Mixed-severity fire in lodgepole-dominated forests: Are historical regimes sustainable on Oregon's Pumice Plateau, USA?

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Abstract: In parts of central Oregon, coarse-textured pumice substrates limit forest composition to low-density lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) with scattered ponderosa pine *(Pinus ponderosa* Lawson & C. Lawson) and a shrub understory dominated by antelope bitterbrush (*Purshia tridentata* (Pursh) DC.). We reconstructed the historical fire regime from tree rings and simulated fire behavior over 783 hectares of this forest type. For centuries (1650-1900), extensive mixed-severity fires occurred every 26 to 82 years, creating a multi-aged forest and shrub mosaic. Simulation modeling suggests that the historical mix of surface and passive crown fire were primarily driven by shrub biomass and wind speed. However, a century of fire exclusion has reduced the potential for the high-severity patches of fire that were common historically, likely by reducing bitterbrush cover, the primary ladder fuel. This reduced shrub cover is likely to persist until fire or insects create new canopy gaps. Crown fire potential may increase even with current fuel loadings if the climate predicted for mid-century lowers fuel moistures, but only under rare extreme winds. This study expands our emerging understanding of complexity in the disturbance dynamics of lodgepole pine across its broad North American range.

Introduction

Lodgepole pine forests *(Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) are broadly distributed in western North America and historically sustained a range of fire regimes (Loope and Gruell 1973, Schoennagel et al. 2008, Amoroso et al. 2011). While these fire regimes have been well documented at the high-severity end of this range (e.g., in portions the Greater Yellowstone Area and parts of the northern Rocky Mountains), they are not as well documented in mixed-severity systems (Pierce and Taylor 2011), such as central Oregon's Pumice Plateau Ecoregion. This region covers over a million hectares in the south-central portion of the state and is characterized by thick deposits of pumice and ash that combine with generally flat topography to favor lodgepole pine, but restrict the establishment of other overstory and understory species (Geist and Cochran 1991, Thorson et al. 2003, Simpson 2007).

A lack of surface fuels historically limited fire spread in some pure lodgepole forests in central Oregon (Geiszler et al. 1980, Stuart 1983, Gara et al. 1985). Tree-ring reconstructions in these forests suggest that their multi-aged tree mosaic resulted primarily from outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkin), similar to one that caused widespread lodgepole mortality in this region in the 1980s (Preisler et al. 2012). However, lodgepole forests on pumice flats in central Oregon are more commonly not fuel limited, but rather have shrub understories dominated by antelope bitterbrush (*Purshia tridentata* (Pursh) DC.; hereafter bitterbrush), a shade-intolerant, highly flammable woody shrub that acts as a ladder fuel and facilitates passive crown fire (i.e., torching of individual trees or small patches of trees; Rice 1983, Busse and Riegel 2009). Bitterbrush is the primary understory fuel in these forests because the coarse-textured, nutrient-poor pumice substrate limits the growth of grass and herbaceous fuels (Geist and Cochran 1991). The presence of fire scars and a general lack of cone serotiny (Mowat 1960) also suggest that mixed-severity fires may have influenced the structure and demography of these forests historically (Keeley and Zedler 1998).

The behavior of mixed-severity fires is driven by a complex mix of fuels and weather, with the relative importance of these two factors varying through time and across space (Halofsky et al. 2011). Both fuels and weather varied in many central Oregon lodgepole forests in the past. Although fire initially reduces the abundance and biomass of bitterbrush it also stimulates regeneration and populations can recover to pre-fire levels via a combination of sprouting and germination from seed caches (Ruha et al. 1996), especially where fire creates canopy gaps (Busse and Riegel 2009). Individuals can be long lived, but bitterbrush productivity and recruitment decline with increasing shrub age as well as increasing tree canopy cover so that without disturbance bitterbrush becomes senescent and decadent (Clements and Young 1997). Further, post-fire resprouting is most successful when individuals of this species are young (5-40 years; Busse et al. 2000), suggesting that old bitterbrush individuals may be less resilient to fire when they grow in fire-excluded stands than when they grow in stands with frequent fire.

In the interior Pacific Northwest, including central Oregon, forest fires were excluded by land-use changes beginning in the late 19th century combined with a relatively wet climate early in the 20th century (Heyerdahl et al. 2008). The effects of this fire exclusion have been documented for some forest types in the region, but not others. For example, the structure and composition of many dry mixed-conifer forests has been significantly altered (Merschel 2012, Hagmann et al. 2013). However, the effects of fire exclusion on lodgepole-dominated forests have not been well-characterized. For example, the few existing studies of the long-term response of bitterbrush to fire have focused on ponderosa pine forests *(Pinus ponderosa* Lawson & C. Lawson) that differ from lodgepole-dominated sites in composition, climatic regime, and substrate (Ruha et al. 1996, Busse et al. 2000, Busse and Riegel 2009). Unlike ecosystems in which fire exclusion has likely increased the risk of widespread crown fire via increased fuel loads, such as central Oregon's dry mixed-conifer forests (Merschel 2012, Hagmann et al. 2013), fire exclusion in central Oregon's lodgepole-dominated forests may instead have reduced the potential for crown fire by reducing bitterbrush, the primary understory fuel facilitating fire spread in this system.

