Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests

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Citation: Johnston, J. D., J. D. Bailey, and C. J. Dunn. 2016. Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests. Ecosphere 7(11):e01581. 10.1002/ecs2.1581

Abstract. Fire frequency is assumed to have exerted a strong influence on historical forest communities in the inland Pacific Northwest. This study reconstructs forest structure and composition in the year 1890 and fire frequency from 1760 to 1890 at 10 sites spanning a broad productivity gradient in the southern Blue Mountains of eastern Oregon. We tested for the relative influence of fire frequency, climate, soils, and topography by fitting variables to ordinations of forest structural and compositional configurations. We also built formal statistical models using non-parametric permutational multivariate analysis of variance. Because fire disturbance and biophysical influences on forest structure and composition may vary depending on the scale at which relationships are examined, we tested the influence of variables at the scale of 4- to 12-ha sites and at the scale of three equal-sized areas within each site. The proportion of fire-intolerant species basal area reconstructed within sites in the year 1890 ranged from 0% to 43%. The proportion of fire-intolerant species basal area reconstructed within equal-sized areas within sites ranged from 0% to 75%. Despite significant differences in historical species composition between and within sites, fire frequencies were relatively similar. Mean fire return intervals (MFRIs) calculated for sites ranged from 10.6 to 21.2 yr. MFRIs calculated for equal-sized areas within sites ranged from 10.6 to 28.8 yr. Fitting fire frequency and biophysical variables to ordinations and model building with perMANOVA showed that topographic position index and vapor pressure deficit had stronger influences on site-scale forest structure and composition than fire frequency metrics. Available soil water was the most important influence on forest structure and composition within equal-sized areas within sites. Relatively frequent fire across a broad range of forest types in the southern Blues appears to have been a relatively uniform influence on forest dynamics modulated by fine-scale biophysical heterogeneity. If return to historical conditions is a goal of management, treatments to reduce fuel and restore frequent fire are appropriate across a broad productivity gradient in the southern Blues.

Key words: Blue Mountains; dendroecology; fire frequency; forest composition; forest structure; mixed conifer; non-metric multidimensional scaling; perMANOVA; ponderosa pine; productivity.

Received 9 July 2016; revised 25 September 2016; accepted 26 September 2016. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

While climate variability controls the distribution of vegetation at broad spatial scales (>10^6 ha^2) (Omernik 1987), ecologists frequently emphasize the role of disturbance in shaping biotic communities at intermediate and fine scales (1^-1 to 10^6 ha^2) where most land management planning occurs (Woodward 1987, Huston 1994, Bond et al. 2005, Keane et al. 2015). Of particular interest to managers and researchers in the inland Pacific Northwest is the relationship between fire frequency and forest structure and composition prior to extensive Euro-American

In contrast to drier forests where frequent fire maintained stands dominated by large old ponderosa pine, more productive mixed conifer forests east of the Cascades are believed to have experienced longer fire-free intervals that allowed the development of relatively dense, late-seral, fire-intolerant forest structure, especially grand and white fir (Hessburg et al. 1999, 2007, Saab et al. 2005, Spies et al. 2006, Stine et al. 2014). However, despite strong interest in using knowledge of historical forest dynamics to guide the development of treatments to restore resilient forest conditions, there has been little or no empirical research that examines the relationship between historical fire frequency and forest structure/composition in eastern Oregon and Washington (Brown et al. 2004, Spies et al. 2006, Franklin and Johnson 2012, Stine et al. 2014). We are aware of only one study that explicitly tested the hypothesis that fire frequency mediates inland Pacific Northwest forest composition. In that study, Keane et al. (1990) adapted a successional process model to test the effects of different fire frequencies on stand-level species composition. Simulated stands burning at average intervals of less than 20 yr were composed almost entirely of ponderosa pine and western larch while fire intervals greater than 50 yr were associated with significant cover of fire-intolerant species.

Disentangling the effects of fire and biophysical variation on forest dynamics poses a number of challenges. First, reconstructing accurate fire histories is time-consuming and thus typically limited in spatial extent, and the lack of replication across highly variable environmental settings may lead to ambiguous results about the influence of fire on forest dynamics (Fritts and Swetnam 1989, Beckage and Stout 2000). Second, reconstructions of historical fire usually rely on fire-scar evidence that may overestimate return intervals in areas where tree species that readily record fire events in cambial tissue are less common (Arno and Sneck 1977, McBride 1983), or underestimate intervals when fire-scar evidence is composited across a broader area than the actual spatial extent of past fires (Baker and Ehle 2001). Third, fire disturbance and biophysical influences on forest structure and composition may vary depending on the scale at which these relationships are examined (Simard 1991, Reed and Johnson 2004, Falk et al. 2007). Finally, strong correlation between biophysical variables and interactions among variables can complicate statistical hypothesis testing. More generally, fire frequency and forest structure is an example of a self-reinforcing relationship between ecological pattern and process that can be difficult to characterize in cause and effect terms (Turner 1989, Peterson 2002, Scholl and Taylor 2010).

