

Spatial interpolation and mean fire interval analyses quantify historical mixed-severity fire regimes

Gregory A. Greene^{A,B} and Lori D. Daniels^A

^AForest and Conservation Sciences Department, University of British Columbia,
3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

^BCorresponding author. Email: gagreene@alumni.ubc.ca

Abstract. Tree-age data in combination with fire scars improved inverse-distance-weighted spatial modelling of historical fire boundaries and intervals for the Darkwoods, British Columbia, Canada. Fire-scarred trees provided direct evidence of fire. The presence of fire-sensitive trees at sites with no fire scars indicated fire-free periods over their lifespan. Sensitivity analyses showed: (1) tree ages used in combination with fire-scar dates refined fire boundaries without biasing mean fire return intervals; and (2) compared with derived conservative, moderate and liberal thresholds (i.e. minimum burn likelihood cut-off values), fixed thresholds generated area burned estimates that were most consistent with estimates based on the proportion of plots that recorded historical fires. Unweighted and weighted spatial mean fire intervals (50–56 and 58–68 years respectively) exceeded dendrochronological plot-level (38-year) estimates based on fire scars only. Including tree-age data from fire-sensitive trees to calculate landscape-level fire interval metrics lengthened the mean return intervals, better representing historical high-severity fires. Supplementing fire scars with tree ages better reflects the spatiotemporal diversity of fire frequencies and severities inherent to mixed-severity fire regimes.

Additional keywords: Darkwoods, fire scars, fire size, GIS, inverse distance weighting, montane forests, subalpine forests, tree ages.

Received 28 May 2015, accepted 23 December 2016, published online 7 February 2017

Introduction

Forest managers are increasingly mandated to conserve biodiversity and sustain ecosystem function while maintaining renewable resources (Christensen *et al.* 1996). Efforts have redoubled in light of a changing global climate and as contemporary research unveils the degree to which forest structures have changed as a result of 20th-century management (Stephens *et al.* 2013). With fire as a dominant agent of disturbance, understanding the temporal and spatial patterns of historical fires can inform management strategies that aim to sustain or restore the resilience of fire-adapted ecosystems (Turner 2010). Reconstructing historical fires is a first step in achieving these goals (Swetnam *et al.* 1999).

Fire interval statistics are the traditional tools used to describe the temporal variability of surface fire regimes, as recorded by fire-scarred trees (Dieterich 1980; Swetnam *et al.* 1999). The mean fire interval (MFI), the mean number of years between successive fires at a site, is a common measure of fire frequency (Dieterich 1980; Agee 1993). MFI describes fire occurrence at various temporal (e.g. annual, decadal and centennial) and spatial (e.g. tree, stand and landscape) scales (Falk 2004; Falk *et al.* 2007).

At the individual tree level, the smallest unit of measure in studies of fire history, fire frequency is quantified by the mean point fire interval (MPFI) (Agee 1993; Baker and Ehle 2001).

The MPFI is calculated by averaging the time between fire events on trees with multiple fire scars. Although fire scars provide affirmative evidence of the occurrence of fire at discrete point locations, trees are not perfect recorders of fire (Dieterich and Swetnam 1984; Swetnam and Baisan 1996). Fire scars may fail to form if cambial damage does not occur (Van Hone and Fulé 2006; Stephens *et al.* 2010), or may be erased from the record by subsequent fires, mechanical damage, or wood decay (Parsons *et al.* 2007). Therefore, the intervals calculated from individual trees are subject to false negatives (Farris *et al.* 2010), potentially overestimating fire intervals and underestimating fire frequency (Baker and Ehle 2001).

Errors in fire frequency calculated at the tree level can be offset by combining fire interval data from multiple trees into composite mean fire interval (CMFI) records representing broader spatial scales (Dieterich 1980; Parsons *et al.* 2007). The CMFI is typically generated at the plot or study site level, representing intermediate-scale assessments, but may also be generated across a watershed or landscape, representing coarse-scale assessments. Composited fire interval data have been shown to increase the likelihood of obtaining complete inventories of major fires (Baker and Ehle 2001; Farris *et al.* 2010). However, the composite approach also has limitations, as fire frequency varies with spatial scale (Falk 2004; Falk *et al.* 2007) and is highly dependent on research, sampling design and the

statistical methods of analysis (Baker and Ehle 2001; Reed and Johnson 2004; Farris *et al.* 2010). As frequency metrics depend on the size of the sample unit, the CMFI approaches 1 year as the sampling area increases from plot to watershed and landscape scales (Falk 2004; Kou and Baker 2006; Falk *et al.* 2007). Thus, to directly compare CMFI statistics within and among studies, the research design, the size of sampled units, methods for selecting trees and sample sizes within sample units must be carefully considered.

Kernan and Hessl (2010) introduced the spatial mean fire interval (SMFI) as a technique for investigating spatiotemporal variability in fire, using a geographic information system (GIS). An SMFI is a spatially explicit method for calculating and representing MFI and is constructed by interpolating between fire-scar point data. Though an SMFI cannot address false negatives associated with individual tree-level analysis, it compensates for the potential loss or lack of fire-scar evidence by estimating burn perimeters in unsampled areas between fire-scarred trees (Kernan and Hessl 2010). SMFI maps supplement traditional fire interval statistics by providing spatially continuous and heterogeneous estimates of fire frequency, enabling managers to better characterise historical fire regimes and visualise the relationships between fire and topography (Kernan and Hessl 2010).

Mapping fire boundaries

Hessl *et al.* (2007) compared several techniques for mapping historical fire boundaries. The most common approach, the 'expert' approach, requires fire behaviour experts to draw fire boundaries by hand based on point locations of fire-scarred trees, relative to their topographic situation and surrounding fuel loads. This method provides ecologically meaningful results, but is time-consuming and subject to human bias due to differing interpretations of fire behaviour among experts. Three less-subjective, computer-based techniques for mapping historical fire boundaries from point data were also assessed: Thiessen polygons, indicator kriging and inverse distance weighting (IDW). Although the simplest to parameterise and the least computationally intensive, the Thiessen polygon method produced results that were not ecologically meaningful in broad-scale studies. Fire burn shapes were unrealistic, preventing additional analysis on spatial pattern. The indicator kriging method produced ecologically meaningful results, but suffered from a high degree of subjectivity in model parameterisation and was computationally intensive. IDW was found to produce the best overall results, requiring some subjective parameterisation, but was otherwise the most efficient, ecologically interpretable and relatively accurate method for reconstructing spatial patterns of historical fires (Hessl *et al.* 2007; Swetnam *et al.* 2011).

Using presence of fire-sensitive trees to reconstruct historical fires

In areas subject to mixed- and high-severity fire regimes, fire-scar evidence may be uncommon or missing from forest stands, limiting the use of fire scars in reconstructions of the historical fire regime. This is particularly problematic in subalpine forests that are dominated by fire-sensitive tree species including Engelmann spruce (*Picea engelmannii* Parry ex Engelm.),

subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and lodgepole pine (*Pinus contorta* Doug. ex Louden) (Alexander 1987; Keeley 2012). Attributes such as thin bark, shallow root systems, the persistence of dead lower limbs, and the horizontal and vertical arrangements of fuels make stands of these species highly susceptible to severe injury and death by fire (Alexander 1987; Schoennagel *et al.* 2004; Keeley 2012). Given the cool, mesic climate of high-elevation forests, the risk of fire is lower than in warmer, low-elevation forests. During the subsequent long intervals between consecutive fires, forests mature and accumulate fuels, contributing to high-severity impacts on fire-sensitive trees when they do burn (Alexander 1987; Schoennagel *et al.* 2004). In these forests, the presence of fire-sensitive species that rarely form scars or survive fire provides strong evidence of an absence of fire over their lifespans.

