

At all sites combined, 37 fire years between 1600 and 2009 were identified based on fire scars (n = 31 years) or cohorts only (n = 6 years). Fires in 1721, 1847, 1865, 1869 and 1910 were recorded at ≥ 4 sites, with a 1910 fire detected at 12 of 20 sites. Only six fires were recorded since the widespread 1910 fire and they were detected at single sites only, unlike many fires in the 1700 and 1800s that resulted in scars at multiple sites. TSLF ranged from 56 to 350 years (Table 1, Fig. 2). While 75% of sites burned in the last 150 years, the remaining 25% of the sites have not burned in >250 years.

3.2. Comparison among fire history groups

Eleven of 20 sites had evidence of mixed-severity fire histories (fire history group I; Table 1, Fig. 2a). Fire scars provided evidence of 2–15 fires per site. Each of these sites also had 14 cohorts, with 74% of the cohort dates corresponding with fire years denoted by a scar. All group I sites burned during the 1910 fire but had multiple fire scars that pre-dated 1910 and 22–100% of their canopies included veteran trees. TSLF ranged between 56 and 99 years, but the oldest veterans originated in the late 1200s to early 1300s, or in the 1600 and 1700s.

The remaining nine sites were assigned to the high-severity fire history groups since each had even-aged cohorts that included the oldest trees per site, and fire scars and veteran trees were absent.


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<th>Fire history group</th>
<th>Site Elev. (m)</th>
<th>Aspect index (0–180)$^a$</th>
<th>Number of Cohorts</th>
<th>Last fire (year)</th>
<th>Time since last fire (years)</th>
<th>Species$^b$ importance values$^c$</th>
<th>Density (individuals per ha) Live trees 5–24.9 cm</th>
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<td>117</td>
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<td>(98) (0) (75) (51) (12) (732) (194) (3) (10)</td>
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<td>1 0</td>
<td>1735</td>
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<td>117</td>
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</table>

$^a$ Aspect was converted into a linear index representing warm (0 = southwest) to cool (180 = northeast) aspects.

$^b$ Species abbreviations are Psme = Pseudotsuga menziesii, Laoc = Larix occidentalis, Pico = Pinus contorta, Pien = Picea engelmannii, and Abla = Abies lasiocarpa.

$^c$ Species importance values (relative density + relative dominance) reported as an index from 0 to 200, where 0 = absent and 200 = one species present only.

$^d$ Excluding Pinus contorta snags killed by mountain pine beetle.

$^e$ Scar was on a charred dead tree.
(Table 1). Four sites were assigned to group II (Fig. 2b). Some of these sites last burned during fires in 1910 and 1869, like sites in group I, but the fire years 1905 and 1920 were unique to this group. TSLF ranged from 89 to 144 years and veteran trees were absent, except at Site 9. The remaining five sites were assigned to group III (Fig. 2c). These sites last burned 274 to 350 years ago and no veteran trees were present.

3.3. Topographic attributes among fire history groups

Mean elevation varied significantly among the three fire history groups \((p < 0.001; \text{Table 1})\). Group I occurred at lower elevations than groups II \((p = 0.01)\) and III \((p < 0.001)\). Mean slope and aspect did not vary significantly among the groups \((p = 0.21 \text{ and } p = 0.30, \text{ respectively})\).

3.4. Species composition and tree establishment following fire

All five dominant tree species were present in fire history group I, but not in groups II and III (Table 1). In group I, 9 of 11 sites were dominated by Pseudostuga menziesii or L. occidentalis. Both high-severity fire groups (II and III) lacked L. occidentalis, but only group III lacked P. menziesii. In Group III, 4 of 5 sites were dominated by A. lasiocarpa with some Picea engelmannii and 1 site was composed entirely of P. contorta. This variation in composition was also reflected in species importance values among fire groups (Table 1).
The importance values for *P. menziesii* were significantly greater in group I than III, while the opposite was true for *A. lasiocarpa* (*p* < 0.05 for both species). The importance values for *L. occidentalis* were significantly greater in group I than groups II and III (*p* < 0.05).