Future climate change may further alter fire and forest dynamics in this region, with important implications for land management (Loehman et al. 2013).Anticipating the future requires an understanding of long-term drivers of forest and fire dynamics. The unique character of central Oregon’s lodgepole-dominated forests means that we cannot extrapolate historical fire regimes from lodgepole forests elsewhere. Furthermore, our documentary knowledge of wildfire in this region is currently limited to written records that post-date late 19th-century fire exclusion. Fortunately, tree rings can be used in central Oregon's lodgepole-dominated forests to infer the historical fire regimes that occurred under a range of climatic conditions and in the absence of landscape-scale management activities such as logging and domestic livestock grazing. These historical fire regimes can in turn be used to corroborate simulations of past fire behavior, increasing our confidence in the ability of models to simulate potential current and future fire behavior under a range of fuel and weather scenarios.

Our first objective was to characterize historical fire regimes and their spatial complexity in lodgepole pine-dominated forests in central Oregon's Pumice Plateau Ecoregion by sampling fire scars and tree demography across a grid of plots. Our second objective was to infer whether fire exclusion has changed current fire behavior relative to the behavior we inferred from tree rings, and to assess the relative importance of fuels and weather as drivers of fire severity. To do this, we used a fire behavior model to simulate both historical and current fire behavior. Our third objective was to use the same model to simulate the behavior of future fires and infer whether projected climate change could trigger a shift in fire regimes.

Methods

Study area

The study area is on the Bend-Fort Rock Ranger District of the Deschutes National Forest, 47 km southeast of Bend, Oregon, USA (43° 43.9' N, -120° 56.6' W; Figure 1) at an elevation of 1,485 m (range 1,461 to 1,510 m). We identified potential sampling sites dominated by lodgepole that had no recent fires (which can destroy the tree-ring record of old fires), and road access, but no record or evidence of extensive logging (such as abundant stumps), and made a final selection during field reconnaissance. In Bend (elevation 1,108 m) mean annual precipitation averages 25 cm, only 12% of which falls in summer (July-September). Monthly temperatures range from an average minimum of -6°C in January to an average maximum of 28°C in July (1914-2012; Western Regional Climate Center 2013).

The site we selected (Potholes), lies on a deep layer of coarse pumice that was ejected from Newberry Crater ~1,300 years ago and overlays the much older Mazama ash (Figure 1; MacLeod et al. 1995). The pumice is nutrient poor, which limits grass growth (Geist and Cochran 1991). It also has low thermal conductivity and slopes that rarely exceed 10% so that growing season radiation frosts are common (Geist and Cochran 1991); such frosts typically occur on clear, windless nights when the ground surface is chilled below the dew point of the overlying air. About 3 km northeast of Potholes and at a similar elevation, temperatures were below freezing 15% of summer days (Tepee Draw Remote Automated Weather Station, July-September, 2004-2012; Western Regional Climate Center 2013). Lodgepole pine is resistant to damage from these frosts and so dominates areas where they are common, whereas ponderosa pine is not resistant and is thus limited to slight rises and other areas above the frost line (Geist and Cochran 1991).

Central Oregon has a long history of Native American land use, including fire, but any intentional burning was likely curtailed by the late 1800s when native people were largely confined to reservations (Brogan 1964, MacLeod et al. 1995). In the early 1800s, scattered explorers and miners passed through central Oregon, followed by Euro-American settlers with domestic livestock in the early 1860s (Brogan 1964). Sheep and cattle were soon abundant (Wentworth 1948, Oliphant 1968) and, along with deer, likely browsed bitterbrush (Blaisdell and Mueggler 1956). In 1886, George Millican homesteaded north of Pine Mountain (Figure 1) and the surrounding area was densely settled by the early twentieth century (Brogan 1964). Fire atlas records compiled by the Pacific Northwest Region and Fire and Aviation Management, U.S. Forest Service, show that only a small portion (9%) of the Lodgepole Pine-Dry plant association group near Potholes burned during the past century (1908-2008; Volland 1988; Figure 1c).

Forest composition, structure and demography

We sampled 30 plots over 793 ha on a grid with 500 m spacing (Figure 1e). At the plots, we visually estimated total tree cover and recorded plot location and elevation. We sampled 30 to 32 live or dead trees ≥20 cm diameter at breast height (1.3 m, DBH) and closest to plot center from which we could remove intact wood, and recorded tree species, DBH (diameter at cut height for stumps), and canopy base height. From live trees, we removed increment cores at ~15 cm height, aiming for a field-estimated maximum of 10 rings from pith; we removed no more than four cores per tree and retained the one closest to pith. From intact dead trees, we used a chain saw to remove a partial cross section generally including pith from ~15 cm height. For the remaining trees ≥20 cm DBH, i.e., those lacking intact wood, we recorded species and diameter.

We sanded all wood samples until the cell structure was visible with a binocular microscope. We assigned calendar years to tree rings by visual crossdating using ring-width chronologies we developed from trees in our plots along with an existing chronology (Pohl et al. 2002), assisted occasionally by cross-correlation of measured ring-width series.

