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RESEARCH ARTICLE

Influence of landscape structure, topography, and forest type on spatial variation in historical fire regimes, Central Oregon, USA

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Abstract
Context In the interior Northwest, debate over restoring mixed-conifer forests after a century of fire exclusion is hampered by poor understanding of the pattern and causes of spatial variation in historical fire regimes.
Objectives To identify the roles of topography, landscape structure, and forest type in driving spatial variation in historical fire regimes in mixed-conifer forests of central Oregon.
Methods We used tree rings to reconstruct multi-century fire and forest histories at 105 plots over 10,393 ha. We classified fire regimes into four types and assessed whether they varied with topography, the location of fuel-limited pumice basins that inhibit fire spread, and an updated classification of forest type.
Results We identified four fire-regime types and six forest types. Although surface fires were frequent and often extensive, severe fires were rare in all four types. Fire regimes varied with some aspects of topography (elevation), but not others (slope or aspect) and with the distribution of pumice basins. Fire regimes did not strictly co-vary with mixed-conifer forest types.
Conclusions Our work reveals the persistent influence of landscape structure on spatial variation in historical fire regimes and can help inform discussions about appropriate restoration of fire-excluded forests in the interior Northwest. Where the goal is to restore historical fire regimes at landscape scales, managers may want to consider the influence of topoedaphic and vegetation patch types that could affect fire spread and ignition frequency.

Keywords Dendroecology · Landscape structure · Fire history · Fire regimes · Eastern Cascades · Reference conditions · Forest restoration

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Introduction

Understanding the drivers of spatial and temporal variation in fire is key to ecosystem management and restoration because fire modifies forest development, structure, and composition in many landscapes. In the interior Northwest, fires have been excluded from mixed-conifer forests for more than a century by land-use changes that include logging, grazing, and fire suppression. As a result, the density of large fire- and drought-tolerant trees has decreased while the density of small-diameter and shade-tolerant trees has increased (Hagmann et al. 2013; Hagmann et al. 2014; Merschel et al. 2014). Managers are using landscape-scale approaches to restoring fire-dependent forests (Hessburg et al. 2016), but are hampered by a lack of information on landscape-scale variation in historical fire regimes and the factors that controlled it (Spies et al. 2006).

At regional scales, climate controls fire regimes and forest types, but at landscape and patch scales where fire ignition and spread occur, microclimate, topography, and the spatial distribution of fuels and vegetation control fire spread and behavior, and hence regimes (e.g., Heyerdahl et al. 2001; Sugihara et al. 2006; Kellogg et al. 2008; Morgan et al. 2001). For example, dry topographic facets with ample fuel may burn frequently because fuel moisture is low (Heyerdahl et al. 2001) or less frequently if they are so hot and dry that fuel production is limited (Taylor and Skinner 2003). Microclimate can also affect forest types hence fuel types and fire regimes. Prominent topographic features that may act as barriers to fire spread include rocky un-vegetated areas (Arabas et al. 2006), steep incised stream valleys (Taylor and Skinner 2003), mires (Hellberg et al. 2004), lakes (Nielsen et al. 2016) or ridges and headwalls (Camp et al. 1997; Holsinger et al. 2016). The structure, composition, and development of forests are influenced by soils, topography, and microclimate, but not necessarily at the same spatial and temporal scales as fire ignitions, fire spread, and behavior.

Fire regimes operate in the context of surrounding abiotic and biotic features because fire spreads across landscapes. Fire regimes may vary little across landscapes lacking structure that might inhibit fire spread across microclimates and forest types (Heyerdahl et al. 2001; Johnston et al. 2017). But when barriers to burning do exist, these landscape structures may play a key role in driving spatial variation in fire regimes. For example, fire intervals were longer and fires were smaller in mire-rich than mire-free parts of a Scots pine (*Pinus sylvestris*) landscape in Sweden (Hellberg et al. 2004). When fire regimes are assigned to forest types at regional scales, the influence of the surrounding landscape is often not considered (e.g., Rollins 2009). Although we recognize the importance of landscape context in models and observations of contemporary fire, we rarely have the opportunity to examine these landscape effects in dendrochronological fire histories that are developed to inform reference conditions.

Spatial variation in historical fire regimes is often associated with forest types (Schoennagel et al. 2004), but evidence is mounting that a given forest type may have supported a range of fires regimes in the past. For example, we assume that cool-moist forests historically sustained climate-limited, infrequent, high-severity fire regimes while warm, dry forests historically sustained fuel-limited, frequent, low-severity fire regimes. In the interior Northwest, we expect cool-moist grand fir (*Abies grandis*) forests to have burned less frequently than warm-dry ponderosa pine (*Pinus ponderosa)* forests. The grand fir forests have compact surface fuels and large woody fuels that are dry enough to burn only under a narrow range of weather conditions (Agee et al. 1978; Howard and Aleksoff 2000). In contrast, ponderosa pine forests have open canopies and continuous well-aerated surface fuels that are often sufficiently dry to burn. However, fire regimes were similar among juxtaposed true fir and ponderosa pine forests in some parts of the interior Northwest (Heyerdahl et al. 2001; Wright and Agee 2004; Johnston et al. 2017) challenging our assumption that a given forest type supports a single fire regime type.

Our objective was to identify the roles of topography, forest type, and landscape structure in driving spatial variation in historical fire regimes prior to twentieth century changes in land use in mixed-conifer forests of central Oregon. Forests on the eastern slope of the Cascade Range in central Oregon are well suited to investigating all three. Tree-ring evidence of past fire is abundant and the region includes gradients in elevation punctuated by volcanic features like small volcanic cinder cones and fuel-limited pumice basins. The forests include a range of types that vary with local climate, topography, and soil in their composition, structure and establishment history (Merschel et al. 2014). To understand spatial variation in fire regimes we reconstructed a multicentury history of fire from tree rings collected on a grid of plots over 10,393 ha.

Methods

Study area, forest structure and composition, and historical fire regimes

We sampled 10,393 ha southwest of Bend, Oregon, 10 km southeast of Mount Bachelor on the Deschutes National Forest (121 31′54.072″W, 43 56′10.463″N; Fig. 1a and d). A gentle southeast to northwest increase in elevation is punctuated by small volcanic cinder cones surrounded by flat pumice basins. This topography drives local variation in annual precipitation and mean maximum temperature (60–120 cm and 10–14 °C, respectively, Fig. 1b), but not in summer climate which is uniformly hot and dry (Fig. 1c). Only 10% of annual precipitation falls from June to September (PRISM 2016).