In the current study, we reconstructed historical fire boundaries and generated SMFI surfaces using a GIS, and fire-scar and tree-age data that were collected in mixed-conifer forests under a mixed-severity fire regime. These forests spanned a broad elevation gradient, including warmer, drier forest types in the lowest elevations, and cooler, wetter subalpine forests in the highest elevations. Although previous studies have used IDW analyses to investigate the spatial attributes of historical low- and mixed-severity fires (Hessl *et al.* 2007; Kernan and Hessl 2010; O'Connor *et al.* 2014), these studies were based on fire-scar evidence alone. Multiple lines of evidence, including fire-scar and tree-age data, have been shown to benefit reconstructions of historical mixed-severity fire regimes (Margolis *et al.* 2007, 2011; Margolis and Balmat 2009). Currently, only one study has investigated the effects of including ages of fire-sensitive trees in IDW interpolations to model the high-severity components of a mixed-severity fire regime (Yocom-Kent *et al.* 2015). In their analysis, Yocom-Kent *et al.* (2015) applied tree-age data from fire-sensitive trees as surrogates for the lowest value for the year of the last stand-replacing fire. As the tree species in our study can establish following a range of disturbances (Kulakowski *et al.* 2003; Axelsson *et al.* 2009, 2010) and in relation to climatic variation independently of disturbance (Brown and Wu 2005; Brown 2006; Brown *et al.* 2008; Swetnam and Brown 2011; Heyerdahl *et al.* 2014), we developed methods that required no *a priori* claims as to the causal agent or date of origin of high-elevation stands. Specifically, we incorporated the ages of fire-sensitive trees as proxies for fire-free periods in our spatial analyses.

To assess the efficacy of reconstructing mixed-severity fire regime attributes using a GIS and IDW, we tested the effects of novel input data and model parameterisation on model outputs. We first tested the effect of including fire-sensitive tree ages (evidence of fire absence) with fire scars (evidence of fire presence) on modelled fire boundaries and SMFI estimates. Second, we tested how parameterisation of the model changed the number of fire polygons, area burned and SMFIs. Specifically, we contrasted three derived thresholds (i.e. minimum burn likelihood cut-off values; Hessl *et al.* 2007) with a fixed fire-boundary threshold. Finally, to assess the quality of the spatially interpolated fire metrics, we compared the modelled area burned and fire interval estimates against metrics derived from composited fire-scar data using standard dendrochronological methods (after Farris *et al.* 2010). We predicted that including

age data from fire-sensitive trees would: (1) produce generally smaller burn polygons as compared with IDW methods that only include fire-scar data; and (2) lengthen fire return intervals across the study area compared with traditional CMFI calculations.

Methods

Study area

The study site is a 3870-ha portion of the south-easternmost watershed of the Darkwoods, a 55 000-ha property owned and managed by the Nature Conservancy of Canada. Located on the leeward side of the Selkirk Range and the western side of the Creston Valley (49°12'N, 116°41'W; mean elevation 1670 m above sea level (asl)) (Fig. 1), the study site is generally east-facing, with terrain varying from barren, rocky peaks and gentle-to-moderate slopes in the high elevations (maximum 2875 m asl), to steep drainages and exposed rocky outcrops in the lower elevations (valley bottom 468 m asl). From valley bottom to altitudinal tree-line, vegetation is a complex mix of conifers. The lower elevations are dominated by ponderosa pine (*Pinus ponderosa* Doug. ex C. Laws. var. *ponderosa* Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) in the warmer and more complex terrain (e.g. rocky outcrops), and by western red cedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in the cooler, more mesic areas (e.g. along drainages). Mid-elevations are co-dominated by western larch (*Larix occidentalis* Nutt.) and Douglas-fir on the warmer aspects, and western red cedar and western hemlock on the

cooler aspects. Subalpine forests in the highest elevations are co-dominated by Engelmann spruce and subalpine fir, with isolated stands of western larch. Lodgepole pine is subdominant across the mid- and high elevations.

Research design and sampling

In the summer of 2010, we established a 1 × 1-km systematic grid, spanning 11 km east–west, 8 km north–south, and the full elevation gradient of the study area (Fig. 1). The south-east corner of the grid was randomly placed within 500 m of the south-easternmost corner of the Darkwoods property using a GIS. Within a 500 m-radius surrounding each grid intersection point ($n = 40$), we established a 1-ha research plot (Fig. 1). Following field reconnaissance, each plot was centred on fire-scarred trees that showed minimal degradation due to decay, were safe to sample and were not wildlife trees. Five ‘supplemental’ plots were also established at intermediate points within the grid. Two supplemental plots were at elevations >1700 m asl, and included trees with multiple fire scars, although the surrounding plots did not include scarred trees. Three supplemental plots were at lower elevations and were used to enhance the resolution of fire boundary reconstructions.

At 30 plots with fire-scarred trees (hereafter ‘fire-scar’ plots), we removed full or partial cross-sections from up to seven snags, stumps, logs and live trees (hereafter ‘trees’) with the greatest number of visible fire scars (mean $\pm$ s.e. = 4.6 ± 0.2 trees plot⁻¹). At 15 plots with no fire scars (hereafter ‘tree-age’ plots), the 10 canopy-dominant trees closest to the plot centre were sampled for species and age. Trees were cored at 20 cm above

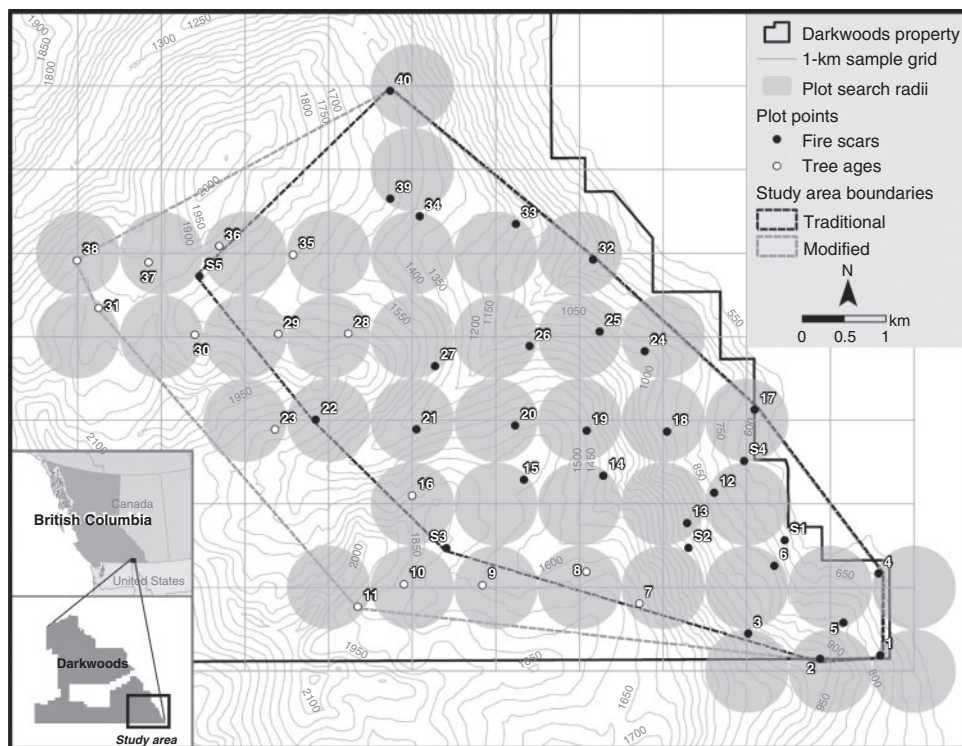


Fig. 1. Location of 45 fire history plots in the Darkwoods of British Columbia. Plots were located within 500 m of grid intersection points after surveying each area for fire-scarred trees.

ground level and multiple cores were extracted per tree to ensure they were within ~ 10 years of the pith. One plot yielded only one fire-scar sample, so 10 trees were cored as well. Plot reference points were recorded with a handheld global positioning system unit, from which the distance and bearing of each sampled tree were measured.

Dendrochronological analyses

Fire-scar samples and increment cores mounted on wooden supports were sanded with 80- to 600-grit sand paper (Stokes and Smiley 1996). Calendar years were assigned to tree rings using a combination of visual cross-dating of ring-widths and cross-correlation of ring-width series using the program COFECHA (Holmes 1983; Grissino-Mayer 2001). We used existing regional chronologies for the dominant species (Mather 2010) from which we created new study area- and species-specific chronologies. Ten cores and five cross-sections could not be crossdated and were excluded from further analysis.

Fire history was reconstructed from crossdated fire-scar samples using methods comparable with other studies in the fire history literature, as follows. We used the position of each scar relative to the dated sequence of annual rings to determine the inner ring or pith date, year(s) of fire, and the outer year or bark date. We assigned dormant-season fires to the previous calendar year owing to the modern pattern of late-season fires in the area (J. Naylor, BC Wildfire Service, unpubl. data). The fire recording period for each tree began with the year of the first fire scar and ended in the year of sampling or death of the recording tree, representing the period when the tree had open cambial scars and was susceptible to repeated scarring by fire (Swetnam and Baisan 1996). Fire records were composited at the individual plot level and filtered to include only fires that were recorded on two or more trees in the study area (Heyerdahl *et al.* 2012; O'Connor *et al.* 2014). Analyses were restricted to the period between 1700 and 2010, when $>25\%$ of plots were recording fire. We used the *Fire History Analysis and Exploration System* (FHAES 2.0; Brewer *et al.* 2015) to calculate the mean, standard deviation and range of fire intervals (i.e. the number of years between consecutive fire scars) for the composited fire record.