This study uses cross-dated tree ring evidence to investigate the relationship between historical stand structure/composition, fire frequency, and biophysical heterogeneity. We account for the challenge posed by the lack of replication across diverse environmental settings by reconstructing historical forest dynamics within 10 different sites that span a broad productivity gradient within a large (688,000 ha) study area in eastern Oregon. We address the potential for scale-dependent responses by analyzing the relationships between forest structure/composition and fire frequency and biophysical variables both at the scale of 4- to 12-ha sites and at the scale of three slope positions of equal area within each site. We use data reduction techniques that map forest structural/compositional configurations, fire frequency metrics, and biophysical variables in a multidimensional space that allows interpretation of relationships without assumptions about cause and effect. We also build formal statistical models that test for interactions among variables using only explanatory variables that are not strongly correlated. We address the following research questions: (1) Does fire frequency vary significantly by forest type? (2) What are the key drivers of forest structure/composition? and (3) Do relationships between forest structure/composition, fire frequency, and biophysical heterogeneity vary at different spatial scales?
Study area

Data were collected on the Malheur National Forest (MNF), which encompasses 688,000 ha of federal lands in the southern Blue Mountains of eastern Oregon (Fig. 1). Three quarters of annual precipitation in the southern Blues falls between November and May. The 30-yr average maximum summer temperature was 29°C and the 30-yr average monthly minimum winter temperature was −5°C (PRISM 2014). Convective storms are common in the summer months, and lightning from these events frequently ignites wildfires from July through September (Rorig and Ferguson 1999).

The MNF ranges in elevation from 998 to 2756 m. Approximately 90% of the total land area of the MNF is found between 1300 and 2000 m, where precipitation ranges from 420 to 775 mm annually. This elevation range is dominated by long-lived conifers of the ponderosa pine, Douglas-fir, and grand fir potential vegetation types (PVTs). PVTs are often subdivided into dry and moist environmental settings, for example, moist grand fir and dry grand fir (Franklin and Dyrness 1988, Agee 1994, Simpson 2007, Hemstrom et al. 2012).

Ponderosa pine (Pinus ponderosa Dougl. ex Laws) is a common early seral, fire-tolerant, shade-intolerant species throughout the southern Blues. Western larch (Larix occidentalis Nutt.) is a
highly fire-tolerant, shade-intolerant, early seral species found in cooler, moister sites (McCune 2006, Touzel 2013). Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) exhibits high fire tolerance, intermediate shade tolerance, and is a common mid- and late-seral species. Grand fir (Abies grandis (Dougl.) Lindl.) is the major late-seral, fire-intolerant, shade-tolerant tree species of the southern Blue Mountains (Franklin and Dyrness 1988, Johnson and Clausnitzer 1992).

Site selection
To avoid the effects of past timber harvest on historical reconstructions, data were collected within 10 randomly selected inventoried roadless areas (IRAs) delineated in Forest Service databases. PVT maps from the Integrated Landscape Assessment Project (ILAP; http://ecoshare.info/ilap/; Hemstrom et al. 2012) were overlaid on selected IRAs. Because fire can remove forest structures of interest, we rejected sites that showed evidence of fire over the past 100 years. Study sites were located by randomly placing a point within one of the following PVTs within each IRA: xeric ponderosa pine, dry ponderosa pine, Douglas-fir, dry grand fir, and moist grand fir. The location of points was constrained so that at least one and no more than three sites were located in each of these PVTs. These procedures resulted in the selection of sites that spanned the full range of forest types found on the MNF (Table 1, Figs. 2, 3).

Field sampling
Each study site consisted of an area of relatively consistent aspect delineated around each randomly located point using a GIS system (ArcMap 10.2, Redland, California, USA). These areas, which ranged in size from 4.1 to 12.3 ha (mean = 7.9 ha), were divided into equal-sized lower, mid-, and upper slope positions. A randomly located point within each slope position served as the midpoint of a 178-m transect running parallel to the slope contour. Five 17.8 m radius (0.1 ha) plots were located at equal intervals along each transect (Fig. 4). Species and diameter at breast height (DBH) were recorded for all live trees >40 cm DBH in each plot to estimate historical structure and composition. The 40-cm threshold was selected because a pilot study demonstrated that most (95%) trees <40 cm sampled in plots were established after the last recorded fire in the late 19th century and the few trees that were older contributed little to overall plot basal area prior to the last fire.

Species, diameter, and decay class were recorded for all dead trees >40 cm DBH in each plot. Of the dead trees, 96% could be confidently identified to species based on physical attributes or examination of a wood sample in the laboratory (Parks et al. 1997). The remaining dead trees were assigned to the species of the nearest dead tree of similar size (±10 cm) for which the species could be determined. Within each plot, the four closest trees to a randomly generated point and four of the largest trees in the plot were cored with a hand-powered increment borer. Five additional large trees within 60 m of the transect that were not sampled in plots were also cored, resulting in tree cores from 45 trees within each slope position (135 trees per site). Most trees were cored multiple times in order to intercept the pith or extract a ring estimated in the field to be within five rings from the pith (minimum laboratory-determined rings to pith = 0, maximum = 15, mean = 1.6). When a tree could not be