Forest composition varies with elevation, aspect, and soil. Grand fir and white fir (*Abies concolor*) hybridize in the study area and we refer to this hybrid as grand fir hereafter (Simpson 2007). Nearly pure ponderosa pine forests are found at low elevations (1350 m), a mixture of grand fir and ponderosa pine dominates intermediate elevations, and a mixture of grand fir, mountain hemlock (*Tsuga mertensiana*), and western white pine (*Pinus monticola*) with occasional ponderosa pine is found at high elevations (1850 m). The grand fir/ponderosa pine forests on the cinder cones vary with aspect; grand fir dominates north and east aspects more so than south and west aspects. Soils vary from fine to coarse sandy loams where abundant surface fuels of pine needles, bunchgrass, and shrubs recover quickly following fire (Volland 1985). Forests near the toe slopes include lodgepole pine (*Pinus contorta*). Adjacent flat basins have coarse-textured, nutrient-poor pumice soils that undergo extreme variation in diurnal temperature (Geist and Cochran 1991) which limits forest composition to lodgepole pine with sparse understories of sedges and herbs, but few shrubs (Volland 1985).

The study area has a patchwork of harvest history. Half of the 10,393 ha study area was heavily logged between 1920 and 1940 before being acquired by the U.S. Forest Service. Subsequently, about 800 ha within a 1920s slash fire was terraced and planted; large ponderosa pine were logged selectively on most cinder cones; and second-growth stands were thinned (personal communication). Many areas dominated by lodgepole pine were harvested following heavy mountain pine beetle (*Dendroctonus ponderosae*) mortality in the 1980s.

We systematically sampled the variation in topography and spatial variation in climate of the study area, while maximizing our likelihood of sampling areas with intact fire history records. In the office, we located 105 plots on a 1 km grid centered on the middle of two management planning areas, including one plot sampled for another study (Heyerdahl et al. 2014a, b; Fig. 1d). Many plots fell in areas where intensive management had destroyed the historical record; using air photos, we were able to move 55 of these to the nearest area lacking plantations, terracing, or roads (mean distance 156 m). Our plots captured the range of variation in precipitation, temperature, slope, and elevation of the study area (SI, Online Appendix S1).

Our grid sampled forest structure and composition in 83 plots; the remaining 22 plots lacked intact forest. We sampled variable radius plots scaled to local tree density in three diameter classes: small, medium, and large (5–29 cm diameter at a breast height of 1.4 m (DBH); 30–49 cm DBH and > 50 cm DBH respectively). We tallied small trees within a 7.28 m radius plot by status. We attempted to sample 12 medium and 12 large trees per plot, recording species, DBH, and status (live, log, snag, or stump). However, if fewer than 12 such trees occurred within 28.2 and 40.0 m of plot center, respectively, we sampled additional medium and then small trees within these radii until we sampled 24 trees total. This allowed us to capture establishment history in plots lacking large trees. We estimated tree density by species, status, and size by dividing the number of trees by plot area ($\pi \times$ [distance from plot center to farthest tree sampled]^2).

We estimated tree establishment dates at 83 plots by removing wood samples from the 24 live or dead medium and large trees described above, plus the 3 live small trees nearest to plot center. From live trees, we removed increment cores at a stem height of 40 cm, aiming for a field-estimated maximum of 10

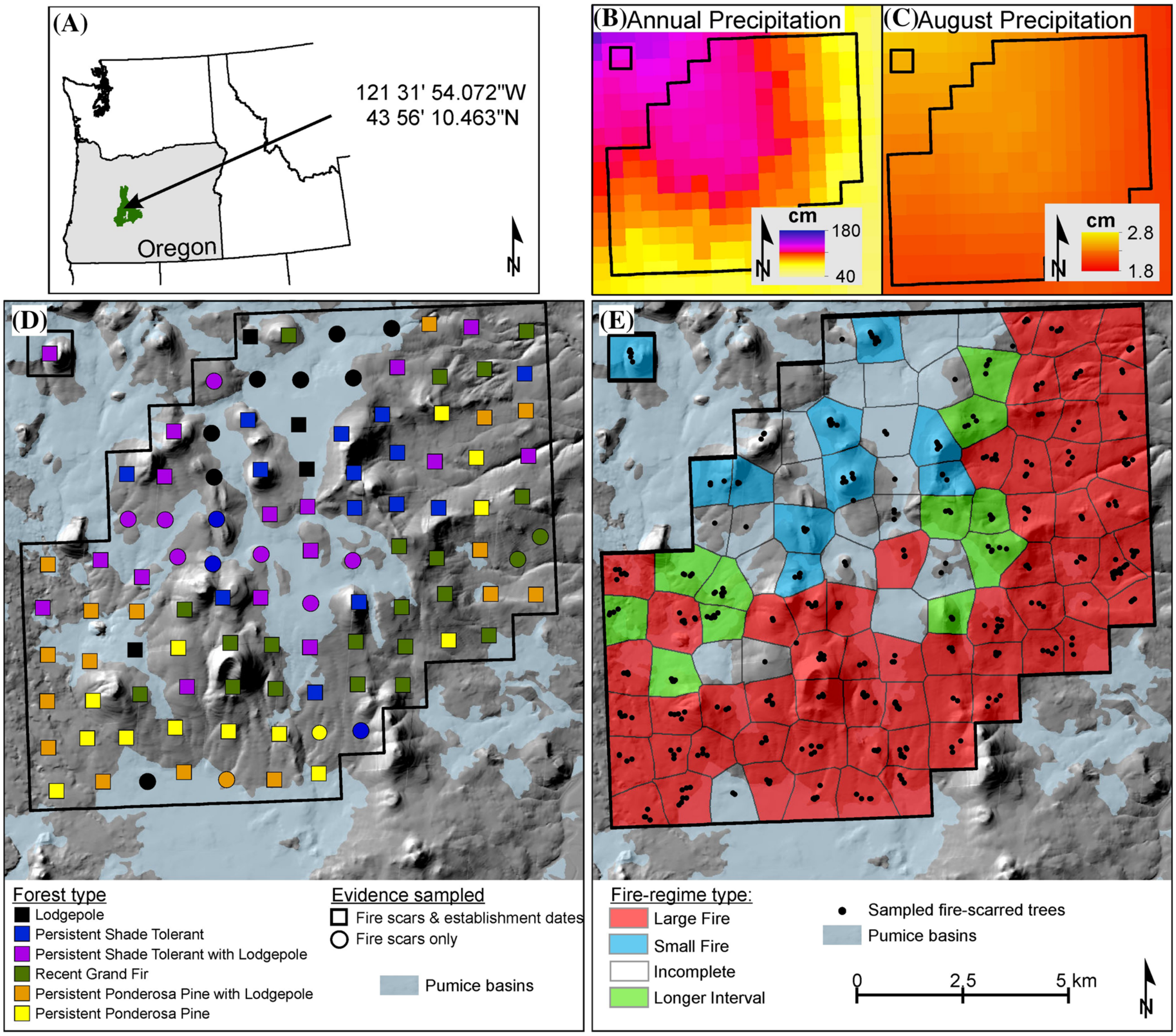


Fig. 1 **a** The study area lies on the east slope of the Cascade Range on the Deschutes National Forest, Oregon, USA. **b** Precipitation varies with elevation across the study area at annual time scales, but not during the fire season (**c**). **d** Plots sampled for fire history and forest composition, showing the location of fuel-limited pumice basins that inhibited the spread of fire (Volland 1985). Elevation varies from 1350 m in the southeast to 1850 m in the northwest. **e** Classification of Thiessen polygons surrounding sample plots by fire-regime type. (Color figure online)