Of the 150 increment cores from tree-age plots, 71 did not intercept the pith; we estimated the number of missed rings to pith (4 ± 1 years) using a geometric correction (Duncan 1989). All pith dates were corrected for the number of years for trees to grow to coring height (5 ± 0.2 years) using species-specific age-height regression models (L. D. Daniels, unpubl. data). Owing to the absence of fire-scarred trees in all but one of the tree-age plots, the predominance of thin-barked, fire-sensitive species, and the location of these trees in the highest elevations, we assumed these trees would have scarred ($n = 20$ thick-barked, fire-tolerant trees) or been killed by fire ($n = 130$ thin-barked, fire-sensitive trees) had a fire burned. For these reasons, we considered the presence of these trees over their lifespan to represent fire-free periods in all subsequent analyses. The estimated age of the oldest tree in each plot represented the fire-free period for each discrete tree-age plot location.

Defining study area boundaries for spatial analyses

All spatial analyses were conducted in *ArcGIS 10.3.1* (ESRI 2015) using composited plot-level data. We defined two

separate study area boundaries for our analyses: (1) a smaller boundary around the 30 fire-scar plots (hereafter referred to as the 'traditional' boundary); and (2) a larger boundary encompassing the 45 fire-scar and tree-age plots (hereafter referred to as the 'modified' boundary). Both study area boundaries were defined using convex hulls (Swetnam and Holmes 1994; Kernan and Hessl 2010) constructed around plot reference points (Fig. 1). This approach is different from methods used in recent studies, where study area boundaries were generated by buffering plot reference points by the minimum distance necessary to create a single polygon (e.g. 750 m; Hessl *et al.* 2007; Kernan and Hessl 2010; O'Connor *et al.* 2014; Yocom-Kent *et al.* 2015). Our attempts to use boundaries derived from this buffering method resulted in extensive overlap with landscape features that act as barriers to fire spread (e.g. non-vegetated peaks at high elevations and a river along the eastern edge of the study area). Using these derived boundaries would have overestimated fire sizes and underestimated intervals for our study area. Instead, we used convex hulls because their smaller sizes and compact shapes minimised estimation errors. These study area boundaries were used to 'clip' subsequent GIS outputs.

Traditional estimates of fire boundaries and spatial mean fire intervals

We used IDW algorithms to interpolate fire occurrence between plot reference points, and to generate burn likelihood surface maps for each fire year (Hessl *et al.* 2007; Kernan and Hessl 2010). IDW interpolations were based on binary $\text{year} \times \text{fire}$ matrices (fire = 1, no fire = 0; Swetnam *et al.* 2011) for all plots. Initially, we used the 'traditional' methods reported in the fire history literature (Hessl *et al.* 2007; Kernan and Hessl 2010; Swetnam *et al.* 2011; O'Connor *et al.* 2014). Fire likelihood surfaces were calculated using data from fire-scar plots ($n = 129$ trees in 30 plots), and clipped using the 'traditional' study area boundary. For each fire year, plots including scarred trees were assigned a value of 1, plots that had trees actively recording but not scarred were assigned a value of 0, and plots that did not contain actively recording trees were not included in interpolations. IDW then generated a continuous likelihood surface for each fire year; unsampled areas were assigned values based on distance-weighted likelihood averages that were interpolated between the 12 nearest plots. We used a power function of 2 and a raster cell size of 50 m in all IDW interpolations (Hessl *et al.* 2007; Kernan and Hessl 2010; Yocom-Kent *et al.* 2015).

To estimate fire boundaries, threshold values (i.e. burn likelihood cut-off points) were applied to likelihood surfaces as minimum selection criteria (Hessl *et al.* 2007; Kernan and Hessl 2010). Used in this manner, threshold values represented the minimum likelihood that a given raster cell was within a fire boundary. Likelihood values exceeding these threshold values were reclassified as areas that burned (fire = 1), whereas those less than the threshold values were reclassified as unburned areas (fire = 0). The boundary dividing these two areas was interpreted as the fire perimeter. Following methods established by Kernan and Hessl (2010), we then used map overlay operations to convert fire perimeter and fire interval data into SMFI surfaces. Two types of fire intervals can be calculated from SMFI surfaces: (1) the 'unweighted' SMFI is the mean of the

range of interval values generated over the SMFI surface; and (2) the 'weighted' SMFI is the mean of all interval values weighted by the number of raster cells occupied by each interval value. The unweighted SMFI is similar to MFI, calculated using dendrochronological methods, whereas the weighted SMFI is spatially explicit and can only be provided through spatial modelling methods. We calculated both unweighted and weighted SMFI values in subsequent analyses.

Analysis 1: Effect of fire-sensitive trees on estimates of area burned

We assessed the effects of including tree-age data on fire boundary and interval estimates. In this analysis, fire likelihood surfaces were calculated by combining data from both fire-scar and tree-age plots ($n = 279$ trees in 45 plots); these surfaces were clipped using the 'modified' study area boundary (hereafter referred to as the 'modified' dataset). In this dataset, the ages of fire-sensitive trees represent fire-free intervals at their locations, and a value of 0 was assigned to tree-age plots with living trees during each fire year. This approach is similar to Yocom-Kent *et al.* (2015), who assigned a value of 0 to plots with fire-sensitive trees that pre-dated the fire year. Applied in this manner, tree-age plots prevented IDW interpolations from extending burn likelihood values into areas with living, fire-sensitive trees; we predicted this would reduce the extent of modelled fire perimeters for many fire years. Conversely, IDW interpolations were allowed to extend burn likelihood values into these areas, uninhibited, in years before tree establishment.

We generated fire perimeters and SMFI surfaces using likelihood outputs from both the 'traditional' and 'modified' datasets. To ensure model results were comparable, fire perimeters were calculated using a fixed threshold value of 0.5. As the modified dataset encompassed a larger area than the traditional dataset, comparisons of estimated area burned (total, mean and range) and SMFI (both unweighted and weighted) were made between the overlapping portions of the two datasets (Fig. 1). Owing to the non-normal distribution of fire sizes and SMFI, we used a non-parametric paired Wilcoxon signed-rank test to identify significant differences ($P < 0.05$) in (i) estimated area burned for each fire year, and (ii) paired raster cell values for the weighted SMFI. We used a non-parametric unpaired Mann-Whitney rank sum test to identify significant differences ($P < 0.05$) in unweighted SMFI. Statistical analyses were conducted with SYSTAT (2011).

Analysis 2: Effect of alternative likelihood thresholds on area burned and SMFI estimates

To assess the effects of fire boundary thresholds on spatial fire metrics, we derived three sets of thresholds from the modified dataset to estimate fire boundaries. In general, the derived thresholds adjust perimeters to be smaller around fires scarring few trees in few plots relative to fires scarring many trees in many plots. Calculating derived thresholds is analogous to the dendrochronological method of filtering fire-scar datasets to emphasise fires of different magnitudes. (1) 'Liberal' fire boundary thresholds were calculated as one minus the ratio of (i) the number of fire-scar plots that recorded a scar to (ii) the total number of recording, previously scarred fire-scar plots

(i.e. 'recorder plots' in fire-scar analyses, Swetnam and Baisan 1996). These liberal thresholds originally were applied by Hessl *et al.* (2007; Kernan and Hessl 2010); we compare them with two other derived thresholds that account for the tree-age data. (2) 'Moderate' thresholds were calculated as one minus the ratio of (i) the number of fire-scar plots that recorded a scar to (ii) the number of recording fire-scar plots, plus the number of recording tree-age plots. Given the inclusion of tree-age plots as recorders, we expected the moderate thresholds would be equal to or larger than corresponding liberal thresholds, and would generate fire perimeters that were equal to or smaller than liberal fire perimeters. (3) 'Conservative' thresholds were calculated and applied to each fire year as one minus the ratio of (i) the number of fire-scar plots that recorded a scar to (ii) the number of fire-scar plots with living trees, including previously unscarred trees, plus the number of recording tree-age plots. The addition of living but previously unscarred trees in fire-scar plots is equivalent to including the origin-to-scar interval (Baker and Ehle 2001). This interval is the period between establishment of the tree and the occurrence of the first fire scar (Keeley and Stephenson 2000), spanning a time when these young trees were highly susceptible to fire and would have died were one to occur (Baker and Ehle 2001). For this reason, the origin-to-scar interval can be interpreted as a fire-free interval in this system (Baker and Ehle 2001). Given the more inclusive group of recorders, we expected that conservative thresholds would be equal to or larger than corresponding 'moderate' thresholds, and would generate the smallest fire perimeters. We also applied a 'fixed' fire boundary threshold of 0.5 to each fire year (following Yocom-Kent *et al.* 2015). This approach is similar to that of Morrison and Swanson (1990), who estimated burn perimeters for each fire by drawing a line midway between plots that recorded a scar, and adjacent, unscarred recorder plots. Fire perimeters were generated by selecting cells that exceeded the minimum threshold (Hessl *et al.* 2007; Kernan and Hessl 2010). The four fire boundary thresholds were applied to each of the 20 fire years, and the number of polygons per fire, area burned (total, mean and range) and unweighted and weighted SMFIs were compared.