Table 1. Location, dominant PVT, and topographic characteristics of study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Easting</th>
<th>Northing</th>
<th>Dominant PVT</th>
<th>Elevation (m)</th>
<th>Aspect</th>
<th>Slope (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thompson</td>
<td>−118°58′42</td>
<td>44°31′16</td>
<td>PIPO Xeric</td>
<td>1248</td>
<td>NW</td>
<td>9</td>
</tr>
<tr>
<td>North Fork</td>
<td>−118°23′10</td>
<td>44°11′53</td>
<td>PIPO Dry</td>
<td>1490</td>
<td>E</td>
<td>10</td>
</tr>
<tr>
<td>Myrtle</td>
<td>−119°5′23</td>
<td>43°56′48</td>
<td>PIPO Dry</td>
<td>1641</td>
<td>W</td>
<td>15</td>
</tr>
<tr>
<td>Malheur</td>
<td>−118°34′44</td>
<td>44°4′56</td>
<td>PIPO Dry</td>
<td>1497</td>
<td>E</td>
<td>17</td>
</tr>
<tr>
<td>Stink</td>
<td>−118°22′32</td>
<td>44°12′17</td>
<td>PSME Dry</td>
<td>1550</td>
<td>NW</td>
<td>18</td>
</tr>
<tr>
<td>Reynolds</td>
<td>−118°29′39</td>
<td>44°25′34</td>
<td>ABGR Dry</td>
<td>1588</td>
<td>SW</td>
<td>26</td>
</tr>
<tr>
<td>Crane</td>
<td>−118°28′49</td>
<td>44°6′17</td>
<td>ABGR Dry</td>
<td>1863</td>
<td>NW</td>
<td>9</td>
</tr>
<tr>
<td>Dry Cabin</td>
<td>−119°24′2</td>
<td>44°21′1</td>
<td>ABGR Dry</td>
<td>1785</td>
<td>NW</td>
<td>15</td>
</tr>
<tr>
<td>Jugow</td>
<td>−118°57′37</td>
<td>44°34′48</td>
<td>ABGR Moist</td>
<td>1730</td>
<td>NW</td>
<td>5</td>
</tr>
<tr>
<td>Dearborn</td>
<td>−118°34′25</td>
<td>44°35′22</td>
<td>ABGR Moist</td>
<td>1460</td>
<td>NE</td>
<td>11</td>
</tr>
</tbody>
</table>

Note: PVT, potential vegetation type; PIPO, Pinus ponderosa; PSME, Pseudotsuga menziesii; ABGR, Abies grandis.
cored to the pith or near the pith because of rot or deformities (9.8% of trees), a nearby replacement tree of the same species with similar DBH (±5 cm) and crown architecture was cored.

The area within 200 m of plots was systematically searched for evidence of historical fire occurrence and partial cross sections were removed with a chainsaw from at least 17 fire-scarred trees within each site. Fire-scarred wood samples were well distributed across sites, with at least two samples collected uphill and downhill of each transect, and at least one sample within 100 m of the beginning, end, and midpoint of each transect (Fig. 4). Sites were revisited to collect additional partial cross sections if collector curves of fire years suggested additional fire years could be detected by collecting additional samples (Falk and Swetnam 2003, Sutherland et al. 2015).

Mean fire return intervals (MFRIs) were calculated both for sites and for each of the equal-sized slope position areas within sites. Site MFRIs were calculated using all fire years recorded by all trees sampled within sites, and slope position MFRIs were calculated using all fire years recorded by trees sampled within individual slope positions.

Forest structure, composition, and fire occurrence reconstructions

Tree cores and partial cross sections were polished with progressively finer grades of sandpaper and visually cross-dated using a master chronology for the southern Blues developed following a pilot study (Stokes and Smiley 1968, Holmes 1983). All wood samples were measured to 0.001-mm precision using a computer-controlled Velmex or Acu-Gage linear measuring system (Velmex, Bloomfield, New York, USA; Acu-Gage Systems, Hudson, New Hampshire, USA). Cross-dating accuracy was verified using COFECHA software (Grissino-Mayer 2001). Each fire scar found in partial cross sections was assigned to a calendar year. A number of tree cores also contained fire scars, and these scars were included in fire return interval calculations provided the scar could be definitively dated to the same calendar year as a cross-dated fire scar found in a cross section.
Only those fire years recorded by trees more than 200 m apart within sites and 50 m apart within slope positions were used in MFRI calculations to ensure that only fires that spread throughout a significant portion of each spatial scale contributed to fire frequency metrics used to explain forest structure and composition. MFRI was calculated as the arithmetic mean interval between fires that occurred between 1760 and 1890. The year 1890 was selected as the end year for historical reconstructions because only two sites recorded fire after 1890 and less than 2% of all cross-dated fire scars were formed after 1890. The year 1760 was selected as the beginning year for historical reconstructions because we hypothesized that fire frequency influenced species composition and none of the fire-intolerant trees sampled were established prior to 1760. Weibull median fire return intervals (Grissino-Mayer 1999) were virtually identical to the arithmetic mean intervals (<1 yr difference), so arithmetic mean intervals are reported throughout this study. We also calculated the minimum and maximum return intervals between 1760 and 1890, as well as the difference between minimum and maximum fire return intervals (Table 2).