Age-structure indices varied significantly among the three fire history groups (Table 2), but complexity and continuity differed. Groups I and III had more occupied 15-year age classes, making them more complex than group II (*p* = 0.04 and *p* = 0.01, respectively). Group I had the most discontinuous age structures. It had more unoccupied 15-year age classes than groups II and III (*p* = 0.01 and *p* = 0.03, respectively), which were not significantly different from each other (*p* = 0.81).

Establishment lags varied among species following fires of different severity, inferred from fire scars and post-fire cohorts within sample sites (Fig. 3). The majority of *P. contorta* (63%) established...

---

**Table 2**

Comparison of age structure indices, complexity and continuity, among fire history groups. Different superscripts indicate significant differences in the number of 15-year age classes among groups (*α* = 0.05).

<table>
<thead>
<tr>
<th>Fire history group</th>
<th>n</th>
<th>Age complexity (number of occupied age classes per site)</th>
<th>Age continuity (number of unoccupied age classes per site)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean (SE)</td>
<td>Range</td>
</tr>
<tr>
<td>I</td>
<td>11</td>
<td>8.0 (0.8)a</td>
<td>3–12</td>
</tr>
<tr>
<td>II</td>
<td>4</td>
<td>3.3 (1.5)b</td>
<td>2–5</td>
</tr>
<tr>
<td>III</td>
<td>5</td>
<td>10.4 (4.6)a</td>
<td>3–14</td>
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</table>
after higher-severity fires that generated cohorts but no scars. In contrast, 84% of *L. occidentalis* established after less severe fires that generated scars. Regardless of fire severity, both species established almost exclusively within 15 years of fire as part of a cohort. Most *P. menziesii* (63%) established after fires that generated scars and fewer than half established in a cohort or within 15 years of a fire. Of the two most shade-tolerant species, more *P. engelmannii* (67%) than *A. lasiocarpa* (16%) established after fires that generated cohorts (Fig. 3). Prolonged establishment of the latter two species was prevalent at 4 of 5 high-severity sites where fires had not burned in >150 years.

3.5. Structural attributes among fire history groups

Densities of live canopy trees ranged from 71 to 543 ha\(^{-1}\) and subcanopies included up to 5600 trees ha\(^{-1}\) (Table 1), with no significant differences among fire history groups (\(p = 0.41\) and 0.57, respectively). In fire history group I, 21–100% of canopy trees had survived at least one fire and were considered veterans. Among the fire history groups, all sites in group I but only 50% and 80% of sites in groups II and III, respectively, included large trees (dbh ≥ 45 cm); however, the mean density of large trees did not differ significantly among groups (\(p = 0.20\)). Similarly, group I had the largest trees and greatest variability in tree size, but these attributes did not vary significantly among fire history groups (\(p = 0.27\) and 0.12, respectively).

Snags with dbh ≥ 25 cm that were not killed by mountain pine beetle were more common at sites in fire history group III (80%) than in groups I (27%) and II (50%) (Table 1). Snag density was significantly greater for group III than I (\(p = 0.04\)); however, density in group II was not significantly different from either of these groups (\(p > 0.05\) for both pairwise tests).

3.6. Species composition relative to topography and stand structure

Based on the PCA of species importance values, sites were associated with three compositional gradients, which were primarily driven by elevation and to a lesser degree, aspect (Table 3). The cumulative proportion of variance explained by all three components was 85% (PC1 = 38%, PC2 = 28%, PC3 = 19%). Principal Component 1 (PC1) was negatively correlated with importance values of...
P. menziesii ($r = -0.53$) but positively correlated with those of A. lasiocarpa ($r = 0.52$). PC1 scores were strongly correlated to elevation ($r = 0.77$). Snags densities were also positively correlated to PC1 ($r = 0.64$), suggesting they were more commonly associated with A. lasiocarpa than P. menziesii. P. contorta was the dominant species associated with Principal Component 2 (PC2, $r = -0.81$); however, axis scores were not correlated to any topographical or structural attributes. Principal Component 3 (PC3) was negatively correlated with L. occidentalis ($r = -0.79$). PC3 scores were positively correlated with aspect ($r = 0.71$), suggesting L. occidentalis was more common on sites with warm, southwest aspects (low values) rather than cool, northeast aspects (high values, Table 3).