We estimated tree recruitment dates from pith dates at sampling height. For samples that did not intersect pith (76%), we estimated years to pith geometrically (5 ± 4 years, average ± standard deviation). We did not correct for age at sampling height, but 274 lodgepole growing on pumice near Potholes required fewer than 7 years to reach 34 cm height (Stuart 1983). We could not estimate pith dates for some trees (15%) and so excluded them from analyses requiring recruitment dates (e.g., identification of cohorts), but retained them in those that did not (e.g., current tree density). We determined death dates for stumps, logs, and snags with intact outer rings.

We identified the dates of cohort initiation in our plots when five or more trees recruited within 20 years, preceded by at least 30 years without recruitment (Figure 2). We identified death cohorts when five or more trees (excluding stumps, i.e., trees cut by humans) died in the same year.

We estimated current tree density in our plots by dividing the number of trees alive in 2009 by plot area (area of plot = $\pi \times$ [distance from plot center to farthest tree sampled]^2). The distance of the farthest tree from plot center varied among plots from 16 to 39 m (23 ± 5 m) resulting in plots that varied from 0.1 to 0.5 ha (0.2 ± 0.1 ha).

To describe current fuel loadings at each plot, we characterized understory fuels by averaging estimates of fuel loadings from four, 1-m^2 microplots placed 4.5 m in the cardinal directions from plot center. In each microplot, we used calibrated photographs to visually estimate the loadings of woody fuels (particles with diameters of <1 cm, 1 to 2.5 cm, and 2.5 to 7 cm, equivalent to 1-, 10-, and 100-hour fuels, respectively) and the biomass of shrubs and herbs (Keane and Dickinson 2007). We measured the depth of litter and duff at two corners of each microplot.

Historical fire regime

We removed fire-scarred partial cross sections from up to 7 live or dead trees within 80 m of plot center (~2 ha search area), but fire-scarred trees did not occur in all plots. To assist in mapping fire extent, we also sampled fire-scarred trees that we encountered between plots. Although mountain pine beetle scarring of ponderosa pine has not been documented, these insects can scar lodgepole pine (Stuart et al. 1983) so we sampled only scars that were basal, lacked bark on the scar face, and were charred if the tree had been scarred more than once. We sanded and crossdated these samples as described above and excluded samples we could not crossdate from further analyses.

We identified the calendar year of fire occurrence as the date of the tree ring in which a scar formed. In this region the season of cambial dormancy (the period corresponding to the ring boundary) spans two calendar years, from cessation of cambial growth in late summer or fall of one year (first year) until it resumes in spring of the following year (second year). We assigned ring-boundary scars to the preceding calendar year (first year) because most modern fires in central Oregon burn late in the cambial growing season (Short 2013).

We mapped the historical fire regime and its spatial complexity by combining fire-scar and cohort dates during the period when at least 25% of the plots had living trees, but preceding recent fire exclusion (1650-1900). We excluded fire years there were recorded only on a single tree (4 scars or 3% of scars, eliminated) because such scars may result from non-fire injuries. If the earliest recruitment date in a cohort followed a fire-scar date at the site by <15 years, we assumed the cohort established in response to the same fire that created the scars. We estimated plot-composite fire intervals as the years between fires in plots.

Simulated fire behavior

We simulated historical, current, and future fire behavior at Potholes using FlamMap (Finney 2006), a landscape-scale fire behavior mapping and analysis program. We implemented a factorial experiment with three factors, each with two levels: historical and current surface fuels, current and future weather, and two wind speeds derived from modern weather records. We input surface fuels to FlamMap in the form of a raster data layer of "fire behavior fuel models" mapped by LANDFIRE (2010 refresh, lf_1.2.0, 30-m resolution, Rollins 2009). Fire behavior fuel models (hereafter "fuel models") are a classified set of fuel bed characteristics that are used by many fire behavior and fire spread models, including FlamMap (Scott and Burgan 2005). Each fuel model describes fuel characteristics, including fuel load by size class and category (live or dead), live woody, live herbaceous, and dead 1-hr surface area to volume ratio, fuelbed depth, dead fuel extinction moisture content, and the heat content of live and dead fuels. LANDFIRE has classified most of the current fuels at Potholes into one of three fuel models: (1) moderate load, dry climate grass shrub (GS2, 42%), (2) high load conifer litter (TL5, 28%), or (3) moderate load broadleaf litter (TL6, 18%). In these fuel models, the primary fuels are grass and shrubs (GS2), conifer litter (TL5), or broadleaf litter (TL6), and live shrub fuel loads are very low, consistent with our field estimates of current fuel loads. We input this layer to FlamMap as "current fuels". We created an alternative layer (hereafter "historical fuels") to explore whether the relatively high cover of bitterbrush that we inferred for historical forests may have facilitated a mixed-severity fire regime in the past. To recreate historical fuels we re-assigned all GS2 pixels at Potholes to fuel model TU5, a very high load, dry climate timber shrub model in which shrubs, small tree understory, and forest litter are the primary fuels that facilitate fire spread. Most of the original GS2 pixels (90%) had moderate tree cover (25 to 45% canopy cover), indicating an open forest structure. In this re-assignment from GS2 to TU5 we retained this moderate cover, as well as other overstory characteristics including canopy base heights of 1.3 to 2.0 meters and canopy bulk densities of 0.05 to 0.09 $kg \cdot m^{-3}$.