We reconstructed basal area in the year 1890 for all cored trees. First, the number of rings between the oldest ring of each tree core and the pith (if missing) was estimated using the geometric method described by Duncan (1989). Most trees were cored between 20 and 140 cm, and we subtracted rings between coring height and breast height based on a regression equation that modeled the number of annual rings between breast height and other locations on the tree trunk based on species, coring height, and radial growth rate. Next, measured tree ring widths at breast height and any additional rings estimated between the pith and last measured ring were converted to basal area increment (m$^2$). Then, each basal area increment was standardized so that the sum of all basal area increments from tree cores was equal to the basal area of each tree at breast height when sampled. This procedure ensured that basal area calculations derived from tree ring widths compensated for different coring heights, differences in bark thickness, the
The total reconstructed basal area of sampled trees in the year 1890 was used to create a simple linear model that predicted 1890 basal area of the remaining unsampled live and dead trees >40 cm recorded in plots based on diameter, species, site, last ring present, and decay class (live or decay class 1–5). The last ring present for dead trees that were not cross-dated was estimated by randomly selecting a year from a distribution of the last annual rings present on cross-dated partial cross sections from dead trees of the same decay class, same site, same species, and similar (±10 cm) diameter.

Western juniper (*Juniperus occidentalis* Hook.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud) trees established during or prior to the year 1890 were found in only seven of 150 plots and made up <1% of those plots’ total reconstructed basal area. These species were excluded from statistical analyses because they were not an important component of stands in 1890, and inclusion of these species significantly increased the heterogeneity of dispersion in the multivariate response modeled using perMANOVA and potentially skewed explanatory variable estimates.

**Biophysical variables**

In addition to calculating fire frequency statistics for sites and slope positions, we assembled 20 different types of biophysical variables describing the physical location, recent climate characteristics, soil characteristics, and topography for each plot (Table 2). Slope position biophysical variables were calculated as the average value across the five plots located within each slope position. Site variables were calculated as the average value of all 15 plots within each site. Most variables were calculated at different spatial or temporal scales. For example, minimum, maximum, and average vapor pressure deficit (VPD) values were calculated at annual, seasonal (e.g., summer), bimonthly (e.g., June and July), and monthly intervals. Topographic position index, a measure of the unevenness of terrain surrounding each plot, was calculated as the average height above the minimum elevation at 75, 300, 450, and 1000 m neighborhood distances from plots (Gallant and Wilson 2000).

Many of these variables were strongly correlated or incorporated redundant information, for instance, solar insolation calculations integrate elevation, aspect, slope, and the shading effect of surrounding topography. For the purposes of statistical analysis, when variables incorporated redundant information or when correlation between variables calculated with Pearson’s *r* exceeded 0.60 or −0.60, we selected the variable that best explained the structure/composition response as measured by a combination of statistical significance (*P*) and the coefficient of determination (r²) (Harris and Taylor 2015). The −0.60/0.60 correlation threshold is arbitrary, but it corresponds to a variance inflation factor of 2.5, which is often associated in statistical literature with an increase in estimate variance that gravitates against identification of an optimal set of explanatory variables in models (Greene 1993).

**Forest groups and fire frequency**

We used hierarchical agglomerative cluster analysis to determine whether historical forest structure/composition of sites and slope positions fell into statistically significant groups.
Cluster analysis was performed using a Euclidean distance measure with Ward’s linkage method (McCune et al. 2002) on both site and slope position matrices that consisted of reconstructed 1890 basal area of ponderosa pine, western larch, Douglas-fir, and grand fir. Statistically significant groups were identified using approximately unbiased (AU) $P$-values computed from multiscale bootstrap