rings from pith. From dead trees we removed partial cross sections at 40 cm with a chain saw, including the pith where possible. For trees lacking intact wood, we recorded species and diameter, then sampled a proxy tree of the same species, status, and similar diameter within 100 m. We sanded all increment cores and cross sections until cell structure was visible under a binocular microscope. Calendar years were assigned to annual rings using visual crossdating and cross-correlation of measured ring-width series using a ring-width chronology we developed from our samples (Holmes 1983; Swetnam et al. 1995). Samples from a few trees did not crossdate (2%) so we excluded them from analyses that required a date. For samples that did not intersect the pith (68%) we estimated the number of rings to pith geometrically (average 5 years, range 1–20 years; Applequist 1958). We did not attempt to estimate pith dates from samples that were more than an estimated 20 years from the pith (5% of samples).

We sampled fire-scarred trees in 97 plots; the remaining eight plots lacked fire scars. We searched for fire-scarred trees within a radius of 250 m of plot center ($\sim$ 20 ha) and removed partial cross sections with a chain saw from 1 to 13 trees per plot (average 4; Arno and Sneck 1977). We sanded and crossdated samples as described above, excluding 6% from further analyses because they did not crossdate. We identified the calendar year of fire occurrence as the year of the annual ring in which a scar formed. For scars that formed on the boundary between two rings, we assumed historical fires burned during the same late summer or fall season as do modern fires in the eastern Cascades (Bartlein et al. 2008) and generally assigned ring-boundary scars to the preceding calendar year. However, scars created by a single fire may have a range of intra-annual positions. On 107 samples, scars from four extensive fires occurred on a ring boundary after the latewood of one year or in the earlywood of the following year. We assigned all these scars to the calendar year of the earlywood inferring that growing season fires created the scars in both positions. We included a small amount of indirect evidence of fire (2% of fire dates) from abrupt decreases in radial growth that were synchronous with fire-scar dates in adjacent plots during years of extensive fire (i.e., fires recorded at more than 25% of plots).

We reconstructed a stand-replacing fire at a plot using multiple lines of evidence: (1) a cohort of four or more trees established within 20 years after a fire-scar date in adjacent plots and followed a gap of 20 years without establishment (Heyerdahl et al. 2014a; Stevens et al. 2016); (2) mature fire-killed logs and snags were alive prior to the fire; and (3) no (stand replacing) or few (partial stand replacing) trees survived the fire.

We analyzed fire history from 1650 to 1871. During this period, most plots with a multicentury fire record were recording (96% of plots), i.e., at least one tree had been scarred at least once. We eliminated fires recorded by only a single tree (8% of fire events eliminated). We computed fire intervals as the number of years between fire-scar dates composited at each plot.

We extrapolated five extensive fires (> 2000 ha, 1653–1717) to two plots dominated by ponderosa pine where logging followed by terracing likely removed this early record. All five fires were recorded by scars in all adjacent plots. We did not extrapolate fires to 23 plots that had incomplete fire records over the entire period of analysis (1650–1871). Most of these plots are dominated by short-lived lodgepole pine (22 plots) and most lie in pumice basins (19 plots; Fig. 1d). The last plot is dominated by ponderosa pine and a patch of recent (1868) stand-replacing fire likely removed the record of earlier fires.

We estimated fire extent using tessellation (Farris et al. 2010) by fitting Thiessen polygons to our grid of 105 plots (average 98 ha per polygon, range 61–148 ha; Euclidean Allocation Distance tool in ArcGIS 10, ESRI, Redlands, California, USA; Fig. 1e). We summed the area of all polygons recording fire in a given year into a record of annual fire extent. Our calculation of fire extent may include unburned islands within the polygons.

Our tree-recruitment dates, fire-scar dates, and associated metadata are available from the International Multiproxy Paleofire Database, a permanent, public archive maintained by the Paleoclimatology Program of the National Oceanic and Atmospheric Administration in Boulder, Colorado (www.ncdc.noaa.gov/paleo/impd/paleofire.html).

Classification of forest and fire-regime types

We classified our plots into forest and fire-regime types using hierarchical agglomerative clustering. We used the Sørensen distance measure with a flexible beta of $\beta = 0.25$ (McCune and Grace 2002) in the PC ORD version 6 software (McCune and Mefford 2010). For forest type, we repeated the analysis of Merschel et al. (2014) with modified species-size classes because Douglas-fir *(Pseudotsuga menziesii)* did not occur in our study area, but lodgepole pine did. For the 83 plots with intact forest structure, we classified a species-size matrix of the density of live and dead trees by assigning the three major species (ponderosa pine, grand fir, and lodgepole pine) to four diameter classes: small, medium, large, and very large (10–29; 30–49; 50–69 cm; and > 70 cm DBH, respectively). Rare species occurred in four plots, but were excluded (mountain hemlock, Engelmann spruce, and western white pine). Large and very large lodgepole pine did not occur, resulting in 10 unique species-size variables. In the matrix, we replaced all zeros with ones, then log-transformed because density varied by more than an order of magnitude within some classes (McCune and Grace 2002). We named forest types based on their historical composition and development following fire exclusion (SI, Online Appendix S3).

We classified our plots into fire-regime types using a matrix of plot-composite fire-regime metrics describing frequency, variation in frequency, and fire extent at the 82 plots with complete fire records. We excluded the remaining 23 plots because they had incomplete records. We considered frequency metrics of mean and median fire intervals; variation metrics of coefficient of variation, minimum and maximum intervals, and standard deviation of intervals. We considered fire extent metrics of the mean extent of all fires that burned a plot, the number of small fires (i.e., less than 400 ha), and the number of large fires (more than 2000 ha).We calculated fire regime metrics using R software (R Development Core Team 2008). Prior to cluster analysis, we used scatterplots to eliminate metrics that were highly correlated ($R > 0.40$) while retaining uncorrelated metrics. The final matrix included median fire interval, the coefficient of variation in fire intervals, the number of small fires, and the number of large fires. In the matrix, we relativized each variable by its maximum observed value (McCune and Grace 2002).

Did historical fire regimes vary with local topography, landscape structure, or forest type?