No structural attributes were correlated with PC3.

4. Discussion

4.1. Prevalence of mixed-severity fire

Mixed-severity fire regimes are increasingly recognized as important drivers of mixed-conifer forest dynamics (Hessburg et al., 2007; Margolis and Balmat, 2009; Perry et al., 2011). We found mixed- and high-severity fire histories at individual sites in the JGC watersheds over the past 400 years. Over half of sites (11 of 20) were classified as mixed-severity (group I) with fire scars, even-aged cohorts and veteran trees. The remaining nine sites were classified as high-severity, given the presence of a single even-aged cohort combined with the absence of fire scars or veteran trees. Four of the high-severity sites had burned in the last 150 years (group II); whereas five sites had not burned in over 250 years (group III).

The term “mixed-severity” can describe (1) variation in severity of different fires at one site through time, or (2) variation in severity within the perimeter of one fire (Perry et al., 2011). We found evidence of both types of variation, as has been noted in other mixed-conifer forests (Brown et al., 1999, 2008; Heyerdahl et al., 2012). Fires of differing severity burned at each mixed-severity site over time (Fig 2a). Most reconstructed fires (73%) were documented solely by scars, indicating surface fires of relative low-severity. The remaining fires were severe enough to create conditions suitable for cohort establishment (Heyerdahl et al., 2012). The widespread, well-documented “Great Fire of 1910” (Pyne, 2008) burned into our study area, with heterogeneous impacts. The 1910 fire initiated a new stand at one (site 16) of the 11 sites that were burned by this fire. Cohorts established at eight sites, while also producing scars at most. The remaining three sites had fire scars only. One-quarter of 215 veteran trees that survived the 1910 fire were thin-barked fire-intolerant species (Agee, 1993), suggesting a low-severity, patchy fire in at least some stands (Taylor and Skinner, 2003).

Spatial patterns of fire severity were primarily controlled by elevation, with a mixed-severity regime at lower-elevations and transitioning into a high-severity regime at upper-elevations. While the watersheds as a whole could be classified as a “mixed-severity regime”, the separation of fire severity along an elevation gradient suggests two fire regimes are present. This pattern is consistent with other mountain landscapes (e.g. Taylor and Skinner, 2003; Margolis and Balmat, 2009), although we found evidence for mixed-severity fire at sites at much higher elevations (600+ m higher) than previously described for this landscape (B.C. Ministry of Forests, 1995; Marcoux et al., 2013). However, the transition between fire regimes was not abrupt along the elevational gradient. All three fire history groups were present at sites between c. 1400 and 1650 m.a.s.l., indicating variable spatial and temporal patterns of fire severity in this transitional ecotone (Perry et al., 2011).

4.2. Insights from age-structure indices of continuity and complexity

The ability to differentiate mixed- and high-severity fire regimes is dramatically improved when multiple lines of evidence are used (Hessburg et al., 2007; Heyerdahl et al., 2012). Two newly-developed forest age-structure indices corroborated our site-level inferences based on fire scars and cohorts and provided additional insights. The index of continuity was most effective for differentiating mixed-severity from high-severity sites, independent of time since last fire. Mixed-severity sites (group 1) contained numerous discontinuous age classes (Table 2), likely driven by lower-severity fires periodically thinning stands by eliminating fire-susceptible trees, and releasing growing space in which trees established (Beaty and Taylor, 2007). This age structure pattern can result from factors unrelated to fire, including disturbance by insects like mountain pine beetle (Axelson et al., 2009), interannual to decadal variations in climate (Brown, 2006), or availability of viable seed or growing space (Johnson and Fryer, 1989; Crotteau et al., 2013). However, two lines of evidence suggest fires of mixed severity primarily explain the discontinuous age structures we observed. First, fire scars were common and frequent at many sites (2–15 per site) with mean return intervals of 7–56 years (Fig 2a; Da Silva, 2009; Marcoux et al., 2013). Second, 233 of 308 (76%) trees established within 15 years of a fire scar (Fig 3), providing a strong linkage between fire and tree establishment.