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description (units)</th>
<th>Source/references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disturbance history</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean fire return interval</td>
<td>Average interval between fires during the period 1760–1890 CE (yr)</td>
<td>This study</td>
</tr>
<tr>
<td>Minimum return interval</td>
<td>Minimum number of years between fires during the period 1760–1890 CE (yr)</td>
<td>This study</td>
</tr>
<tr>
<td>Maximum return interval</td>
<td>Maximum number of years between fires during the period 1760–1890 CE (yr)</td>
<td>This study</td>
</tr>
<tr>
<td>Return range</td>
<td>Difference between minimum and maximum interval between fires (yr)</td>
<td>This study</td>
</tr>
<tr>
<td>Physical location</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Easting</td>
<td>$x$-coordinate in Universal Transverse Mercator North American Datum 1983 projection</td>
<td>Digital Elevation Model (DEM); <a href="http://spatialdata.oregonexplorer.info/">http://spatialdata.oregonexplorer.info/</a></td>
</tr>
<tr>
<td>Northing</td>
<td>$y$-coordinate in Universal Transverse Mercator North American Datum 1983 projection</td>
<td>DEM</td>
</tr>
<tr>
<td>Climate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>Thirty-year average annual and monthly minimum, maximum, and average temperature (°C)</td>
<td>PRISM Climate Group (2014); <a href="http://www.prism.oregonstate.edu">http://www.prism.oregonstate.edu</a></td>
</tr>
<tr>
<td>Precipitation</td>
<td>Thirty-year average annual and monthly minimum, maximum, and average precipitation (mm)</td>
<td>PRISM (2014)</td>
</tr>
<tr>
<td>Vapor pressure deficit</td>
<td>Thirty-year average annual and monthly minimum, maximum, and average difference between actual vapor pressure and saturation vapor pressure at the same temperature (hPa)</td>
<td>PRISM (2014)</td>
</tr>
<tr>
<td>Water climate deficit</td>
<td>Precipitation minus evapotranspiration modeled from MODIS satellite imagery</td>
<td>Mildrexler et al. (2016)</td>
</tr>
<tr>
<td>Soils</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Available soil water</td>
<td>Total growing season water holding capacity of soil column estimated from soil depth, soil texture, and parent material (mm)</td>
<td>NRCS (2014); <a href="http://www.nrcs.usda.gov/wps/portal/nrcs/site/soils/home/">http://www.nrcs.usda.gov/wps/portal/nrcs/site/soils/home/</a>; Carlson (1974)</td>
</tr>
<tr>
<td>Ash content</td>
<td>Total depth of soil ash (mm)</td>
<td>NRCS (2014)</td>
</tr>
<tr>
<td>Soil type</td>
<td>Categorical description of soil type</td>
<td>NRCS (2014)</td>
</tr>
<tr>
<td>Parent material</td>
<td>Categorical description of mineral type from which soils were derived</td>
<td>NRCS (2014)</td>
</tr>
<tr>
<td>Topography</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>Height above sea level (m)</td>
<td>DEM</td>
</tr>
<tr>
<td>Slope</td>
<td>Steepness of slope (%)</td>
<td>DEM</td>
</tr>
<tr>
<td>Slope variability</td>
<td>Difference between minimum and maximum slope at different neighborhood distances</td>
<td>DEM</td>
</tr>
<tr>
<td>Slope position</td>
<td>Categorical description of position on slope</td>
<td>USDA (1993)</td>
</tr>
<tr>
<td>Landform</td>
<td>Categorical description of location with respect to geomorphological features</td>
<td>This study</td>
</tr>
<tr>
<td>Transformed aspect</td>
<td>Aspect, transformed to a continuous variable ranging from 0 to 2 (aspect = 1 + cos(45° − aspect))</td>
<td>This study; Beers (1966)</td>
</tr>
<tr>
<td>Topographic position index</td>
<td>Focal pixel height above minimum elevation at different neighborhood distances</td>
<td>This study; Weiss (2001), Gallant and Wilson (2000)</td>
</tr>
<tr>
<td>Direct incident radiation</td>
<td>Maximum potential annual solar radiation</td>
<td>This study; McCune and Dylan (2002)</td>
</tr>
<tr>
<td>Heat load</td>
<td>Index of potential direct incident radiation adjusted for aspect and slope</td>
<td>This study; McCune and Dylan (2002)</td>
</tr>
<tr>
<td>Solar insolation</td>
<td>Total solar radiation derived from hemispherical viewshed algorithms</td>
<td>This study; Fu and Rich (2002)</td>
</tr>
</tbody>
</table>
resampling using the pvclust package in R (Suzuki and Shimodaira 2014, R Core Team 2016). We also tested for statistically significant differences between groups identified by cluster analysis using multiple response permutation procedures (MRPP) in R’s vegan package using a Sørensen distance metric (Oksanen et al. 2015). MRPP provides a non-parametric test of the statistical difference between pre-determined groups using random permutations of the original data set (Zimmerman et al. 1985). We used a variety of non-parametric tests including a Kruskal–Wallis test, a Mann–Whitney–Wilcoxon test, and permutation-based tests to determine whether fire frequency metrics differed among the groups identified by cluster analysis (Mann and Whitney 1947, Kruskal and Wallis 1952, Conover 1980).

**Drivers of forest structural and compositional variation**

Variation in forest structure and composition was evaluated by ordination of both site and slope position tree basal area matrices (Bekker and Taylor 2010). Site ordination was performed on a matrix that consisted of reconstructed basal area in the year 1890 of the four major overstory tree species (western larch, ponderosa pine, Douglas-fir, and grand fir) in all plots in each site. Slope position ordination was performed on a matrix that consisted of reconstructed 1890 basal area of the four major overstory tree species in plots within each slope position. Ordination was performed using non-metric multidimensional scaling (NMDS) in R’s vegan package using a Sørensen distance metric (Oksanen et al. 2015). NMDS iteratively searches for positions of \( n \) entities, in this case 1890 forest structure/composition of either 10 sites or 30 slope positions, on \( k \) axes that best minimize stress, defined as departure from monotonicity in the relationship between the distance in the original \( P \)-dimensional space and distance in the reduced \( k \)-dimensional space (McCune et al. 2002). The location of sites and slope positions in ordination space was plotted in relation to the four major overstory tree species.

We examined the relationship between fire frequency metrics, biophysical variables, and site and slope position structure/composition by fitting each fire frequency and biophysical variable as an ordination projection using vegan’s envfit function (Oksanen et al. 2015). Permutation tests were used to evaluate the statistical significance of projection fits. Tests of slope position statistical significance were constrained within sites because slope positions within sites were likely not independent sample units. The top-performing variables were overlaid on ordinations as smoothed surfaces using a thin-plate spline general additive model which allows visualization of non-linear relationships between explanatory variables and structure/composition configurations (Wood 2003, Oksanen et al. 2015).

We used non-parametric permutational multivariate analysis of variance (perMANOVA) implemented with the adonis function in R’s vegan package to build formal statistical models of relationships between forest structure/composition and fire frequency and biophysical variables. The significance of explanatory variables was computed with an \( F \)-test based on sequential sums of squares from permutations of the raw data (Anderson 2001, McArdle and Anderson 2001). Permutations to evaluate the significance of slope position explanatory variables were constrained within each site because slope positions within sites were likely not independent sample units. In addition to accounting for a nested study design, perMANOVA allowed us to test for interactions of explanatory variables.