Assessment of area burned estimates

As the actual size of the reconstructed fires is unknown (i.e. a fire atlas for our study area over the time period of the reconstruction does not exist), we assessed the quality of burn estimates using the following indirect method. We compared the percentages of the study area burned estimated using IDW with the percentage of recording plots that included fire-scarred trees, a traditional index of fire extent used in dendrochronological studies (e.g. Morrison and Swanson 1990; Taylor and Skinner 1998; Hessl *et al.* 2007; Farris *et al.* 2010; Farris *et al.* 2013). Because we used the modified dataset to estimate area burned, we adjusted the percentage of recording plots scarred to incorporate tree-age data. The numerator was the number of fire-scar plots that recorded a scar and the denominator was the number of recording fire-scar plots plus the number of recording tree-age plots. The area burned by each fire was estimated using fire perimeters generated from the conservative, moderate, liberal or fixed fire boundary thresholds. We used linear regression with

an intercept of zero to quantify the relationships between the percentages of scarred recorders against the estimated percentage of the study area burned. Departures from a 1 : 1 relationship (slope = 1.0) indicate differences between the two area burned estimates resulting from over- or underestimates of fire size (Hessl *et al.* 2007; Farris *et al.* 2010). We used the slope of the

regression model and a minimisation of the sum of squared errors of the data points relative to a slope of 1.0 to assess the accuracy of area burned estimates from the four data-threshold combinations.

Analysis 3: Comparison of fire interval metrics

We compared fire intervals (mean, standard deviation and range) calculated using dendrochronological (i.e. fire scars only) and spatial analyses for the 20 fires that scarred ≥ 2 trees in the study area between 1700 and 2010. For the dendrochronological summary, the grand mean and standard deviation of the 20 plot-level CMFIs were calculated. CMFI ranges were calculated as the minimum and maximum scar-to-scar intervals observed among the plots. SMFIs were generated for the modified dataset and the conservative, moderate, liberal and fixed fire-boundary thresholds. We compared CMFI with both the unweighted and weighted forms of SMFI. We predicted that SMFI would be longer than CMFI owing to the inclusion of tree-age plots with long fire-free intervals.

Results

Fire history

Trees with external fire scars were present in 30 of 45 plots (Table 1). Fires causing scars burned between 1406 and 1966. Twenty fires scarred ≥ 2 trees after 1700 when $>25\%$ of plots were recording fire.

Analysis 1: Effect of fire-sensitive trees on area burned estimates

Differences in estimated area burned between the overlapping portions of the traditional and modified datasets were significant ($P < 0.001$; Table 2). Based on the traditional and modified datasets, a total of 12 492 and 11 651 ha burned during the 20 fire years respectively. These estimates differed by 841 ha, or 42 ha in mean area per fire year. However, differences in SMFI between the two datasets were not significant; unweighted SMFI decreased slightly from 51 to 50 years ($P = 0.85$), and weighted SMFI increased slightly from 49 to 51 years ($P = 0.62$) for the traditional and modified datasets respectively.

Analysis 2: Effect of alternative likelihood thresholds on area burned estimates

Fixed thresholds resulted in the greatest total area burned (13 194 ha, mean 426 ha), and shortest spatial mean return

Table 1. Historical fire metrics for the 30 plots containing trees with external fire scars

Metrics are for fires that scarred ≥ 2 trees in the study area per fire year. The fire recording period and number of fires reported are for the full recording period (1406–2010); the fire interval information is for the truncated period, 1700–2010. NA, not applicable

Plot no.	Fire recording period	No. fires	Intervals(years)		
			<i>n</i>	Mean	Range
1	1823–2010	4	3	27	15–43
2	1823–2010	5	4	20	6–43
3	1823–2008	5	4	17	3–25
4	1739–2010	5	4	38	20–84
5	1823–2010	3	2	33	23–43
6	1886–1981	2	1	18	NA
12	1886–2004	2	1	18	NA
13	1795–2003	5	4	23	7–46
14	1718–2010	6	5	24	17–56
15	1869–2010	1	0	NA	NA
17	1823–2010	3	2	41	25–56
18	1795–1974	5	4	27	8–55
19	1718–1989	7	6	31	8–84
20	1831–2010	2	1	38	NA
21	1869–1971	2	1	35	NA
22	1665–2007	3	1	40	NA
24	1831–1996	3	2	37	18–55
25	1739–2010	6	5	37	20–56
26	1642–2005	7	4	33	17–63
27	1768–2010	3	2	51	26–75
32	1635–1986	8	5	37	18–63
33	1739–2010	7	6	30	16–63
34	1635–1975	5	2	76	16–136
39	1665–2007	7	5	38	17–101
40	1665–2010	4	2	37	35–38
S1	1739–2010	4	3	49	28–63
S2	1795–2010	4	3	30	17–46
S3	1642–2002	3	1	130	NA
S4	1795–1979	4	3	30	17–46
S5	1869–1943	1	0	NA	NA

Table 2. Comparison of area burned and spatial mean fire interval estimates between the traditional and modified datasets

Analyses were for 20 fires that scarred ≥ 2 trees in the study area between 1700 and 2010. The traditional dataset included only fire scars from fire-scar plots; the modified dataset included data from fire-scar and tree-age plots. Summaries are for the overlapping 2687 ha of the two datasets. Differences in area burned between the two datasets were significant ($P < 0.001$), but differences in unweighted and weighted spatial mean fire intervals (SMFIs) were not ($P = 0.85$ and 0.62 respectively)

Dataset	Area burned (ha)				SMFI (years)			
	<i>n</i>	Total	Mean $\pm$ s.d.	Range	<i>n</i>	Unweighted	Weighted	Range
						Mean $\pm$ s. d.	Mean $\pm$ s. d.	
Traditional	29	12 492	431 $\pm$ 621	12–2369	30	51 $\pm$ 28.6	49 $\pm$ 2.1	24–136
Modified	31	11 651	376 $\pm$ 573	0.3–2134	31	50 $\pm$ 28.5	51 $\pm$ 2.1	24–136

Table 3. Comparison of plot-level fire metrics derived from spatial analyses of the modified dataset using conservative, moderate, liberal and fixed burn thresholds

Analyses were for 20 fires that scarred ≥ 2 trees in the study area between 1700 and 2010. Area burned metrics include the number of burn polygons, the total area burned, mean and standard deviation, and the area burned ranges. Spatial mean fire interval (SMFI) metrics include the number of fire intervals, the unweighted and weighted means and standard deviations, and the interval ranges

Dataset	Threshold	<i>n</i>	Area burned (ha)			<i>n</i>	SMFI (years)		
			Total	Mean $\pm$ s.d.	Range		Unweighted Mean $\pm$ s. d.	Weighted Mean $\pm$ s. d.	Range
Modified	Conservative	38	9889	260 $\pm$ 799	0.3–2796	28	56 $\pm$ 29.3	68 $\pm$ 5.2	25–136
	Moderate	36	10 932	304 $\pm$ 862	0.3–2850	28	50 $\pm$ 28.6	68 $\pm$ 5.7	25–136
	Liberal	33	12 164	367 $\pm$ 921	0.7–3057	27	54 $\pm$ 29.3	68 $\pm$ 6.2	25–136
	Fixed	31	13 194	426 $\pm$ 810	12.0–2773	31	50 $\pm$ 28.5	58 $\pm$ 3.4	24–136