Weather (temperature and precipitation) influences fire behavior in FlamMap via its effect on fuel moistures. We tested the effects of fuel moistures derived from current climate and predicted future climate on fire behavior, using August weather because more modern fires initiated in this month than in other months in the eastern Bend-Fort Rock Ranger District (30% of 1,322 fires, 1992-2011, Short 2013). We obtained current weather (2004-2012) from observed daily minimum, maximum, and mean temperature, and total precipitation from the Tepee Draw Remote Automated Weather Station (Western Regional Climate Center 2013). We modeled future weather (2039-2050) by offsetting the Tepee Draw daily observations by monthly deltas that we obtained from an ensemble average of regionally downscaled global climate models (~6 km^2 resolution) derived from the Coupled Model Intercomparison Project (CMIP3) and driven by the Intergovernmental Panel on Climate Change AR4 A1B emissions scenario (Littell et al. 2011). We used Fire Family Plus (Main et al. 1990) to calculate mean fuel moistures for current and future weatherand to compute the 50^{th} and 99^{th} percentile peak wind gust speeds (2004-2012) at 6 m height (6 and 11 $m \cdot s^{-1}$, respectively, equivalent to 14 and 25 miles per hour at 20 feet; Table 1). Peak gusts are the maximum wind speeds passing a sensor within an observation window, important for assessing rate of spread, fire intensity, and flame lengths. We chose these two percentiles to represent mean and extreme wind conditions.

We produced eight FlamMap simulations using all combinations of fuels (historical or current fire behavior fuel models), weather (current or future fuel moistures), and wind speed (mean or extreme). For all simulations, we held constant the other FlamMap parameters (wind azimuth of 270 degrees, 100% foliar moisture content, and method of crown fire calculation; Scott and Reinhardt 2001) and other spatial data layers (elevation, slope, aspect, canopy cover, canopy base height, and canopy bulk density, acquired from LANDFIRE). We report fire behavior as the percentage of the simulation landscape that was assigned to surface fire, passive crown fire, and active crown fire. Passive crown fire, or torching, burns an individual or small group of trees, but does not move continuously through the canopy (Scott and Reinhardt 2001) whereas active crown fire does move continuously through the canopy.

Results

Forest composition, structure, and demography

All 30 plots at Potholes are dominated by lodgepole pine (92% of 909 trees), but ponderosa pine occurred in nearly half of them (13 plots; Figure S1). Lodgepole pine occurred at a much higher density than ponderosa pine (255 ± 67 trees·ha^{-1} versus 64 ± 68 trees·ha^{-1}, respectively). Tree cover was sparse in all plots, with all but one having <50% canopy cover and about half (16 plots) with <30% canopy cover.

Most sampled trees were alive (83%); the rest were logs (12%), snags (5%), or stumps (<1%). The pith dates we estimated from 752 of these live or dead trees ranged from 1624 to 1962. Logs and snags were widely distributed; they occurred in 63% of plots and were mostly lodgepole that died between 1980 and 1989 (63 of 74 trees). We tallied 174 undatable trees (average 6 per plot; range 1 to 20 trees), ranging from 20 to 94 cm in diameter. Most were lodgepole (79%) logs (87%) that were not charred (90%).

We identified 21 cohort initiation dates (Figure 4a). All but one cohort initiated between 1822 and 1888; the remaining cohort initiated in 1752. They occurred in two-thirds of our plots, most of which had a single cohort except for one plot with two (Figure 2d). We identified two death cohorts in 1988, during a widespread outbreak of mountain pine beetles in central Oregon (Preisler et al. 2012).

Shrubs were common in the understory but forbs and gramminoids were sparse (Figure 1g and h). Bitterbrush was the only shrub that occurred in every plot, mostly with cover exceeding 10%. Mountain big sagebrush (*Artemisia tridentata* Nutt. *ssp. vaseyana* (Rydb.) Beetle) and wax currant (*Ribes cereum* Douglas) occurred in about half the plots, mostly covering less than 10%. Rubber or yellow rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird; *Chrysothamnus viscidiflorus* (Hook.) Nutt., respectively) also occurred in a few plots and covered <10% cover. Buckwheat (*Eriogonum* sp.) and blue eyed Mary (*Collinsia* sp.) occurred in more than half the plots. Grasses occurred in only 5 plots, but were not identified to species.

Downed woody fuel loadings were low, averaging 6 ± 5 Mg·ha^{-1} per plot for the three size classes combined (<1 to 7 cm). The highest shrub biomass we measured occurred at plots with the lowest tree densities, although overall the relationship between shrub biomass and tree density was not strong (r^2=0.2; Figure 3). Overall shrub and herb biomass were low (<1 Mg·ha^{-1}) compared to understory biomass in other bitterbrush habitat types in Oregon (Busse and Riegel 2009). Litter and duff were shallow (2 ± 3 cm and 3 ± 2 cm, respectively). Fuels were patchy; many of the 120 microplots contained no shrubs or herbs (53% and 78%, respectively) and some contained no litter or duff (16% and 24%, respectively). We observed similarly patchy surface fuel loads between plots (Figure 1g and h).