We selected variables for perMANOVA models using manual forwards and backwards variable selection procedures. First, we tested each of the five top-performing variables identified by ordination fitting independently. The most explanatory of these variables were then added sequentially to create a full model. Variables were retained in subsequent models if they explained 10% or more of the variance associated with the forest structure/composition multivariate response. We also built a full model with all five of the top-performing variables identified by ordination. Variables were retained in subsequent models if their removal from the full model resulted in a 10% or greater decline in the explanatory power of the full model. We manually tested for interactions among all variables that were statistically significant when tested independently or when tested with other variables. We built parsimonious final models with top-performing variables,
rejecting additional variables that explained less than 10% of the structure/composition response. The 10% threshold was arbitrary, but our experience suggested that including model terms that explained less than 10% of the variance in the multivariate response significantly reduced the precision of the estimates of remaining explanatory variables.

Estimates of the effect of the explanatory variables identified using these model selection procedures were used to evaluate the influence of fire frequency and biophysical variability on the abundance of each of the four major overstory tree species recorded in plots. We bootstrapped confidence intervals for the estimated effect of each variable on each of the four major overstory species that formed the multivariate response and considered the variable to have a statistically significant effect on species abundance if confidence intervals for the estimate did not include zero.

Results

Forest groups

Between 46% and 95% of all live trees >40 cm within plots were cored. Computer-assisted quality control of cross-dating showed strong correlation between 96% of samples and a master chronology, and no better dating for the remaining samples was possible. A linear model using DBH, species, site, last annual ring, and decay class as predictor variables provided a robust estimate of the 1890 basal area of unsampled live and dead trees (\(P < 0.01, r^2 = 0.78\)).

Three statistically significant groups (AU with \(P\)-value < 0.05) were identified by cluster analysis. MRPP analysis confirmed significant structural and compositional differences between sites (\(A = 0.35, P < 0.01\)) and between slope positions (\(A = 0.48, P < 0.01\)) that fell within the three groups. The first group consisted of sites and slope positions that were dominated almost exclusively by ponderosa pine in 1890. Ponderosa pine made up 96% to 100% of site 1890 reconstructed basal area and 97% to 100% of slope position reconstructed basal area of this group.

A second group was also dominated by ponderosa pine in 1890 (71% to 88% of site basal area and 67% to 94% of slope position basal area), but also contained a modest amount of Douglas-fir or western larch, and occasionally small amounts of grand fir. The third group consisted of mixed conifer stands with a significant grand fir component in 1890 (20% to 40% of site basal area and 24% to 93% of slope position basal area). There was often considerable variation in forest structure/composition between slope positions within the same site, potentially reflecting different disturbance histories or biophysical influences on forest dynamics at relatively fine (<3 ha) scales (Fig. 5).

Fire frequency

An average of 19.1 fire-scarred trees were sampled per site (minimum = 17, maximum = 25), for an average of 2.6 fire-scarred trees sampled ha\(^{-1}\) (minimum = 1.7 trees/ha, maximum = 3.7 trees/ha). Site MFRIs ranged from 10.6 to 14.9 yr for the first ponderosa pine group, from 13.1 to 18.0 yr for the second ponderosa pine group, and from 11.8 to 21.2 yr for the mixed conifer group. Slope position MFRIs ranged from 10.6 to 16.9 yr for the first ponderosa pine group, from 11.6 to 27.0 yr for the second ponderosa pine group, and from 19.7 to 28.2 yr for the mixed conifer group (Fig. 6). At the site scale, a Kruskal–Wallis test failed to detect a statistically significant difference between MFRIs of groups derived from cluster analysis (\(P \geq 0.1\)). However, the sample size for site group membership was small and did not closely follow a chi-square distribution, an important assumption of the Kruskal–Wallis test statistic.

Neither a Kruskal–Wallis nor a Mann–Whitney–Wilcoxon test detected a statistical difference in site MFRIs between the two pine-dominated groups combined and the grand fir group (\(P \geq 0.09\)). A non-parametric permutation-based test (Fay and Shaw 2010) showed no statistical difference in MFRIs between sites belonging to different groups (\(P = 0.14\)) and a marginally statistically significant difference in MFRIs between the mixed conifer group and the combined ponderosa pine groups (\(P = 0.06\)). At the slope position scale, the Kruskal–Wallis test and permutation tests for differences between group MFRIs were statistically significant (\(P \leq 0.01\)). However, both the Kruskal–Wallis and permutation test significance statistics are potentially biased by lack of independence among slope positions.
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Fig. 5. Cluster analysis of 1890 species composition of sites and slope positions within sites. Photographs show representative plots of the three groups derived from cluster analysis. The first ponderosa pine group is “PIPO1.” The second ponderosa pine group is “PIPO2.” The mixed conifer group is “ABGR” (see Results — Forest groups). The sites column shows proportion of basal area (x-axis) in the year 1890 for each of four major overstory tree species in each of 10 sites. The column slope positions shows proportion of basal area in the year 1890 for each of the three slope positions in each site, ordered from (top to bottom) upper, middle, and lower slope positions (see Fig. 4). Note that some slope positions fell into a different forest group than other slope positions within the same site, potentially indicating fine-scale controls on structure/composition within 4- to 12-ha sites. ABGR, *Abies grandis*; PSME, *Pseudotsuga menziesii*; LAOC, *Larix occidentalis*; PIPO, *Pinus ponderosa*. 