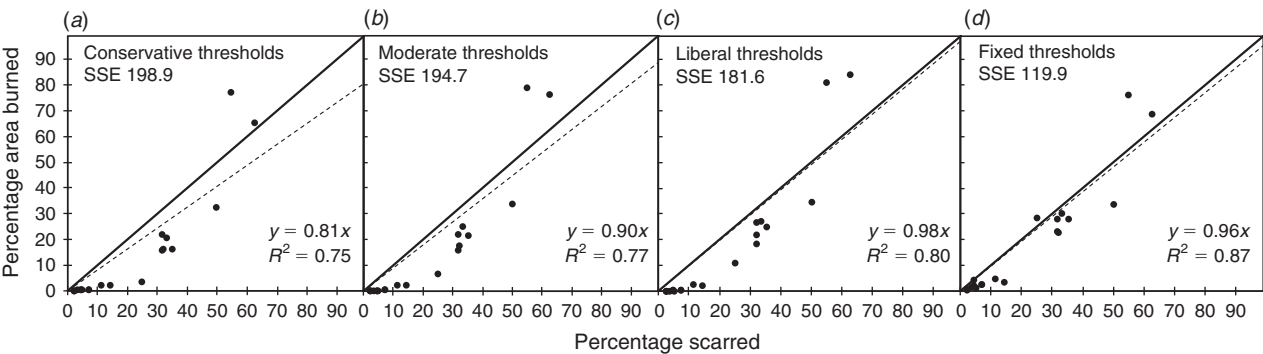


Fig. 2. Comparison of the percentage of plots scarred versus estimated percentage of the study area burned for the 20 fires between 1700 and 2010. Fire extent was modelled using conservative (a); moderate (b); liberal (c); and fixed (d) thresholds. The solid lines depict a 1 : 1 relationship; dashed lines, equations and R^2 describe the linear trends of the modelled data. The sum of squared errors (SSE) of the modelled percentage area burned is relative to a 1 : 1 relationship with percentage of plots scarred.

interval (unweighted = 50 years, weighted = 58 years, n = 31 intervals) (Table 3 and Table S1, available as online supplementary material). The conservative thresholds (0.49–0.98) produced the most polygons (n = 38), lowest area burned (9889 ha, mean 260 ha) and longest return intervals (unweighted = 56 years, weighted = 68 years, n = 28 intervals). Moderate thresholds (0.38–0.98) yielded intermediate values, but generated area burned estimates that were slightly larger than conservative estimates for all fires up to 1869. Thereafter, moderate area burned estimates were identical to conservative estimates. Liberal thresholds (0.23–0.97) also produced intermediate values, but generated the largest individual burn polygons in 1739 (3057 ha) and 1869 (2937 ha). Fixed and conservative thresholds resulted in similar maximum area burned polygons (2773 and 2796 ha respectively). Conservative, moderate and liberal thresholds produced similar minimum area burned polygons (0.3–0.7 ha), but the smallest area burned in a single year using fixed thresholds was 12 ha.

Assessment of area burned estimates

Fixed thresholds produced area burned estimates that were most consistent with those derived from the percentage of plots scarred (Fig. 2). Percentage burned estimates were consistently underestimated (slope = 0.81 to 0.98), though fixed thresholds better estimated smaller fires than conservative or liberal thresholds. However, all threshold models overestimated

percentage area burned by the most widespread fires in 1739 and 1869. Fixed thresholds produced the smallest sum of squared error (SSE = 120), whereas conservative thresholds produced the largest error (SSE = 199).

Analysis 3: Comparison of fire interval metrics

The dendrochronological plot-level CMFIs were shorter than SMFIs for all thresholds (24–136 years; Table 4; Fig. 3). Between 1700 and 2010, CMFIs were 3–136 years, with a grand mean of 38 years. Conservative thresholds yielded unweighted SMFI with the longest grand mean (56 years), followed by liberal (54 years), then fixed (50 years) thresholds. Conservative, moderate and liberal thresholds produced weighted SMFIs with the longest grand mean (68 years), followed by fixed (58 years) thresholds.

Discussion

Refined fire boundaries using data from fire-sensitive trees

Using tree-age data in combination with fire-scar dates from fire-scar plots allowed us to refine the fire boundaries without biasing fire interval estimates. The trees in plots that lacked fire scars were primarily fire-sensitive species with thin bark. As they were unlikely to survive had a fire burned (Alexander 1987; Keeley 2012), their presence indicates a lack of fire over their

Table 4. Comparison of plot-level composite mean fire intervals (CMFIs) and spatial mean fire intervals (SMFIs)

The CMFI analysis was based on fire-scar evidence from fire-scar plots. SMFI analyses were based on the modified dataset including data from fire-scar and tree-age plots and were conducted using four thresholds for defining fire boundaries. Mean and standard deviations (s.d.) of the unweighted and weighted fire intervals are presented. All analyses were for 20 fires that scarred ≥ 2 trees in the study area between 1700 and 2010. NA, not applicable

Type of analysis	Dataset	Threshold	Fire intervals (years)			
			Unweighted		Weighted	
			Mean $\pm$ s.d.	Range	Mean $\pm$ s.d.	Range
Dendrochronological (CMFI)	Fire-scars	NA	38 $\pm$ 22	3–136	NA	NA
SMFI	Modified	Conservative	56 $\pm$ 29.3	25–136	68 $\pm$ 5.2	25–136
		Moderate	50 $\pm$ 28.6	25–136	68 $\pm$ 5.7	25–136
		Liberal	54 $\pm$ 29.3	25–136	68 $\pm$ 6.2	25–136
		Fixed	50 $\pm$ 28.5	24–136	58 $\pm$ 3.4	24–136

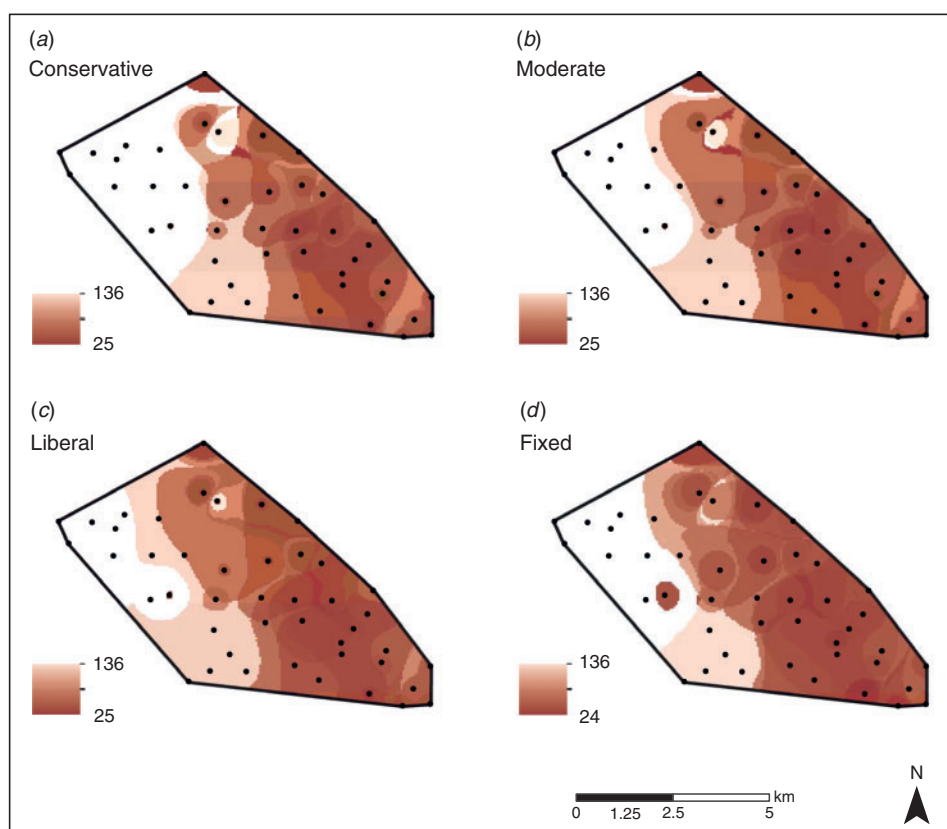


Fig. 3. Comparison of spatial mean fire intervals (SMFIs) derived using the conservative (a); moderate (b); liberal (c); and fixed (d) thresholds. Darker red colours indicate a higher frequency of fires, whereas lighter red colours indicate lower fire frequency. White indicates areas with ≤ 1 fire during the 310-year study period, preventing the calculation of an SMFI.

lifespan. Therefore, tree-age plots represented discrete locations that did not burn. Including these plots in spatial analyses prevented overestimation of fire extent by limiting the distance of fire likelihood interpolations between sampled points.