Historical fire regime

We removed one to four partial cross sections from 69 fire-scarred trees and crossdated samples from 56 of them. These included 44 trees that occurred in half the plots (Figure 4a) plus 12 trees we encountered between plots (Figure 4b). Most crossdated trees were ponderosa (37 trees) and the rest lodgepole. Most were dead when sampled (41% logs and 32% stumps). Of the 144 fire scars, those from ponderosa ranged from 1580 to 1877, but those from lodgepole were limited to either 1819 or 1877, synchronous with widespread fire-scar dates on ponderosa (Supplementary Material). The two most recent fires (1819 and 1877) likely burned more than the 783 ha we sampled because they intersected all four boundaries of the grid (Figure 5).

During the analysis period (1650-1900), we reconstructed 6 fires from 129 fire scars and 19 of the cohort initiation dates (Figure 4a; Figure 5). All but two of the cohorts satisfied our criteria for assignment to fire-scar dates in 1750, 1819, or 1877 (Figure 4a). From these 6 fires, we computed 34 plot-composite fire intervals of variable length (26-82 years; Figure 6). We crossdated fire scars from 5 of these same 6 fires (all but 1700) from the trees we sampled between plots (Figure 4b). There was no consistent relationship between widespread fire dates and interannual variation in PDSI, rather cohorts initiated under a variety of drought conditions (Cook et al. 2004; Figure 4e).

The tree-recruitment dates, fire-scar dates, and associated metadata we collected at Potholes 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).

Simulated fire behavior

FlamMap simulations suggest that fuel loadings and wind speed are the primary drivers of fire behavior at Potholes, while fuel moistures had less influence on crown fire activity except under extreme winds, at least for the range of moistures we simulated. Simulations using historical fuels included some passive crown fire (37 to 39% of the simulation area regardless of fuel moisture) with the greatest area of passive crown fire occurring under extreme wind speeds (57% of the simulation area; Figure 7a-d). In contrast, simulations using current fuels were dominated by surface fire (90-92% of the simulation area; Figure 7e-g) except under extreme wind speeds and low fuel moistures when passive crown fires dominated and surface fire was predicted for only 35% of the simulation area (Figure 7h). Active crown fire was very rare in all eight scenarios, assigned to less than 2% of the simulation area regardless of scenario.

In all scenarios dominated by passive crown fire (Figure 7a-d and h), the spread of fire from the surface to the canopy was facilitated by flame lengths that exceeded the majority of canopy base heights (1.3 to 2.0 m; the lowest height above the ground where there is sufficient canopy fuel to propagate fire vertically, Scott and Reinhardt 2001), whereas the flame lengths associated with surface fire-dominated scenarios (Figure 7e-g) were below that canopy base height. In the absence of the abundant shrub fuels that we assume occurred historically, flame lengths of sufficient height to carry fire into the canopy occurred only with extreme winds.

The fire behavior we simulated with historical fuels is consistent with our tree-ring reconstructions of patchy mixed-severity fire (Figure 5). Furthermore, the area weighted average fire behavior we simulated using historical fuels under high winds (flame length 4 m, rate of spread 5 $m \cdot min^{-1}$, and heat per unit area 800 $kW \cdot m$) are consistent with the behavior of prescribed fires in lodgepole forests with a mature bitterbrush understory elsewhere in central Oregon (Rice 1983).

Discussion

Fire historically mixed in severity

Several lines of evidence support our inference that Potholes historically sustained extensive mixed-severity fires. Although widespread synchrony in fire-scar dates during several years suggests extensive low-severity fires, these scars were also synchronous with cohorts of tree recruitment, suggesting that individual fires included patches of both high- and low-severity fire. Our inference is also consistent with the general lack of serotinous lodgepole cones in central Oregon (Mowat 1960) because extensive high-severity fires select for cone serotiny in pines (Keeley and Zedler 1998). Our fire behavior simulations also support our inference that active crown fire was not common here, but rather that patches of high-severity fire occurred when and where shrub cover and winds were sufficient to carry fire into the canopy. Active, independent crown fire was not a likely fire behavior because the pumice substrate limits tree density at Potholes.

Mixed-severity fires at Potholes were likely limited more by fuels than weather. Despite a lack of topographic complexity, fires we simulated with the abundant shrub understory we infer was present historically produced a mosaic of crown and surface fire under a range of fuel moisture and wind conditions. In contrast, fires we simulated with the sparse shrub understories present today primarily produced surface fire, except under extreme wind. This suggests that mixed-severity fire at Potholes depended on sufficient shrub fuels to both carry fire across the site and torch patches of trees. Historically, fires occurred every 26 to 82 years; these intervals were long enough for bitterbrush to regain sufficient cover and height to facilitate fire spread across the site and into the canopy in a mosaic pattern. In turn, this mosaic pattern would have allowed for post-fire regeneration of bitterbrush by creating canopy gaps while maintaining some unburned plants as seed sources and stimulating vigorous sprouting from undamaged portions of surviving plants (Blaisdell and Mueggler 1956, Ruha et al. 1996, Busse and Riegel 2009). Furthermore, the fires we reconstructed from tree rings at Potholes did not consistently occur during years with warm-dry summers (Figure 4e), nor were they synchronous with climatically driven years of widespread fire across the region (Heyerdahl et al. 2008). Our work supports findings about the drivers of mixed-severity fire regimes elsewhere in the region (Halofsky et al. 2011).