ECOSPHERE  ❧  www.esajournals.org  ❧  November 2016  ❧  Volume 7(11)  ❧  Article e01581
Site structure and composition

A two-dimensional NMDS solution was the best fit for site structure/composition data (stress = 0.08). Fitting fire frequency and biophysical variables to the resulting ordination indicated that topographic and climatic variables best explained site structural/compositional configurations. Statistically significant ($P \leq 0.05$) explanatory variables of the site ordination as assessed with permutation tests were topographic position index (TPI), VPD, and elevation (Fig. 7).

The average height above the minimum elevation within a 300-m radius of site plots (“TPI 300”), a measure of topographic ruggedness, was fit to the site ordination because it was the best explanatory variable of a number of strongly correlated (>0.80) topographic position indexes calculated at different neighborhood distances. The maximum summer VPD variable was fit to the site ordination because it was the best of a number of strongly correlated (>0.90) VPD variables calculated. Elevation was excluded from subsequent models because it was strongly correlated with VPD ($-0.88$), which was more explanatory of the structure/composition ordination as measured with $r^2$. MFRI had marginally statistically significant explanatory power ($P = 0.08$). No other fire frequency metrics were statistically significant ($P \geq 0.25$).

TPI 300 was the most explanatory of site structure/composition variables tested individually using perMANOVA ($P < 0.01$, $r^2 = 0.55$). The most parsimonious of a wide variety of multivariate models tested was a simple additive model consisting of TPI 300 and VPD. This model explained 66% of the total site structure/composition response. Adding MFRI to this model explained an additional 6% of the total variance of the structure/composition response.

Slope position structure and composition

A two-dimensional NMDS solution was the best fit for slope position structure/composition data (stress = 0.15). Fitting fire frequency and biophysical variables to the resulting ordination indicated that soil variables were the most explanatory of slope position structural/compositional configurations (Fig. 7). Available

Fig. 6. Box and whisker plots of mean fire return intervals (MFRIs). The dark line within the box shows the mean value of MFRIs for sites/slope positions within each group. The area of the box above and below the mean line shows the spread of the first and third quartile observations. The “whiskers” show values between the first and third quartiles and the highest or lowest value within a 1.5 interquartile range. Dots indicate any remaining observations. The top panels show MFRIs calculated for sites and lower panels show MFRIs calculated for slope positions within sites. Left-hand panels show MFRIs for all three forest groups derived from cluster analysis and right-hand panels show MFRIs for the two pine groups combined (PIPO) and the grand fir (ABGR) group. ABGR, Abies grandis; PIPO, Pinus ponderosa.
soil water was the best of several statistically significant ($P \leq 0.05$) but strongly correlated (>0.78) soil variables. No other biophysical variables provided statistically significant explanations of slope position structural and compositional configurations. Available soil water was the only statistically significant explanatory variable tested individually using perMANOVA at the slope position scale ($P = 0.02, r^2 = 0.24$). No fire frequency metrics were statistically significant when tested individually using perMANOVA, but an interaction of available soil water and MFRI explained an additional 11% of the total variance associated with slope position forest structure/composition response.

**Species composition**

The top-performing fire frequency and biophysical variables tested with perMANOVA had different influences on the abundance of overstory tree species (Fig. 8). At the site scale, more rugged and variable terrain as measured by TPI was associated with a decrease in ponderosa pine basal area relative to other species and an increase in Douglas-fir and grand fir basal area. An increase in VPD at the site scale was associated with decreased grand fir and Douglas-fir basal area. At the within-site slope position scale, an increase in available soil water was associated with a decrease in ponderosa pine basal area and an increase in grand fir and western larch basal area. An increase in MFRI (less frequent fire) at the slope position scale was associated with a decrease in ponderosa pine and Douglas-fir basal area.

**Discussion**

**Drivers of forest structural and compositional variation**

This study documents less variation in historical fire frequency than anticipated by either ecological theory or recent syntheses of our knowledge of inland Pacific Northwest forest dynamics (Keane et al. 1990, Agee 1996, Brown et al. 2004, Stine et al. 2014). Very different forest structural and compositional configurations were possible within the same general range of fire frequencies reconstructed in forests of the southern Blue Mountains in the 18th and 19th centuries (Fig. 9).
Our dendrochronology methods created the sharpest contrast possible between fire frequency and forest structure/composition in the southern Blue Mountains and it is unlikely that different methods for calculating fire return intervals would show a stronger influence of fire frequency. Calculating MFRIs at a smaller spatial scale than we attempted is not feasible because old trees that record historical fires are not always available in numbers sufficient to reconstruct fire histories at scales smaller than the slope positions utilized in this study. Calculating MFRIs at scales larger than our 4- to 12-ha study sites would result in shorter MFRIs and less variation in MFRIs between forest types than we report in this study. Including fires that were not recorded by more than one tree in fire return interval calculations decreased MFRIs in the ponderosa pine groups by 0% to 6% and decreased MFRIs in the grand fir group by between 4% and 15%, further reducing the ability to detect an influence of fire frequency on different forest structural and compositional configurations.