The effect on area burned estimates within the overlapping portions of the traditional and modified datasets was significant; including tree-age data in IDW interpolations reduced the

estimated area burned by 7% (841 ha). These results suggest a scaling effect on the spatial extent of fires within our study area; expanding analyses into high-elevation forests incorporated longer fire-free intervals, which reduced fire size estimates in adjacent mid-elevation forests. However, SMFIs were similar across datasets, indicating tree-age data did not induce temporal bias in estimated spatial return intervals. Falk *et al.* (2007) state a

similar effect for fires that are consistently large and synchronous across the landscape, where an increase in the sampling area captures few new fire dates. This suggests that tree-age data from high-elevation forests in our study area may represent areas subject to large and synchronous (i.e. high-severity) fires. Given the significant adjustments to area burned estimates, we recommend including tree-age data when conducting spatial interpolation analyses in areas under a mixed-severity fire regime.

Fixed thresholds best represent fire boundaries

Paralleling dendrochronological analyses of historical fires, our derived thresholds were based on the ratio of plots recording each fire to the total number of recorders (Morrison and Swanson 1990; Swetnam and Betancourt 1990; Fulé and Covington 1999; Veblen *et al.* 1999; Farris *et al.* 2010). Subtracting this ratio from 1 yielded thresholds of 0.23 (77% of plots recording fire) to 0.78 (22% of plots recording fire), with the conservative and moderate thresholds consistently exceeding liberal and fixed thresholds. As expected, the largest and fewest polygons and area burned per fire were generated using thresholds <0.5 , whereas thresholds approaching 1.0 generated more and smaller polygons.

Two lines of evidence indicate that the fixed thresholds of 0.5 better represented fire boundaries than the derived thresholds. (1) Fixed thresholds extended fire boundaries farther and generated the greatest overlap amongst the 20 modelled fire boundaries. These overlapping boundaries represented areas that reburned in subsequent fire years, and were consistent with the presence of numerous trees with multiple fire scars, particularly at low and middle elevations in our study area. (2) The fixed thresholds produced fire sizes most consistent with area burned estimates based on the percentage of plots that recorded each fire. We recommend a fixed threshold of 0.5 be used rather than derived thresholds when using IDW to reconstruct historical fires.

Yocom-Kent *et al.* (2015) found that fixed thresholds well represented maximum burn polygon size and total area burned by high-severity fires in mixed-conifer forests. However, interpolations using fixed thresholds underrepresented the total number of high-severity burn polygons (Yocom-Kent *et al.* 2015). We did not specifically model low- or high-severity components of the fire regime separately from each other. Rather, our data allowed modelling of a mix of fire severities, suggesting their findings are applicable to at least a portion of our results. This highlights a limitation in the ability of IDW interpolation methods to model the inherently patchy nature of mixed-severity fires. The sampling design must adequately capture unburned areas within and around high-severity burn patches so interpolation methods can account for this heterogeneity. We suggest the use of 'supplemental' plots within a gridded sampling design to account for this.

Influences of model parameterisation and fire severity on fire area metrics

The estimated percentage of area burned consistently exceeded the percentage scarred by large fires, but percentage scarred exceeded percentage area burned by small fires; the magnitude

of this effect was smallest for the fixed thresholds. We attribute this effect to the inclusion of the 12 nearest neighbours (27% of plots) in interpolations, particularly for smaller fires when $<50\%$ of plots were scarred. In these years, interpolations were overly influenced by numerous plots without scars (i.e. contributing numerous zeros to interpolations), which lowered the likelihood values in raster cells nearest to scarred plots. Conversely, in large fire years when $>50\%$ of plots were recording fires, interpolations were heavily influenced by plots with scars and less so by plots without scars. Understanding these deviations provides insight into the effects of moderate-to-high severity fires on reconstructions of historical fire size using spatial modelling. Additional research is needed to identify an ecologically meaningful number of nearest neighbours for use in spatial reconstructions of historical fires.

Other factors may have contributed to errors in area burned estimations. The percentage scarred exceeded percentage area burned for most small fires that were recorded as fire scars at lower elevations. In this part of the landscape, infrequent but severe fires may remove recorders of past frequent, less-severe fires (Swetnam *et al.* 1999, 2011). In areas dominated by mixed-severity fire regimes, the loss of fire-scar evidence may reduce modelled fire sizes, potentially over-representing small, isolated fires. This effect would be exacerbated by the conservative, moderate and liberal thresholds in years when there were a low number of scarred trees relative to the number of potential recorders. Although we surveyed each 1-ha plot and sampled trees with the most visible scars, our reasonably small sample size of up to seven trees per plot may have missed scars, resulting in underestimated sizes of small fires.

Generally speaking, the modelled percentage area burned was greatest for 1869, although liberal thresholds generated a larger fire in 1739. In 1869, fires were noted to have burned throughout the Pacific Northwest, indicating region-wide synchrony (Heyerdahl *et al.* 2008). In our study area, the 1869 fire generated scars at many mid-elevation plots, and was the last modelled fire to occur in the high-elevations before establishment of 75% of the tree-age plots, suggesting that the 1869 fire may have initiated these stands. Based on the distribution of evidence, the fire most likely ignited at mid-elevation, spread laterally and upslope, and fire severity increased with elevation, all of which are well documented fire behaviour patterns (Agee 1993). This notion is supported by the lack of fire scars on living trees or remnant wood in the high-elevation plots, suggesting that existing recorder trees were either (i) consumed by the most recent high-severity fire (Swetnam *et al.* 1999, 2011), or (ii) that previous fires were also high severity, resulting in few scars (Sibold *et al.* 2006), or both. The lack of scars and the presence of contiguous plots with similar fire history evidence resulted in large modelled fire sizes, particularly at high elevations, which is consistent with fire sizes and effects in upper montane and subalpine forests (Schoennagel *et al.* 2004; Sibold *et al.* 2006; Marcoux *et al.* 2013).

Improved fire interval estimates for mixed-severity fire regimes

Traditional dendrochronological methods that summarise fire return intervals at discrete point locations (e.g. CMFI) are

subject to false negatives (Kilgore and Taylor 1979; Fall 1998; Baker and Ehle 2001; Farris *et al.* 2010) or may be scale-sensitive (Falk 2004; Falk *et al.* 2007), potentially underestimating fire occurrence (Baker and Ehle 2001; Collins and Stephens 2007). In mixed-severity fire regimes, fire histories reconstructed from fire scars only may bias frequency estimates in favour of shorter return intervals (Baker and Ehle 2003). This is problematic when areas between sampled points are not assessed, and particularly if these areas are influenced by high-severity fire effects at longer return intervals. Consequently, fire-scar data may suggest management practices that too frequently disturb forests (Odion *et al.* 2014). However, fire scar data are more commonly viewed as providing a conservative estimate of fire intervals, as they typically capture larger fires (i.e. at the scale of the average distance between plots) and ignore small fires (i.e. those that occur between sampled points) (Farris *et al.* 2010).

Our results suggest that SMFI calculated from both tree-age and fire-scar data are improvements on traditional dendrochronological estimates for forests under a mixed-severity fire regime; weighted SMFIs, in particular, better represent the distribution of intervals over space. Both unweighted and weighted SMFIs of the Darkwoods exceeded CMFIs, reflecting the degree to which fire-free intervals can lengthen mean return intervals across a mixed-fire landscape. However, this finding is in contrast to the results of Kernan and Hessl (2010), who found that SMFIs constructed using only fire-scar evidence produced average values that were intermediate to MPFIs and CMFIs. These differences suggest that the sampling design used in spatial analysis is critical; it must reflect a thorough understanding of the historical fire regime, accounting for both spatial and temporal heterogeneity in fire severities (Lertzman *et al.* 1998). In dry ponderosa pine forests under a low-severity fire regime, a sampling approach using only fire scars seems appropriate; SMFIs calculated from these data may be similar to the results of Kernan and Hessl (2010). However, in forests under a mixed-severity fire regime, fire-scar evidence alone cannot capture the range of severities and subsequent effects on forest structures. Instead, combining fire-scar and tree-age data provides more accurate estimates of fire metrics across a range of severities and subsequent effects on forest structures.

Our results also suggest that including tree-age data in SMFI analyses is especially powerful for mountain landscapes dominated by mixed-severity fire regimes, where fire severity increases with elevation and the number of fire scars decreases (Agee 1993; Schoennagel *et al.* 2004; Marcoux *et al.* 2013, 2015). Supplementing fire scar data with tree-age data provides evidence for the absence of fire and, therefore, better reflects the longer fire-free intervals in the high-elevation forests. Thus, our approach accounts for the spatiotemporal diversity of fire frequencies and severities inherent to mixed-severity fire regimes. For these reasons, managers can clearly benefit from SMFIs; they provide the range of variation and a mean return interval of fire disturbances, and show how and where these metrics are distributed over a landscape.