Given the strong influence of bitterbrush on fire at Potholes, we hypothesize that the historical fire regime at our site was similar to that of the other lodgepole-dominated forests with scattered ponderosa, bitterbrush understories, and discontinuous surface fuels that are common in central Oregon's Pumice Plateau Ecoregion, e.g., in the Ponderosa Pine/Bitterbrush plant association in which ponderosa and lodgepole pine occur in varying amounts (Simpson 2007). However, the historical fire regime we reconstructed at Potholes differs from that of pure lodgepole forests elsewhere in central Oregon where fires of any severity were limited by very low loadings of surface fuels (Geiszler et al. 1980, Stuart 1983, Gara et al. 1985). These forests are similar in elevation (1,490 versus 1,800 m) and climate to Potholes, but grow on ash substrates that support only very low loadings of shrubs and the other surface fuels that carry fire so that mountain pine beetles were likely the primary control of forest structure (Geiszler et al. 1980, Stuart 1983, Gara et al. 1985).

Future fire at Potholes not likely to be mixed in severity given current fuels

Our fire behavior simulations suggest that loadings of modern understory fuels are insufficient to spread the mix of surface and crown fire that occurred historically at Potholes. Reestablishment of such a mixed-severity fire regime is not likely to occur here today unless bitterbrush cover increases; however, bitterbrush's ecophysiological requirements suggest that shrub cover will not increase in the absence of disturbances that create canopy gaps, such as fire or mountain pine beetles. Overstory thinning and prescribed fire have been suggested as wildfire surrogates that can increase bitterbrush cover, particularly if mechanical damage to plants can be limited and slash fuels that can increase burn severity are removed (McConnell and Smith 1970, Ayers et al. 1999). Our simulations suggest that the lower fuel moistures calculated for predicted mid-century climate may allow for a mix of surface and crown fire behavior if fires ignite under high winds and fuel loads have not decreased further. However, regeneration of bitterbrush following fire depends on additional factors such as high soil moisture content, sufficient pre- and post-fire flower and seed production, plant vigor, photosynthetic uptake, and carbohydrate reserves, all of which might be negatively affected by a warmer, drier future climate (Rice 1983, Ayers et al. 1999, Busse et al. 2000, Loik 2007). Thus, active management may be required to perpetuate resilient mixed-severity fire regimes in lodgepole-dominated forests with bitterbrush understories.

Coupling simulation modeling with tree ring reconstructions improves inferences about the past

The fire behavior and fuel models we used approximate natural phenomena, but are inexact because they are built using mathematical models that make simplifying assumptions about complex systems. Further, fire behavior calculations are dependent on model inputs, which can be simplified representations of actual landscape characteristics and may thus be inaccurate. Consequently, simulation modeling alone may not capture the complex spatial and temporal patterns of fire behavior and effects characteristic of mixed-severity regimes. Coupling modeling with tree ring reconstructions of fire history can provide a more complete picture of fire-driven changes in forest structure. For example, FlamMap models fire behavior at the flaming front, but not the residual combustion that occurs after the flaming front has passed (Scott and Burgan 2005), but our tree ring reconstructions capture mortality associated with both torching and residual smoldering. The standard Scott and Burgan (2005) fire behavior fuel models used in this analysis represent fuel beds using a limited set of fuel characteristics that cannot capture the complexity or heterogeneity of actual fuel beds in terms of depth, heat content of fuels, fuel moisture, and fuel loads, and assume homogeneity and continuity of fuels in horizontal and vertical directions. However, corroboration between the fire behavior modeled in FlamMap using reconstructed historical fuels, and the historical fire effects we reconstructed from tree rings gives us confidence that we have adequately represented conditions at Potholes in our model inputs.

The tree-ring record of historical fire at Potholes is robust

Our strongest tree-ring evidence of mixed-severity fire is limited to the 1800s, but we suggest that fires were also mixed in severity for at least several hundred years before that. The earliest lodgepole pine at Potholes recruited in 1745, although the majority recruited in the early 1800s. Lodgepole's ability to withstand frequent radiation frosts means that it dominates coarse pumice substrates in this region (Geist and Cochran 1991). Therefore, it is likely that cohorts of this species established episodically at Potholes in response to the death of older trees by fire in the 1600s and 1700s, but the evidence of these cohorts was destroyed by decay and subsequent fires. Any lodgepole killed by fire at our site would have died at least 130 years ago and are unlikely to still be intact; lodgepole snags on nearby pumice soils fell rapidly and decayed within 60 years (Busse 1994; Mitchell and Preisler 1998).