Our complexity index showed the effects of high-severity fires on forest age structure change with time since fire. This index differentiated the simple and even-aged structures at recently-burned high-severity sites (group II) from the complex, older and uneven-aged high-severity sites (group III), as well as the complex, uneven-aged mixed-severity sites (group I). Well-documented stand development processes and differences in the life histories of the species in our study area explain differences in age structure complexity between the high-severity groups II and III (Oliver and Larson, 1996; Franklin et al., 2002). Within 15 years of high-severity fires, post-fire cohorts composed of P. contorta, P. menziesii and P. engelmannii established (Table 1; Fig 3), as has been observed in other montane and subalpine forests (Romme, 1982; Antos and Parish, 2002; Amoroso et al., 2011). These cohorts were often dominated by P. contorta which is shade-intolerant and regenerates on exposed mineral soil often from serotinous cones (Turner et al., 1997, 1999; Antos and Parish, 2002), but varied in composition likely due to a range of factors including differences in site attributes, fire severity (Lentile et al., 2005; Gass and Robinson, 2007; Crotteau et al., 2013), seed source (Greene and Johnson, 2000), competing vegetation (Doyle et al., 1998) and post-fire interannual variation in climate (Little et al., 1994). This stage was followed by decades with limited tree establishment and recruitment, due to crown closure, competition and self-thinning (Johnson and Fryer, 1989; Oliver and Larson, 1996; Antos and Parish, 2002). High-severity sites that burned <150 years ago were in this stem-exclusion stage, with narrow even-aged cohorts, followed by several decades without canopy recruitment (Fig 2b). At older high-severity sites, uneven-age structures resulted from A. lasiocarpa and P. engelmannii recruitment in canopy openings over the past c.200 years (Table 1; Figs. 2c and 3). Prolonged lags between fire and establishment for both species are consistent with their shade tolerance and slow understory growth rates (Antos and Parish, 2002).

4.3. Western larch and snags as indicators of fire severity

Few fire history studies have included L. occidentalis. Both mixed- and high-severity fire regimes have been suggested for these forest types (Barrett et al., 1991). Our results suggest the
fire-adapted *L. occidentalis* may be a useful indicator of mixed-severity fire. *L. occidentalis* stumps and living trees were found only at mixed-severity sites (group I). Within mixed-severity sites, 84% of *L. occidentalis* established following surface fires leaving scars, and most individuals (68%) were part of a cohort that established ≤15 years after fire (Fig. 3). This shade-intolerant species requires a proximate seed source shortly following disturbance, when it has the competitive advantage of a mineral seedbed over shade-tolerant species (Schmidt et al., 1976). Thus, fires that leave veteran tree seed sources are needed for population survival at a stand-level (Schmidt et al., 1976). Intermediate patch sizes, large amount of edge and patchiness in forest structure associated with mixed-severity fire regimes (Agee, 1998; Lentile et al., 2005; Perry et al., 2011) would also aid the regeneration required to sustain *L. occidentalis* populations.

Few snags were found at sites with mixed-severity fire histories, contrasting our expectation that these sites would have complex stand structures (Hutto, 2006; Spies et al., 2006). However, this result may misrepresent the role of mixed-severity fires on snag creation, given the influences of 20th century management. Widespread selective harvesting of large *L. occidentalis* and *P. menziesii* trees from our study area in the early 20th century likely removed future potential snags. Exclusion of surface fires in recent decades (Daniels et al., 2011; Marcoux et al., 2013) may have also limited snag creation given that densities tend to be greatest <20 years and >250 years after fire (Morrison and Raphael, 1993; Lehmkuhl et al., 2003; Hutto, 2006). Consistent with this temporal pattern, low snag densities were found at most mixed-severity sites where time since last fire was 56–99 years. More frequent fires before 1910 at mixed-severity sites (Da Silva, 2009; Marcoux et al., 2013) may have generated and maintained snags in greater abundance than we observed.