To assess whether fire regimes varied with landscape structure we developed an index of isolation that captures the amount of pumice basin surrounding each plot. We computed this index by centering a circle on each plot (2 km radius) and dividing it into 8 sectors (Fig. 2). We assumed the pumice substrate in a sector isolated the plot from the spread of fire when a straight line could not cross the sector without crossing a pumice basin or when pumice basin occupied > 50% of the sector. We assigned values of 1 to outer sectors (1–2 km radius) and 2 to inner sectors (plot center to 1 km radius) that met one of these criteria then summed these values for each plot [0 (low) to 24 (high) isolation]. We assigned an index of 25 to plots for which all sectors were within a pumice basin.

We determined via generalized linear mixed modeling (GLMM) (Bolker et al. 2009) that spatial autocorrelation did not impact the relationships between variables describing topography (elevation, aspect, and slope) and landscape structure (isolation) and fire regime metrics (SI Appendix, S4). We then

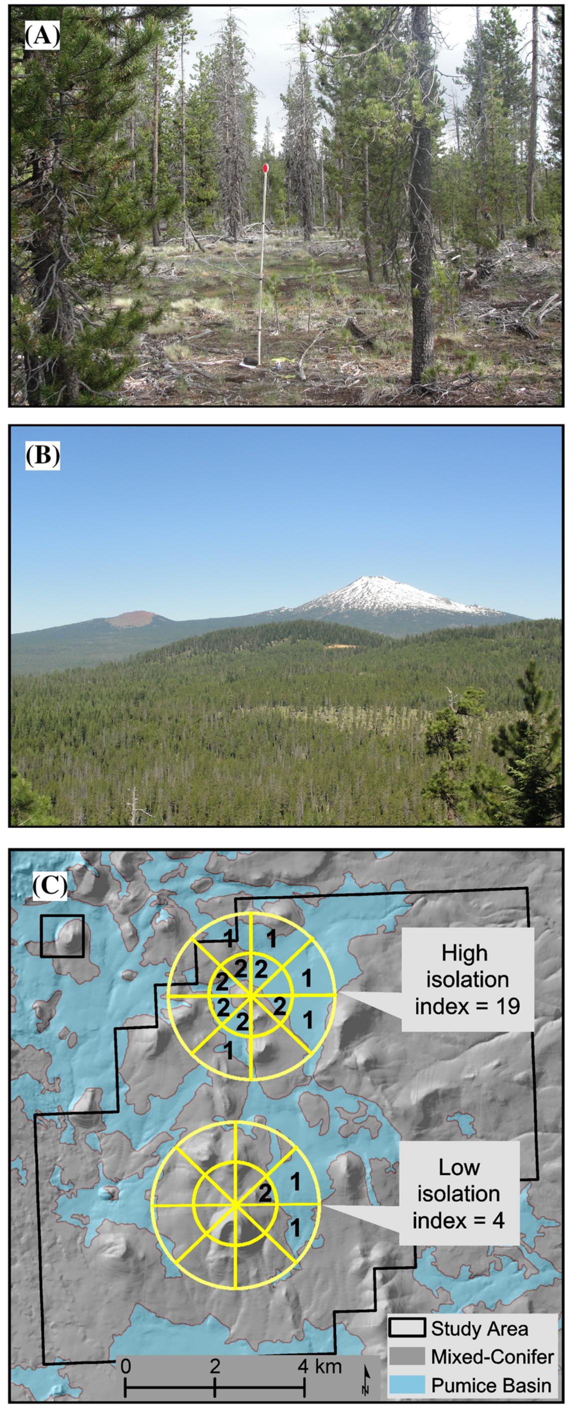


Fig. 2 **a** Fuel-limited pumice basins are common at high elevations in the study area. **b** Portions of these basins were thinned in the 1980s. **c** Examples of computing isolation indices at two plots. Plots surrounded by pumice basins have high isolation while plots in larger patches of mixed-conifer have low isolation. (Color figure online)

assessed whether historical fire regimes (median fire interval, coefficient of variation in fire intervals, number of small fires, and number of large fires) varied with topography and isolation using nonparametric Spearman rank correlation for a total of 16 tests ($\alpha < 0.05$). We transformed aspect to a continuous variable ranging from 0 (southwest) to 2 (northeast; Beers et al. 1966).

We assessed whether fire regime types occurred predominantly in certain forest types. If the spatial pattern of historical fire regimes was driven by forest type, we expected fires to be larger and more frequent in warm-dry, low-elevation ponderosa pine forests and fires to be less frequent and more variable in cool-moist, high-elevation grand fir forests. If the pattern of fire regimes was controlled by landscape structure, we expected isolated plots (i.e., those with high isolation indices) to have lower fire frequency, fewer large fires, and more small fires than plots that are not isolated.

Results

Historical fire regime

Surface fires were historically frequent and often extensive (Fig. 3). Within the analysis period (1650–1871), we crossdated 1995 fire scars and 45 abrupt changes in ring width from 414 trees in the 97 plots containing fire scars. Mean plot-composite fire intervals ranged from 10 to 33 years. Fires (> 400 ha) occurred every 6 years on average and fires > 2000 ha and > 4000 ha occurred every 10 and 28 years on average, respectively (Fig. 4a). The most extensive fire burned 8218 ha in 1695 (Fig. 4d). However, most fires were likely even more extensive than we reconstructed because they intersected the boundary of the sampling grid.

We found strong evidence of partial or stand-replacing fires at 9 of our 82 plots during the analysis period. Most of these occurred as small (< 100 ha) patches within 8 extensive low-severity fires and comprised < 1% of all reconstructed area burned. Two severe patches occurred in adjacent plots in the same fire year and may have burned severely over 100–200 ha. These severe patches occurred in all six forest types (1–3 plots per forest type). The rare occurrence of severe patches precluded us from further analysis of the spatial pattern of severe fire or using severity to identify fire regime types.

Classification of forest- and fire-regime types

We identified six forest types, (13–22 plots per type; SI, Online Appendix S3). The cluster dendrogram was pruned with ~ 50% information remaining and branching was concentrated at short distances (SI Online Appendix S2; McCune and Grace 2002). Three of these types are analogous to those identified by Merschel et al. (2014): Persistent Ponderosa (all sizes classes dominated by ponderosa pine), Recent Grand Fir (dominated by grand fir that established after 1900), and Persistent Shade Tolerant (grand fir present before 1900). The remaining three types include lodgepole pine: Persistent Ponderosa with Lodgepole; Persistent Shade Tolerant with Lodgepole (lodgepole pine dominates small and medium size classes); and Lodgepole (large and very large trees absent, lodgepole pine dominates remaining sizes). These six types occupy distinct environmental settings. On steep slopes, Persistent Ponderosa occupies hot-dry environments, transitioning to Recent Grand Fir and eventually Persistent Shade tolerant with increasing precipitation and decreasing maximum temperature. Persistent Ponderosa with Lodgepole and Persistent Shade Tolerant with Lodgepole occupy analogous environments, but on moderate slopes. Lodgepole Pine occupies flat areas regardless of microclimate.