Conclusions

Combining tree-age data with fire scars to model spatial fire intervals using the IDW method provides a much-needed

solution for quantifying mixed-severity fire regimes. Given new recognition that mixed-severity fire regimes prevail across forest types (Perry *et al.* 2011; Anderson 2012; Marcoux *et al.* 2013), methods to adequately quantify fire frequency, size and magnitude are imperative to guide management efforts aimed at sustaining or increasing forest resilience to environmental change. Metrics derived from fire scars alone have been criticised for overestimating fire frequency (Odion *et al.* 2014); however, quantifying the relative importance of high-severity fires within mixed-severity fire regimes is also contentious (Fulé *et al.* 2014; Stevens *et al.* 2016).

Using the Darkwoods as an example, we have shown that spatial fire intervals derived from fire scars and tree ages can be longer than point intervals derived from fire scars alone, which can better represent landscape-scale mean fire frequencies of mixed-severity fire regimes across elevational gradients, from montane to subalpine forests. In our study area, fire scars provided evidence of repeated low-severity fires at low and mid-elevations. In high-elevation subalpine forests, an absence of fire scars may indicate an absence of fire or it may be the residual effect of high-severity fires removing recorder trees. The presence of fire-sensitive trees helped discriminate between these two causes. Fire-sensitive trees indicated absence of fire over their lifespan, limiting the extent of modelled fire boundaries and reducing bias from over-representing frequent fires. Simultaneously, interpretive power was appropriately afforded to fire-scar evidence to model smaller fires. We recommend combining tree-age data with fire scars to enhance spatial interpolation analyses and better represent the range of spatio-temporal variation inherent in mixed-severity fire regimes.

Acknowledgements

This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (L. D. Daniels) and a Mitacs Accelerate Award (G. A. Greene). We thank the Nature Conservancy of Canada (NCC) for permission to conduct this research, our collaborators H. Page (NCC) and D. Thorburn (Kalesnikoff Lumber Co. Ltd), and our research assistants S. DesRoches, S. T. Martin and R. Chavardes. We also thank two anonymous reviewers for providing comments that greatly improved this manuscript.

References

- Agee JK (1993) 'Fire ecology of Pacific Northwest forests.' (Island Press: Washington, DC)
- Alexander RR (1987) Ecology, silviculture, and management of Engelmann spruce–subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service, Agriculture Handbook No. 659 (Fort Collins, CO).
- Anderson D (2012) The influence of wildfire boundary delineation on our understanding of burning patterns in the Alberta foothills. *Canadian Journal of Forest Research* **42**, 1253–1263. doi:10.1139/X2012-074
- Axelsson JN, Alfaro RI, Hawkes BC (2009) Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia. Canada. *Forest Ecology and Management* **257**, 1874–1882. doi:10.1016/J.FORECO.2009.01.047
- Axelsson JN, Alfaro RI, Hawkes BC (2010) Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. *Forestry Chronicle* **86**, 87–99. doi:10.5558/TFC86087-1
- Baker WL, Ehle D (2001) Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* **31**, 1205–1226. doi:10.1139/X01-046

- Baker WL, Ehle D (2003) Uncertainty in fire history and restoration of ponderosa pine forests in the western United States. In 'Fire, fuel treatments, and ecological restoration: conference proceedings', 16–18 April 2002, Fort Collins, CO. (Eds PN Omi and LA Joyce) USDA Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-29, pp. 319–333. (Fort Collins, CO)
- Brewer PW, Velásquez ME, Sutherland EK, Falk DA (2015) Fire History Analysis and Exploration System (FHAES) version 2.0.0. Available at <http://www.fhaes.org> [Verified 22 January 2017]
- Brown PM (2006) Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. *Ecology* **87**, 2500–2510. doi:10.1890/0012-9658(2006)87[2500:CEOFRA]2.0.CO;2
- Brown PM, Wu R (2005) Climate and disturbance forcing of episodic tree recruitment in a south-western ponderosa pine landscape. *Ecology* **86**, 3030–3038. doi:10.1890/05-0034
- Brown PM, Heyerdahl EK, Kitchen SG, Weber MH (2008) Climate effects on historical fires (1630–1900) in Utah. *International Journal of Wildland Fire* **17**, 28–39. doi:10.1071/WF07023
- Christensen NL, Bartuska AM, Brown JH, Carpenter S, D'Antonio C, Francis R, Franklin JF, MacMahon JA, Noss RF, Parsons DJ, Peterson CH, Turner MG, Woodmansee RG (1996) The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* **6**, 665–691. doi:10.2307/2269460
- Collins BM, Stephens SL (2007) Managing natural wildfires in Sierra Nevada wilderness areas. *Frontiers in Ecology and the Environment* **5**, 523–527. doi:10.1890/070007
- Dieterich JH (1980) The composite fire interval – a tool for more accurate interpretation of fire history. In 'Proceedings of the fire history workshop', 20–24 October 1980, Tucson, AZ. (Eds M Stokes, J Dieterich) USDA Forest Service, Rocky Mountain Research Station, General Technical Report RM-GTR-81, pp. 8–14. (Fort Collins, CO)
- Dieterich JH, Swetnam TW (1984) Dendrochronology of a fire scarred ponderosa pine. *Forest Science* **30**, 238–247.
- Duncan R (1989) An evaluation of errors in tree-age estimates based on increment cores in kahikatea (*Dacrydium dacrydioides*). *New Zealand Natural Sciences* **16**, 31–37.
- ESRI (2015) ArcGIS Desktop 10.3.1, Service Pack 0. (Environmental Systems Research Institute: Redlands, CA)
- Falk DA (2004) Scaling rules for fire regimes. PhD dissertation, University of Arizona, Tucson, AZ.
- Falk DA, Miller C, McKenzie D, Black AE (2007) Cross-scale analysis of fire regimes. *Ecosystems* **10**, 809–823. doi:10.1007/S10021-007-9070-7
- Fall JG (1998) Reconstructing the historical frequency of fire: a modeling approach to developing and testing methods. MS thesis, Simon Fraser University, Burnaby, BC.
- Farris CA, Baisan CH, Falk DA, Yool SR, Swetnam TW (2010) Spatial and temporal corroboration of a fire-scar fire history reconstruction in a frequently burned ponderosa pine forest in Arizona. *Ecological Applications* **20**, 1598–1614. doi:10.1890/09-1535.1
- Farris CA, Baisan CH, Falk DA, Van Horne ML, Fulé PZ, Swetnam TW (2013) A comparison of targeted and systematic fire-scar sampling for estimating historical fire frequency in south-western ponderosa pine forests. *International Journal of Wildland Fire* **22**, 1021–1033. doi:10.1071/WF13026
- Fulé PZ, Covington WW (1999) Fire regime changes in La Michilía Biosphere Reserve, Durango, Mexico. *Conservation Biology* **13**, 640–652. doi:10.1046/J.1523-1739.1999.97512.X
- Fulé PZ, Swetnam TW, Brown PM, Falk DA, Peterson DL, Allen CD, Aplet GH, Battaglia MA, Binkley D, Farris C, Keane RE, Margolis EQ, Grissino-Mayer H, Miller C, Sieg CH, Skinner C, Stephens SL, Taylor A (2014) Unsupported inferences of high-severity fire in historical western United States dry forests: response to Williams and Baker. *Global Ecology and Biogeography* **23**, 825–830. doi:10.1111/GEB.12136
- Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* **57**, 205–221.
- Hessl AE, Miller J, Kernan JT, Keenum D, McKenzie D (2007) Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. *The Professional Geographer* **59**, 87–104. doi:10.1111/J.1467-9272.2007.00593.X
- Heyerdahl EK, McKenzie D, Daniels LD, Hessl AE, Littell JS, Mantua NJ (2008) Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). *International Journal of Wildland Fire* **17**, 40–49. doi:10.1071/WF07024
- Heyerdahl EK, Lertzman K, Wong CM (2012) Mixed-severity fire regimes in dry forests of southern interior British Columbia, Canada. *Canadian Journal of Forest Research* **42**, 88–98. doi:10.1139/X11-160
- Heyerdahl EK, Loehman RA, Falk DA (2014) Mixed-severity fire in lodgepole pine-dominated forests: are historical regimes sustainable on Oregon's Pumice Plateau, USA? *Canadian Journal of Forest Research* **44**, 593–603. doi:10.1139/CJFR-2013-0413
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* **43**, 69–78. Available at <http://hdl.handle.net/10150/261223> [Verified 9 January 2017]
- Keeley JE (2012) Ecology and evolution of pine life histories. *Annals of Forest Science* **69**, 445–453. doi:10.1007/S13595-012-0201-8
- Keeley JE, Stephenson NL (2000) Restoring natural fire regimes in the Sierra Nevada in an era of global change. In 'Wilderness science in a time of change conference'. (Eds DN Cole, SE McCool and J O'Loughlin) USDA Forest Service, Rocky Mountain Research Station RMRS-P-15, pp. 255–265 (Missoula, MT)
- Kernan JT, Hessl AE (2010) Spatially heterogeneous estimates of fire frequency in ponderosa pine forests of Washington, USA. *Fire Ecology* **6**(3), 117–135. doi:10.4996/FIREECOLOGY.0603117
- Kilgore BM, Taylor D (1979) Fire history of a sequoia–mixed conifer forest. *Ecology* **60**, 129–142. doi:10.2307/1936475
- Kou X, Baker WL (2006) Accurate estimation of mean fire interval for managing fire. *International Journal of Wildland Fire* **15**, 489–495. doi:10.1071/WF05113
- Kulakowski D, Veblen TT, Bebi P (2003) Effects of fire and spruce beetle outbreak legacies on the disturbance regime of subalpine forest in Colorado. *Journal of Biogeography* **30**, 1445–1456. doi:10.1046/J.1365-2699.2003.00912.X
- Lertzman K, Fall J, Dorner B (1998) Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. *Northwest Science* **72**(special issue), 4–23.
- Marcoux HM, Gergel SG, Daniels LD (2013) Mixed-severity fire regimes: how well are they represented by existing fire-regime classification systems? *Canadian Journal of Forest Research* **43**, 658–668. doi:10.1139/CJFR-2012-0449
- Marcoux HM, Daniels LD, Gergel SG, Da Silva E, Gedalof Z, Hessburg PF (2015) Differentiating mixed- and high-severity fire regimes in mixed-conifer forests of the Canadian Cordillera. *Forest Ecology and Management* **341**, 45–58. doi:10.1016/J.FORECO.2014.12.027
- Margolis EQ, Balmat J (2009) Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecology and Management* **258**, 2416–2430. doi:10.1016/J.FORECO.2009.08.019
- Margolis EQ, Swetnam TW, Allen CD (2007) A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. *Canadian Journal of Forest Research* **37**, 2227–2241. doi:10.1139/X07-079
- Margolis EQ, Swetnam TW, Allen CD (2011) Historical stand-replacing fire in upper montane forests of the Madrean Sky Islands and Mogollon Plateau, south-western USA. *Fire Ecology* **7**(3), 88–107. doi:10.4996/FIREECOLOGY.0703088
- Mather V (2010) Climate relationships and sub-ring parameters of four conifer species in the Kootenay region of British Columbia, Canada. MS thesis, University of Guelph, ON.