A larger fire frequency and forest structure data set might provide evidence of subtle fire frequency thresholds that modulated historical forest structure and composition. However, the multivariate statistical analysis presented here demonstrates that the influence of fire frequency on tree growth and establishment is less generalizable than the influence of edaphic and climatic variables. The very different structural and compositional configurations reconstructed at the end of the 19th century are more reflective of edaphic and climatic limits on plant growth than differences in fire frequency. Fire, like herbivory, was a ubiquitous and relatively uniform influence whose effects on southern Blues forest structure and composition were entrained by biophysical heterogeneity.

**Influence of scale**

Biophysical heterogeneity and fire frequency influence forest structure and composition at different spatial scales. More rugged and uneven terrain as measured with TPI 300 was associated with an increased abundance of grand fir and Douglas-fir relative to ponderosa pine at the site scale, possibly because more variable topography at 4- to 12-ha scales results in a higher incidence of microclimatic or edaphic conditions suitable for the persistence of fir. At smaller spatial scales, an increase in available soil water was associated with an increased abundance of grand fir and western larch, species that are less drought tolerant than ponderosa pine (Jackson and Spomer 1979, Niinemets and Valladares 2006, Ganey and Vojta 2011). The interactive influence of fire frequency and available soil water at the within-site slope position scale may indicate that frequent surface fire only threatens the persistence of fire-intolerant species in the absence of water resources adequate to promote resistance to the synergistic effects of fire, drought, and insect attack.

The major difference between inland Pacific Northwest forests and the mesic forests of the western Cascades and Coast Ranges may be the scale at which fire disturbance influences forest structure (Ohmann and Spies 1998). In mesic forests with abundant water resources, periodic fire disturbance coupled to decadal and centennial scale climate variability synchronizes forest structure over relatively large areas (Tepley et al.
2013), whereas in drier landscapes the effects of frequent fire are modulated by spatial variability in water availability resulting in fine-scale successional mosaics. While coarse-grain fire-driven patch dynamics are characteristic of mesic forests, fine-grained succession associated with frequent fire was likely characteristic of both dry ponderosa pine-dominated forests and the moister mixed conifer forests embedded within the broader dry inland Pacific Northwest landscape (Franklin et al. 2002).

Management implications

Although emulating historical disturbance is recommended as a technique to restore resilient forest conditions (Brown et al. 2004, O’Hara 2004, Spies et al. 2006, Franklin and Johnson 2012), this study shows that managers may be better informed by stand-scale data about topography, soils, and climate than detailed fire histories. While pre-fire exclusion late-seral, fire-intolerant forest structure was found across a broad range of fire frequencies, no fire-intolerant species established prior to 1890 were found on sites with less than 90 mm of modeled available soil water, nor was pre-1890 fire-intolerant species basal area reconstructed on sites with modeled maximum summer VPD in excess of 29 hPa.

Using these soil water and climate thresholds to parameterize future management may be problematic for several reasons. Tree ring reconstructions of 600 yr of summer temperature and precipitation in the southern Blues show that the historical period considered in this study—the end of the 19th century—was cooler and moister than in any period over at least 300 yr (Youngblood et al. 2004, Garfin and Hughes 1996; J. D. Johnston, unpublished data). Although this study documents frequent fire across a wide variety of forest structural and compositional configurations, fire frequency at most sites declined somewhat from the late 1700s until the 1890s when fire had largely ceased (Johnston 2016). The extent of fire- and drought-intolerant species documented by this study in the late 1800s may reflect anomalous climatic and disturbance conditions unlikely to be encountered by managers in the future.

Most climate change modeling efforts project temperature increases between 2.5° and 3.5°C in the inland Pacific Northwest over the next 50 yr. Future precipitation projections are far less certain, with estimated changes ranging from −10% to +20% over the next 50 yr. Many models predict higher precipitation in the winter and decreased precipitation in the summer months when water availability limits plant growth and establishment (Mote and Salathe 2010). Given the likelihood of substantial increases in temperature and potential changes in precipitation patterns, retaining a lower proportion of late-seral drought-intolerant species than were historically present may be appropriate (Littell et al. 2010, Coops and Waring 2011, Wimberly and Liu 2014). Experimentation and long-term monitoring of restoration treatments will likely be necessary for successful climate change adaptation.

Conclusions

There is little evidence that differences in historical fire frequency among randomly located
sites in the southern Blue Mountains strongly influenced structural and compositional characteristics. Contrary to the expectations of the literature, sites with very different inherent productivity characteristics all historically experienced frequent fire. The abundance of late-seral, fire-intolerant tree structure appears more closely related to biophysical controls on tree growth and establishment than fire frequency. Forest structure and composition varies at fine spatial scales, likely reflecting differences in available soil water and interactions between water availability and fire frequency. Management that emulates the effects of frequent fire is appropriate in a wide range of forest types in the southern Blue Mountains, although basing compositional targets on late 19th century forest structure may not be appropriate given changing climate.

**Acknowledgments**

Emily Comfort, Garrett Meigs, David Peterson, and two anonymous reviewers provided helpful comments on draft manuscripts. Mike Vernon, Virginia Bailey, and David Gardelius provided laboratory assistance. Tim Lillebo provided important insights into the terrain and ecology of the southern Blue Mountains. Funding was provided by the Northwest Advanced Renewables Alliance.

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