We identified three fire-regime types via clustering on fire regime metrics (Fig. 3). The cluster dendrogram was pruned with 55% information remaining and branching was concentrated at short distances (SI Online Appendix S2; McCune and Grace 2002). Fires were frequent in all three types (< 32 year intervals), but were most frequent in the Large-Fire type and least frequent in the Longer-Interval type. Plots in the Large Fire type (61 plots) burned frequently, recorded the most large fires, and burned in relatively few small fires. The remaining plots were evenly divided between the Longer Interval (11) and Small Fire (10) types. Plots in the Longer Interval type burned less frequently and in fewer large and small fires, Plots in the Small Fire type burned with intermediate frequency, in a broad range of large fires, and in the most small fires. Small fires accounted for 24% of fires in the Small Fires type, but only 3 and 5% in the Large Fire and Longer Interval types respectively. The

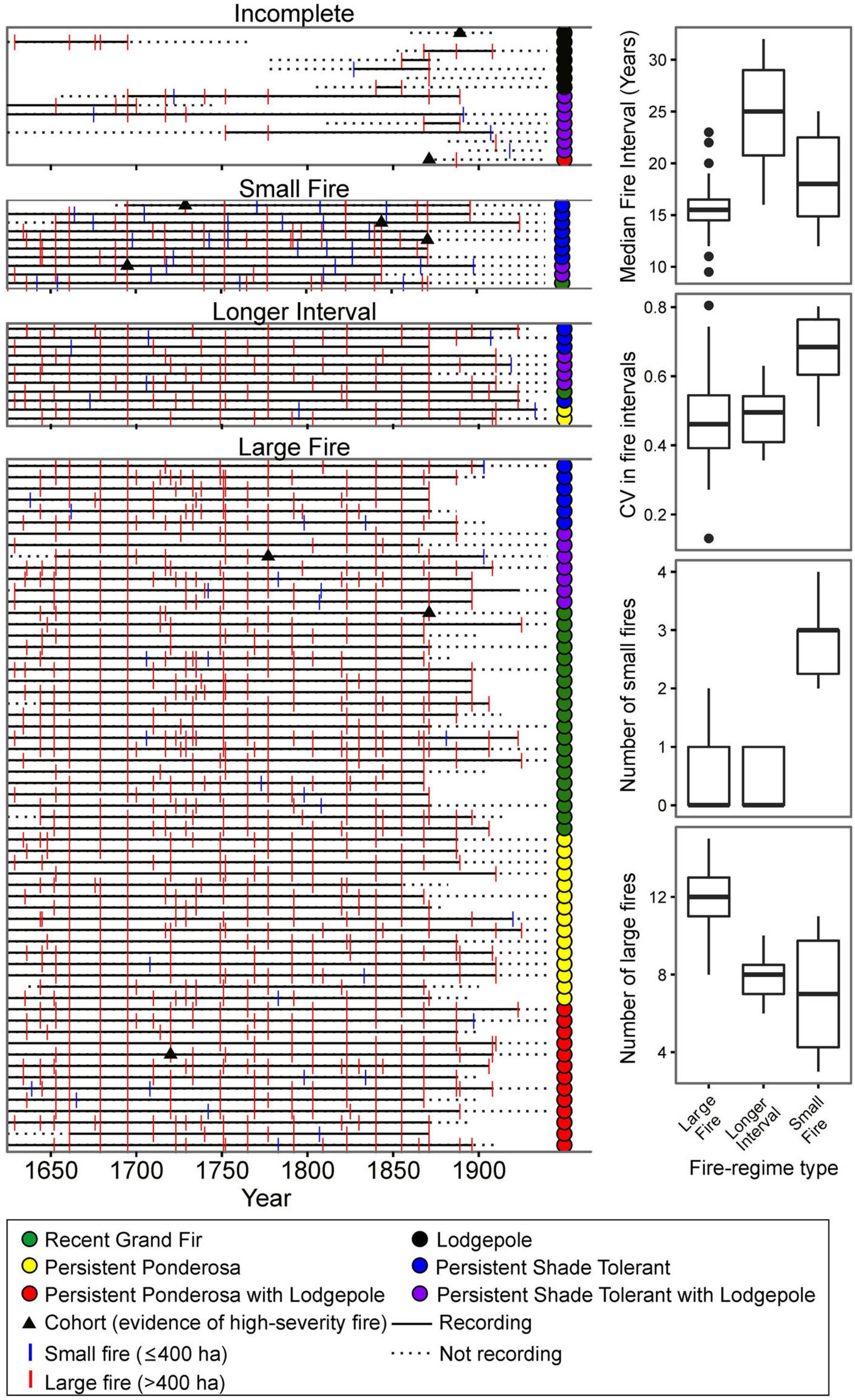
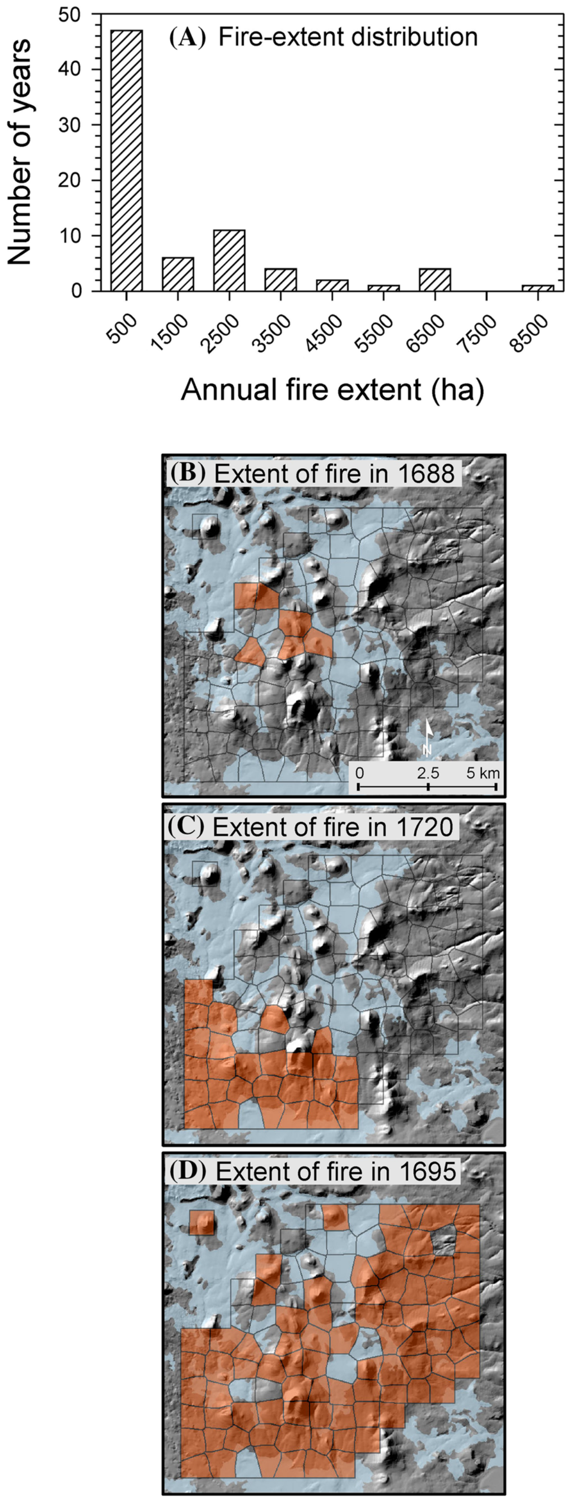