- Morrison PH, Swanson FJ (1990) Fire history and pattern in a Cascade Range landscape. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-254. (Portland, OR)
- O'Connor CD, Falk DA, Lynch AM, Swetnam TW (2014) Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *Forest Ecology and Management* **329**, 264–278. doi:10.1016/J.FORECO.2014.06.032
- Odion DC, Hanson CT, Arsenault A, Baker WL, Della Sala DA, Hutto RL, Klenner W, Moritz MA, Sherriff RL, Veblen TT, Williams MA (2014) Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS One* **9**, e87852. doi:10.1371/JOURNAL.PONE.0087852
- Parsons RA, Heyerdahl EK, Keane RE, Dörner B, Fall J (2007) Assessing accuracy of point fire intervals across landscapes with simulation modelling. *Canadian Journal of Forest Research* **37**, 1605–1614. doi:10.1139/X07-013
- Perry DA, Hessburg PF, Skinner CN, Spies TA, Stephens SL, Taylor AH, Franklin JF, McComb B, Riegel G (2011) The ecology of mixed severity fire regimes in Washington, Oregon and northern California. *Forest Ecology and Management* **262**, 703–717. doi:10.1016/J.FORECO.2011.05.004
- Reed WJ, Johnson EA (2004) Statistical methods for estimating historical fire frequency from multiple fire-scar data. *Canadian Journal of Forest Research* **34**, 2306–2313. doi:10.1139/X04-110
- Schoennagel T, Veblen TT, Romme WH (2004) The interaction of fire, fuels and climate across Rocky Mountain forests. *Bioscience* **54**, 661–676. doi:10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2
- Sibold JS, Veblen TT, Gonzalez ME (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* **33**, 631–647. doi:10.1111/J.1365-2699.2005.01404.X
- Stephens SL, Fry DL, Collins BM, Skinner CL, Franco-Vizcaino E, Freed TJ (2010) Fire-scar formation in Jeffrey pine–mixed conifer forests in the Sierra San Pedro Mártir, Mexico. *Canadian Journal of Forest Research* **40**, 1497–1505. doi:10.1139/X10-083
- Stephens SL, Agee JK, Fulé PZ, North MP, Romme WH, Swetnam TW, Turner MG (2013) Managing forests and fire in changing climates. *Science* **342**, 41–42. doi:10.1126/SCIENCE.1240294
- Stevens JT, Safford HD, North MP, Fried JS, Gray AN, Brown PM, Dolanc CR, Dobrowski SZ, Falk DA, Farris CA, Franklin JF, Fulé PZ, Hagmann RK, Knapp EE, Miller JD, Smith DF, Swetnam TW, Taylor AH (2016) Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS One* **11**, e0147688. doi:10.1371/JOURNAL.PONE.0147688
- Stokes MA, Smiley TL (1996) 'An introduction to tree-ring dating: updated edition.' (University of Chicago Press: Chicago, IL)
- Swetnam TW, Baisan CH (1996) Historical fire regime patterns in the southwestern United States since AD 1700. In 'Fire effects in southwestern forests: proceedings of the 2nd La Mesa fire symposium', 29–31 March 1994, Los Alamos, NM. (Ed. CD Allen) USDA Forest Service, Rocky Mountain Research Station, General Technical Report RM-GTR-286, pp. 11–32. (Fort Collins, CO)
- Swetnam TW, Betancourt JL (1990) Fire–Southern Oscillation relations in the south-western United States. *Science* **249**, 1017–1020. doi:10.1126/SCIENCE.249.4972.1017
- Swetnam TW, Brown PM (2011) Climatic inferences from dendroecological reconstructions. In 'Dendroclimatology: progress and prospects'. (Eds MK Hughes, TW Swetnam, HF Diaz) pp. 263–295. (Springer Publishing: New York)
- Swetnam TW, Holmes RL (1994) Spatial analysis of fire events: description of the computer program SPANFIRE. Laboratory of Tree-Ring Research, University of Arizona. Available at <http://lustig.pp.fi/data/dpl/Spanfire.txt> [Verified 22 January 2017]
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications* **9**, 1189–1206. doi:10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2
- Swetnam TL, Falk DA, Hessl AE, Farris C (2011) Reconstructing landscape pattern of historical fires and fire regimes. In 'The landscape ecology of fire'. (Eds D McKenzie, C Miller, DA Falk) pp. 165–192. (Springer Publishing: New York)
- SYSTAT (2011) SigmaPlot 12.5. (Systat Software, Inc.: San Jose, CA)
- Taylor AH, Skinner CN (1998) Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**, 285–301. doi:10.1016/S0378-1127(98)00342-9
- Turner ML (2010) Disturbance and landscape dynamics in a changing world. *Ecology* **91**, 2833–2849. doi:10.1890/10-0097.1
- Van Horne ML, Fulé PZ (2006) Comparing methods of reconstructing fire history using fire scars in a south-western United States ponderosa pine forest. *Canadian Journal of Forest Research* **36**, 855–867. doi:10.1139/X05-289
- Veblen TT, Kitzberger T, Villalba R, Donnegan J (1999) Fire history in northern Argentina: the roles of humans and climatic variation. *Ecological Monographs* **69**, 47–67. doi:10.1890/0012-9615(1999)069[0047:FHINPT]2.0.CO;2
- Yocom-Kent LL, Fulé PZ, Bunn WA, Gdula EG (2015) Historical high-severity fire patches in mixed-conifer forests. *Canadian Journal of Forest Research* **45**, 1587–1596. doi:10.1139/CJFR-2015-0128