Lodgepole trees scarred by fire are common elsewhere in western North America (e.g., Loope and Gruell 1973, Amoroso et al. 2011). This species can also be scarred when mountain pine beetles attack only one side of a tree, killing a strip of cambium (Stuart et al. 1983), but we have strong evidence that the lodgepole scars at Potholes were created by fire. All the lodgepole scars we crossdated were synchronous with scars on ponderosa created by widespread fires in 1819 and 1877, all were basal, and all trees with more than one scar were charred. Several criteria have been proposed to distinguish lodgepole scars created by mountain pine beetle strip kill from those created by fire (Stuart et al. 1983). Consistent with these criteria, the fire-scarred lodgepole at Potholes lacked both multiple areas of cambial kill around the circumference of a single ring and bark retained on the scar face. They also did not span a narrow cluster of scar dates, but were annually synchronous. However, we found that some of these criteria apply to both agents of scarring. For example, more than half the fire-scarred sections we removed from lodgepole pine (60%) had insect galleries on the scar face and bluestain. Five were logs and snags that were scarred by fire in the 1800s and subsequently died in the 1980s during the last widespread outbreak of mountain pine beetles in the region, suggesting that the bluestain may have been introduced after the tree was scarred by fire. Strip-kill scars on lodgepole are thought to occur mostly on the north and east sides of tree boles and sometimes spiral around the bole (Stuart et al. 1983), but some of the fire-scarred lodgepole we sampled also had these characteristics.

The majority of cohorts at Potholes appear to have recruited in response to fire. However, we may have failed to identify some cohorts because our criteria were conservative. At a few plots, for example, many lodgepole were recruited within a 5-year period immediately following the 1819 or 1877 fires, but were not identified as a cohort because this period was not preceded by a 30-year gap in recruitment. We sampled both live and dead trees to overcome some of the challenges of reconstructing mixed-severity fire regimes from the static age structure of forests.

However, when the re-establishment of lodgepole pine proceeds slowly from the margins of a large severely burned patch, it might be possible to falsely identify more than one pulse of recruitment and conclude that the preceding fire was of mixed severity (Pierce and Taylor 2011). This was not likely at Potholes because almost all the cohorts we identified in mixed-age plots were recruited shortly after widespread fires recorded by fire scars, and our criteria required them to be preceded by a 30 year gap in recruitment. Our cohorts are not likely to have recruited after logging; we selected a site that did not appear to have been heavily logged and of the 967 trees we sampled over 783 ha, only 29 were stumps.

Mountain pine beetles also affected these forests

The ongoing severe outbreak of mountain pine beetles in lodgepole forests across western North America has highlighted the need to understand the complex historical disturbance dynamics of this foundation tree species (Hicke et al. 2012). We observed evidence of modern insect outbreaks at Potholes (galleries, death-date cohorts, and bluestain), but did not attempt to reconstruct past outbreaks. While the overstory composition of these forests is not likely to be altered by climate change in the coming decades, forest structure might be altered by outbreaks of mountain pine beetle. In contrast to some pure lodgepole forests in central Oregon (Geiszler et al. 1980, Stuart et al. 1983), insect outbreaks were not the dominant control of forest structure at Potholes. However, mountain pine beetle outbreaks have occurred at Potholes in the past and will continue to do so. It is likely that the trees in some of the death cohorts we reconstructed were killed by mountain pine beetles during the widespread outbreak of the 1980s (6% of the trees in our plots died between 1980 and 1989), resulting in a new cohort of trees unassociated with fire that we did not detect because we sampled only large trees (≥20 cm DBH). Also, a few of the recruitment cohorts we identified may have recruited after trees were killed by insects, but may also have recruited in response to mortality from wind, drought, or interactions among these disturbances.

Fire may have interacted with mountain pine beetle outbreaks in several ways at Potholes. First, mountain pine beetles have caused widespread tree mortality after modern mixed-severity fires in lodgepole and ponderosa forests elsewhere (Jenkins et al. *in press*). Alternatively, fires may have occurred shortly after widespread tree mortality caused by outbreaks of mountain pine beetle. However, this second possible interaction appears less likely because the potential for torching and active crown fire is high only briefly during the red-needle phase that occurs within a few years of death by mountain pine beetles (Hicke et al. 2012). Further, mixed-severity fires created a mosaic of tree sizes, and hence beetle susceptibility, across Potholes in the past, so we would not expect widespread mortality during outbreaks or the widespread cohorts of lodgepole pine that would result.

Conclusions

The effect of fire exclusion on the fire regime at Potholes is unusual among mixed-conifer forests in the interior Pacific Northwest (Hagmann et al. 2013). While forest composition is topoedaphically limited primarily to lodgepole, our simulations suggest that contemporary, low shrub fuel loads at Potholes are of insufficient loading to spread fire to the canopy. In contrast, our tree-ring reconstructed fire history indicates that patches of high-severity fire occurred periodically at Potholes, generating multi-aged stands that may have been more resilient to beetle attacks. Because topographic relief at Potholes is low, spreading fires were likely wind driven, and would have required sufficient surface fuel loads for horizontal and vertical spread. However, fuel loads, in particular the abundance and cover of bitterbrush - the primary understory species at Potholes - has likely decreased since the exclusion of fire 130 years ago, reducing the ability of the site to support a mixed-severity fire regime. Because bitterbrush is both sensitive to and stimulated by fire, continued lack of fire within the ecosystem is likely to promote a negative feedback cycle, in which canopy gaps are not created and bitterbrush sprouting is not stimulated, thereby restricting shrub growth; in turn, limited shrub abundance and cover restricts horizontal and vertical spread of fire, thus eliminating some opportunities for creation of canopy gaps. However, future changes may introduce different mechanisms for mixed severity fires in this system if fuel moistures become sufficiently low to promote crown fire under current loadings or if bark beetles kill trees and create canopy gaps.