Fig. 3 Plot-composite chronologies of fire reconstructed from tree rings, grouped by fire-regime and forest types (left panels). Each horizontal line shows the composite history of low- and high-severity fires at a plot. Variation in fire regime metrics used to classify fire regime types (right panels). Midlines are medians, box ends are the first and third quartiles, whiskers extend from the 10th to the 90th percentile, and points are outliers. We analyzed fire regimes from 1650 to 1871. (Color figure online)



◀**Fig. 4** **a** Distribution of annual fire extent (1650–1871) computed as the sum of tessellated polygons with evidence of fire in a given year. **b–d** Maps of fire extent (orange shading) in 1688 (576 ha), 1720 (2726 ha) and 1695 (8218 ha), the most extensive year we reconstructed. Pumice basins are indicated with blue shading. (Color figure online)

coefficient of variation was highest in the Small Fire type where periods of frequent fire were followed by relatively long periods without fire (34–66 years). A fourth incomplete type was identified prior to clustering and includes the 23 plots with incomplete fire records. Lodgepole pine dominated 22 of these plots. The plots of each fire-regime type generally occurred in contiguous groups (Fig. 1e) and the boundaries of these groups often coincided with pumice basins.

Did historical fire regimes vary with local topography, landscape structure, or forest type?

The fire regime metrics varied with some aspects of topography, but not others. All four metrics were significantly correlated with elevation ($r = -0.57$ to 0.55; $P = 0.0026$ to < 0.0001;),but not with aspect ($r = -0.12$ to 0.22, $P = 0.0354$ to 0.8846) or slope ($r = 0.15$ to 0.20, $P = 0.0766$ to 0.1557; Fig. 5). The metrics also varied with our measure of landscape structure: all were significantly correlated with the isolation index ($r = -0.62$ to 0.24, $P = 0.0319$ to < 0.0001; Fig. 5). However, this index is also correlated significantly with elevation ($r = 0.60$, $P < 0.0001$; Fig. 6) because the pumice basins happen to occur at high elevation at our site. Therefore, we cannot infer whether elevation or isolation was the primary driver of variation in historical fire regimes from this analysis alone.

Fire regime metrics did not vary monotonically with elevation or isolation (Fig. 6).

Median fire intervals were longer at intermediate elevations and isolations on all landforms. Median intervals were short at lower elevations where large fires were common, and short at upper elevations on cinder cones isolated by pumice basins where small fires were common. High coefficients of variation in fire intervals occurred irregularly throughout the landscape, but were consistently high on isolated cinder cones.

Forest types did not reliably indicate fire-regime types, particularly in environments where grand fir was historically common (Fig. 7). Most plots (61)

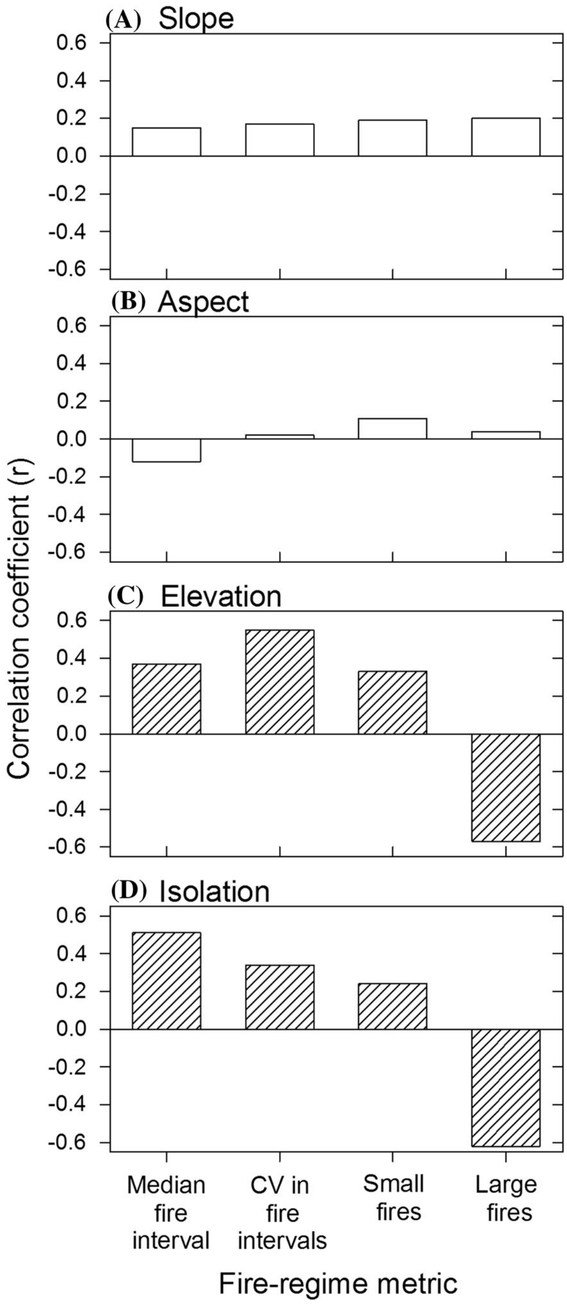


Fig. 5 Relationship of fire-regime metrics to **a** slope, **b** aspect, **c** elevation, and **d** isolation. Hatched bars indicate significant correlations (nonparametric Spearman rank correlation; $P < 0.05$)