The impacts of 20th century management undoubtedly affected other forest size attributes, especially at mixed-severity sites. Stumps from selectively logged canopy dominant trees were generally the largest diameter individuals at our sites. With detailed age-structure data and taper regressions for estimating diameter at breast height (Demearschalk and Omule, 1982), we were able to reconstruct the size of these trees. However, our reconstructions did not account for the release in growing space for intermediate subcanopy trees, which would reduce tree size variation at many sites. Exclusion and suppression of surface fires, indicated by the low occurrence of fire scars during the 20th century (Da Silva, 2009; Marcoux et al., 2013), has further restricted opportunities for size stratification among trees within stands. For example, in seven of our mixed-severity study sites, subcanopy trees formed even-aged cohorts (Fig. 2a) that established following the last surface fire and persist at high densities of 500–5600 trees ha⁻¹ (Table 1). Had low- to moderate-severity fires continued to burn, they would have killed many of these small understory trees, released growing space for dominant trees to accumulate biomass, and contributed to greater variation in tree sizes within stands and forest densities among stands (Miller et al., 2012). The cumulative impacts of harvesting, fire exclusion and suppression have resulted in artificially subtle differences in forest size attributes between mixed- and high-severity sites and homogenized structural attributes across the landscape.

4.4. Fire and topography influences on forest composition and structure

Spatial patterns of fire occurrence and behavior are controlled by interactions between topography and other environmental gradients that influence species composition, fuel characteristics, and their flammability (Heyerdahl et al., 2001; Falk et al., 2007; Moritz et al., 2011). The resulting fire effects and vegetation recovery provide feedbacks that influence subsequent fires and the long-term frequency and severity of the fire regime (Falk et al., 2007). In the JGC watersheds, elevation creates a persistent climatic gradient that governs forest composition (Table 3) and fire regime. At low elevations, warm, dry climate dries fuels and helps promote spread of low-intensity, high-frequency surface fires (Schoennagel et al., 2004), resulting in fire scars and facilitating regeneration of thick-barked, fire-resistant *P. menziesii* and, on warm aspects, *L. occidentalis* (Fig. 3, Table 3). Repeated low- and mixed-severity fires reduce surface and ladder fuels (Bekker and Taylor, 2010) and resulted in stands with discontinuous, complex, uneven age structures (Figs. 2a and 3). Since weather and climate are non-stationary and years with extreme fire weather occur periodically (Da Silva, 2009; Daniels et al., 2011), conditions suitable for higher-severity fires provide opportunities for even-aged, post-fire cohorts to establish in these low-elevation forests as well (Fig. 2a and b).

A contrasting dynamic occurs in *A. lasiocarpa*-dominated forests at high elevation in the JGC watersheds (Tables 1 and 3). Cooler temperatures and deep, long-lasting snow packs increase fuel moisture and shorten the fire season (Schoennagel et al., 2004). Fuels of higher moisture content are effective barriers to the spread of low-severity fires and generally require prolonged drying to burn (Schoennagel et al., 2004; Gedalof et al., 2005). In these forests, infrequent but high-severity fires initiate even-aged cohorts dominated by *P. contorta* and *P. engelmannii* (Figs. 2c and 3). In the long intervals between fires, *A. lasiocarpa* increases in dominance (Fig. 3) creating the continuous ladder and canopy fuels needed to initiate and propagate crown fires (Cruz et al., 2006). Snags are also generated over time through processes other than fire, including partial disturbances and autogenic processes, which are common to *A. lasiocarpa* dominated forests (Table 3) (Antos and Parish, 2002).