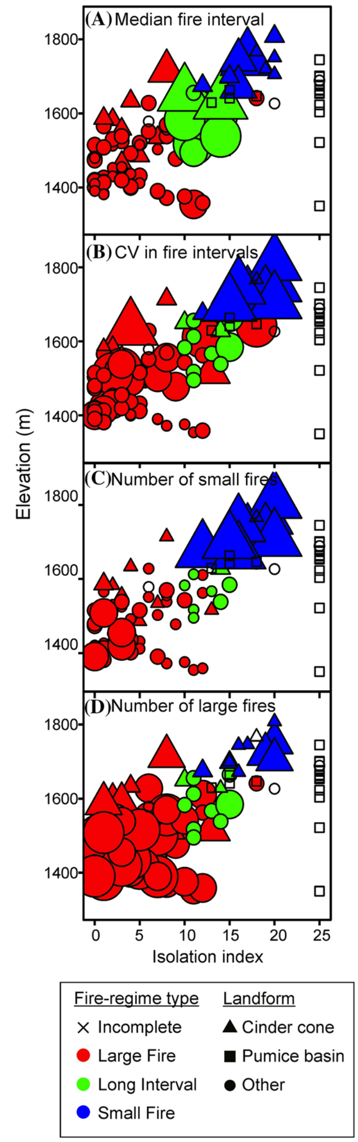


Fig. 6 Relationship of topography, landscape structure, and fire regimes. Symbol sizes are scaled by the variable indicated in the panel label: **a** median fire intervals (< 15, 15–19, 20–24, 25–32 years); **b** coefficient of variation (CV) in fire intervals (< 0.35, 0.35–0.54, 0.55–0.64, > 0.65); **c** number of small fires (0, 1, 2, 3 or 4 fires); and **d** number of large fires (1–6, 7–9, 10–12, 13–15 fires). (Color figure online)

occurred in the Large Fires type and grand fir was historically rare or absent in 48 of these plots. However, fires were large and frequent at the remaining 13 plots, and Persistent Shade Tolerant and Persistent Shade Tolerant with Lodgepole plots occurred in all four fire-regime types. Plots where grand fir was rare or absent historically occurred primarily in the Large Fire type (48 of 53 plots in the Persistent Ponderosa, Persistent Ponderosa with Lodgepole, and Recent Grand Fir forest types). The fire-regime types occurred in geographically contiguous groups, but the forest types did not (Fig. 1d, e).

Discussion

Our tree-ring reconstruction in mixed-conifer forest reveals the persistent influence of landscape structure on spatial variation in historical fire regimes, with local topography and forest composition only weakly related to historical fire-regime type. The fire-regime types we identified varied little in fire frequency (mean MFI 15–25 years) and severity despite a 60 cm gradient in annual precipitation across the study area. Fire-regime types differed more strongly in fire size. The spatial pattern of fire-regime types was clearly associated with topoedaphic landscape structure, in particular with the distribution of pumice basins that intermittently inhibited the spread of fire. In contrast, forest types based on tree composition and establishment history varied at finer scales with local topography that modifies microclimate and soil (SI, Online Appendix S5) consistent with mixed-conifer forests elsewhere in the region (Merschel et al. 2014; Johnston et al. 2016). Our results confirm that fire regimes can be influenced by the surrounding landscape and cannot always be inferred from forest type alone.

Pumice basins occur primarily at high elevation in our study area, confounding efforts to identify their independent effects on fire regimes. Elevational gradients in annual microclimate from relatively cool-moist conditions in the northwest to warm-dry in the southeast relate strongly to a gradient in grand fir which declines in abundance from northwest to southeast (SI, Online Appendix S5). Compact, short-needled litter produced by grand fir is relatively less flammable then the aerated, long-needled surface litter generated by ponderosa pine (Agee et al. 1978; de Magalhães and Schwilk 2012). If the gradients in microclimate and/or surface fuels were driving variation in fire regimes, frequency should decrease continuously with elevation, but this is not what we observed. Rather, fire was frequent at all elevations (Fig. 6; 9 of 14 plots at elevations > 1650 m had a median intervals < 17 years). Long fire-free intervals at high elevations on isolated cinder cones may indicate an intermittent climatic limitation on fire spread and frequency. Because climate is a broad scale

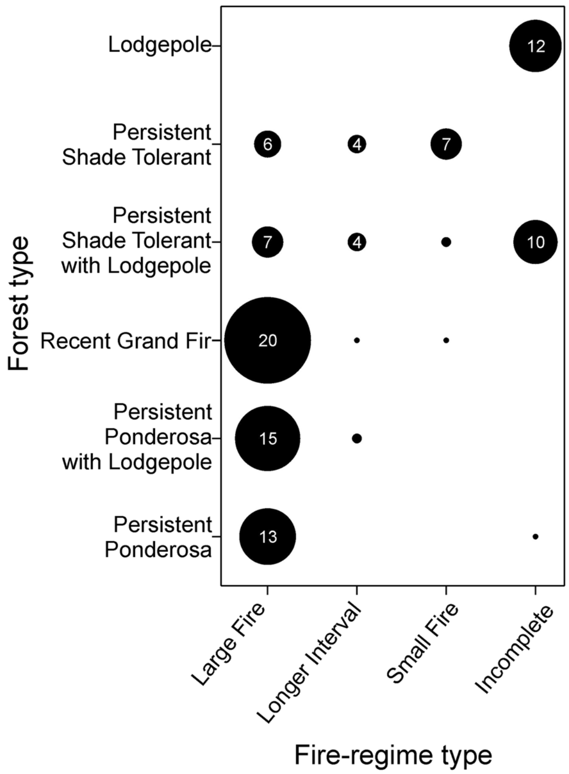


Fig. 7 Distribution of 105 plots by forest and fire-regime type. Size of symbols are proportional to the number of plots in each category and the number of plots are indicated within each symbol for those categories containing more than 2 plots. Grand fir was historically absent from the Persistent Ponderosa, Persistent Ponderosa with Lodgepole, and recent grand fir types, but was common in the Persistent Shade Tolerant types

top-down driver we would expect long fire-free periods to be synchronous among isolated cinder cones. However, fire-free periods were asynchronous among isolated cinder cones in the Small Fires type (Fig. 3) suggesting that fuel-limited pumice basins, a local-scale bottom-up driver, occasionally resulted in longer fire-free periods. For example, no fires were recorded on the isolated cinder cone in the northwest corner of the study area from 1752 to 1817 while fires occurred in 1777, 1786, and 1810 at the nearest isolated cinder cone 3 km to the southeast (Fig. 1).

Pumice basins dominated by lodgepole pine may act as intermittent barriers to fire spread elsewhere in central Oregon and more broadly in the interior Northwest (Agee 1993). There are strong topoedaphic controls on forest structure, composition, and understory fuels in forests on pumice soils, especially in flat basins where cold air pools (Geist and Cochran 1991).

Frost heaving and extreme daily variation in surface temperatures limit the overstory to low-density lodgepole pine forests with sparse understories that can take decades to recover following disturbance (Volland 1985; Geist and Cochran 1991). These stands may only carry fire immediately following mountain pine beetle mortality, after decades of woody fuel accumulation and decay, or during extreme fire weather (Gara et al. 1985; Stuart et al. 1989; Heyerdahl et al. 2014a).