4.5. Management recommendations

In contemporary mixed-conifer forests, stands with historical mixed- versus high-severity fire histories are difficult to distinguish since species composition and structure have been altered by the combined influences of fire exclusion, suppression and high-grade logging (Hessburg and Agee, 2003; Hessburg et al., 2005). In the past, mixed-severity fire regimes produced a multitude of developmental pathways and contributed to stand- and landscape-level heterogeneity (Perry et al., 2011). In the 20th century, surface fires have been effectively eliminated from the JGC watersheds (Da Silva, 2009), as in other locales regionally (Daniels et al., 2011), and in western North America (Perry et al., 2011). This has altered regeneration dynamics of fire-adapted species (Merschel et al., 2014) and yielded stands with persistent, high-density subcanopy trees, which pose a substantive fuel hazard (Miller et al., 2012). In other forests with historical low- to moderate-severity fire regimes, high-severity fires have become more common in: (1) stands composed of small trees relative to those made-up of larger trees, and (2) stands that have burned only once relative to those that burned multiple times during the last 100 years (Miller et al., 2012). An increased chance of high-severity fires in our study area is of serious concern as the JGC watersheds form the wildland-urban interface and provide drinking water to the City of Cranbrook, British Columbia.

Ideally, ecological heterogeneity created by mixed-severity fire regimes at stand- and landscape-levels should influence decisions related to silviculture, wildfire and fuels management. Where historically frequent surface fires are now lacking, silvicultural systems, ecological restoration, and fuels mitigation should emulate the full variability of the mixed-severity fire regime (Stephens et al., 2013). Toward this goal, we suggest managers working in forests with mixed-severity fire regimes consider the following:
1. Differences in contemporary forest structure between mixed- and high-severity regimes are subtle, largely due to the impacts of early 20th century harvesting and subsequent fire exclusion. New approaches are needed to discriminate among historical fire regimes and to emulate their variability.

2. Interpretations of historical fire severity based on age-structure match inferences based on presence of fire scars and even-aged cohorts only when an index of age-structure continuity is used. Reconstructing mixed-severity regimes within stands requires detailed age-structure data and should consider quantifying continuity.

3. Veteran trees and *L. occidentalis* are associated with mixed-severity fire regimes and therefore, may be useful field and landscape-level mapping indicators.

4. In contemporary forests affected by high-grade logging in the early 20th century, high density of large snags (dbh >25 cm) may be a stronger indicator of high-severity fires that burned >150 years ago than of mixed-severity fires, although this will vary by species. This factor can be useful in rapid field evaluations of historical fire regimes.

5. Elevational limits between mixed- and high-severity fire regimes form a complex gradient rather than an abrupt, static boundary. Differentiating fire histories should be based on multiple lines of evidence and delimiting fire regime boundaries must be more nuanced than extrapolation based on elevation alone.

5. Conclusions

Forest and fire management that seeks to emulate historical disturbance regimes requires accurate depictions of fire regimes and associated variability of forest structures. Evaluating the efficacy of methods used to infer historical fire severity will continue to be important as fire histories are re-evaluated throughout western North America. Our research adds new insights to previously understudied forests of British Columbia where mixed-severity fire regimes are more common than previously believed (B.C. Ministry of Forests, 1995; Marcoux et al., 2013). Our new age structure index of continuity, corroborated by the presence of fire scars and veteran trees, effectively differentiates sites with mixed-versus high-severity fire histories. Combined, these multiple lines of evidence provided strong evidence that relatively frequent surface fires mixed with periodic higher-severity fires historically burned in montane forests up to elevations of 1700 m a.s.l. Similarly, the regeneration dynamics of *L. occidentalis* are strongly linked to surface fires, making this species a useful indicator of historical mixed-severity fire regimes throughout its range in the Pacific Northwest and southern British Columbia.

In the absence of surface fires during the 20th century in the JGC watersheds, subcanopy trees have persisted at high density, increasing stand-level fuel hazards and homogenizing montane forests. We conclude that fire exclusion and suppression have altered historical fire regimes and forest structures, strongly contrasting current forest and fire management paradigms for the montane forests of our study area (B.C. Ministry of Forests, 1995). Our findings reveal a critical need to better understand the historical role of surface fires and mixed-severity fire regimes throughout montane forests of the Canadian Cordillera. This information is essential in determining where and how fire regimes have been altered, forest resilience may have been compromised, and management of forests, fires and fuels can help restore ecological integrity.

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References


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