Our reconstruction of historical fire perimeters and the pattern of fire sizes reveals that pumice basins likely influence spatial variation in fire regimes where they are embedded in mixed-conifer landscapes. Small fires prevailed in isolated patches of mixed-conifer forest (e.g., the fire in 1688; Fig. 4b) whereas large fires prevailed in large patches of mixed-conifer forest (e.g., 1720; Fig. 4c). Pumice basins in our study area are rare at low elevations so fires ignited anywhere in the lower elevations spread widely resulting in frequent fires throughout this connected part of the study area as they do elsewhere in large fire compartments (Bergeron 1991; Frost 2006). Fires intermittently crossed pumice basins (e.g., 1695; Fig. 4) perhaps from (1) bark beetle attack, subsequent fuel accumulation, and understory development coinciding with severe fire weather (Geiszler et al. 1980; Lotan et al. 1985), (2) lightning storms igniting multiple fires in the same year across pumice basins (Morris 1934), or (3) spotting from embers carried by wind across pumice basins.

We were surprised that fires were as frequent on many of the small, isolated cinder cones as they were in the large patches of forest (Fig. 6a). In other regions, small isolated landscape units have lower frequencies because fires do not spread to them and must be ignited locally (Bergeron 1991; Frost 2006). A possible explanation is that fires may have been ignited more frequently in the mixed-conifer forests on the cinder cones than they were in the mixed-conifer forests at low elevation. The frequency of cloud-to-ground lightning strikes increases with elevation, slope, and terrain complexity (Vogt and Hodanish 2014), and ignitions are highest where lightning strikes dry fuel in relatively productive mixed-conifer forests (e.g., Van Wagtendonk 1993). Topography and fuels that increase the likelihood of lightning ignitions coincide on steep prominent cinder cones. Notably, periods of more frequent fire occurred when large and logically ignited small fires both occurred during 2–3 decades on a cinder cone in the Small-Fire type, and longer intervals occurred when larges fires did not spread to isolated cinder cones (Fig. 3). The high frequency and variability in frequency of fire on isolated cinder cones may be driven by local ignitions and intermittent spread of fires across pumice basins in the landscape we assessed.

The historical resistance of grand fir to fire varied with environmental setting in our study area. Grand fir persisted despite frequent fire in cool-moist environments, but was rare or absent in warm-dry environments with the same pattern of fire. Microclimate and productivity rather than fire regime also explain the historical distribution of true fir versus ponderosa pine dominated forests elsewhere in the interior Northwest (Taylor and Skinner 2003; Wright and Agee 2004; Johnston et al. 2017).

Forest types and fire regimes clearly have different sensitivity to variation in microclimate at landscape scales where restoration and management planning and implementation occur. The comparatively small influence of topography and microclimate on fire regime in our study area is best explained by relatively homogenous summer microclimates (Fig. 1b, c) and suitable flammability of surface fuels (Banwell et al. 2013) in both ponderosa pine and grand fir dominated forests during uniformly hot-dry fire seasons. Variation in forest composition is thus not necessarily indicative of variation in historical structure, historical fire regime, and restoration needs (Johnston 2017). Accordingly we found that compositional shifts from ponderosa pine to grand fir and the highest densities of trees established after fire exclusion occurred in relatively productive forests that were coupled to drier forests (Johnston 2017) by the same disturbance pattern of frequent fire.

Abundant fire-scarred trees distributed across more than 10,000 ha in our study area are strong evidence that low-severity fires dominated the mixed-conifer forests here, consistent with tree-ring reconstructions of fire regimes in similar forests elsewhere in the region (Heyerdahl et al. 2001; Johnston et al. 2016). Our results are also supported by extensive (> 50,000 ha) and intensive (> 1,000,000 trees inventoried) historical surveys of forest structure and composition from the early 1900s both north (Hagmann et al. 2014) and south of our study area

(Hagmann et al. 2013). These surveys documented that low-density forests dominated by large fire-resistant trees historically dominated the same environmental gradient we sampled. Following the exclusion of frequent fire from the landscape, grand fir increased in density and predominance across our study area (SI, Online Appendix S3), consistent with extensive empirical data on forest development collected across the eastern Cascades and Ochoco Mountains (Perry et al. 2004; Merschel et al. 2014) and the southern Blue Mountains (Johnston et al. 2016). One study based on records from the General Land Office suggested that high-severity fires historically dominated our study area (Baker 2012, 2015), but the methods and conclusions of that study have been challenged (Levine et al. 2017) and are not supported by the abundant physical evidence of low-severity fire we found in our systematically sampled plots.

Fire regimes vary with bottom-up and top-down drivers elsewhere and their relative importance and effects vary with the scale of assessment and the landscape assessed (Heyerdahl et al. 2001; Kellogg et al. 2008; Parks et al. 2012). Our study emphasizes the importance of landscape structure, via edaphic features, as an additional mesoscale bottom-up driver. Volcanic features were the landscape structures driving variation in fire regime in the landscape we assessed, but other features of landscapes can modify fire regimes. In more rugged landscapes boundaries of fires and fire occurrence groups coincided with streams and incised topography in the Blue Mountains of Oregon (Heyerdahl et al. 2001), the Klamath Mountains of California (Taylor and Skinner 2003) and in the southern interior of British Columbia (Jordan et al. 2008). Our work expands these efforts to more gentle terrain and demonstrates that a suite of fire regime metrics and an extensive systematic sample may be required to correctly identify topoedaphic drivers of variation in historical fire regimes. For example, variation in fire regime between a site dominated by ponderosa pine versus one dominated by grand fir could be erroneously attributed to microclimate and forest composition if the repeated pattern of fire perimeters across the landscape were unknown. By sampling grand fir forest in different spatial contexts and environmental settings we determined that these forests may or may not have a more variable fire regime than ponderosa pine forests, and that limitations to fire spread and not immediate microclimate explain this variability.

Our work advances the understanding of the drivers of spatial variation in historical fire regimes and can inform discussions about appropriate restoration of fire-excluded forests in the interior Northwest. Regional-scale classifications of historical fire regimes and assessments of restoration needs (e.g., LANDFIRE; Rollins 2009; Haugo et al. 2015) based on forest composition facilitate prioritization among ecoregions. However, where the goal is to restore historical fire regimes and associated forest structure at landscape scales (Stine et al. 2014; Hessburg et al. 2016), managers may want to consider how fire regimes would or would not vary given the spatial pattern of topoedaphic and vegetation patch types that could affect fire spread and ignition frequency. We identified three historical fire regimes within relatively cool, moist and productive biophysical settings where grand fir was historically common. This demonstrates that restoration plans may need to consider landscape context. We also demonstrated how departure from historical conditions can be scale dependent. In other words, landscape structure may be departed at a large scale, but within the historical range of variability at an individual site. For example, sites on cinder cones isolated by pumice basins had fire frequency similar to the rest of the landscape, but also had the longest fire-free periods that were asynchronous among cinder cones. These productive sites likely supported denser multilayered forests during fire quiescent periods and current structure at the scale of a single isolated patch may be consistent with historical conditions. However, if all isolated patches are considered it is extremely unlikely they would have all simultaneously advanced to a late successional stage as they have during a century of fire exclusion. Landscape-scale perspectives can present a more informative picture of reference conditions than approaches based on individual stand or patch-level assessments.

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