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Tables

Table 1. Fuel moistures used in fire behavior simulations.

	Fuel moisture (percentage) by fuel type				
Weather	<1 cm	1 to 2.5 cm	2.5 to 7 cm	Live herb	Live shrub
Current	4	5	9	111	130
Future (2040)	3	4	9	84	106

Note: Fuel types of <1 cm, 1-2.5 cm, and 2.5-7 cm correspond to 1-, 10-, and 100-hour fuels, respectively.

Figures

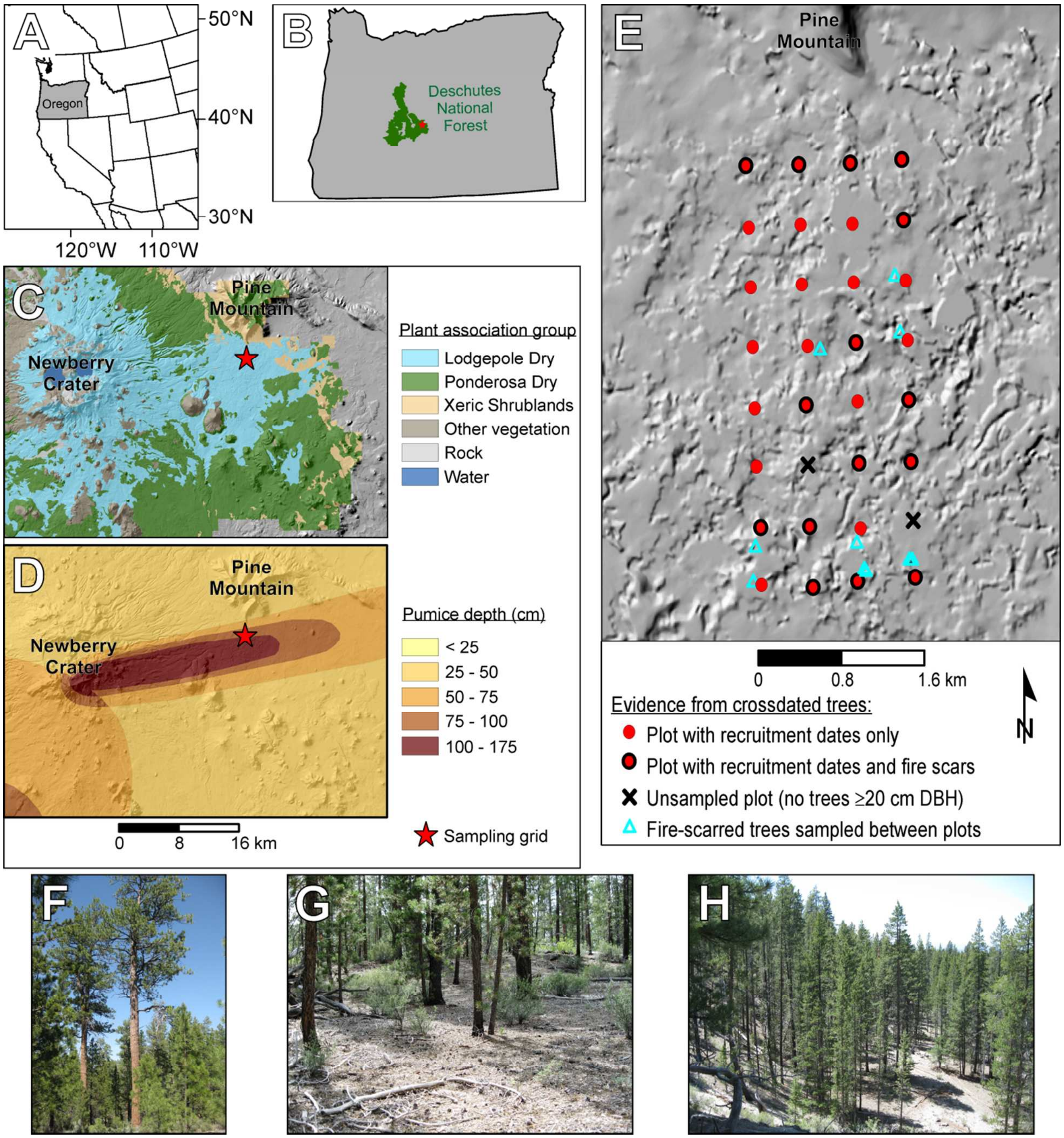

Figure 1. (A and B) Location of Potholes study site on the Deschutes National Forest in central Oregon, USA. (C) Distribution of plant association groups (Volland 1988). The Lodgepole Dry group includes scattered ponderosa pine. (D) Depth of pumice ejected by Newberry Crater

roughly 1,300 years ago (MacLeod et al. 1995). (E) Grid of plots in our relatively flat site (plot elevations 1,460 to 1,500 m, Pine Mountain elevation 1,935 m). (F) The site includes scattered live and dead large ponderosa pine trees. (G) and (H) Low-density forests with shrub understories growing on coarse pumice. Photo credits for F and H: James P. Riser II.

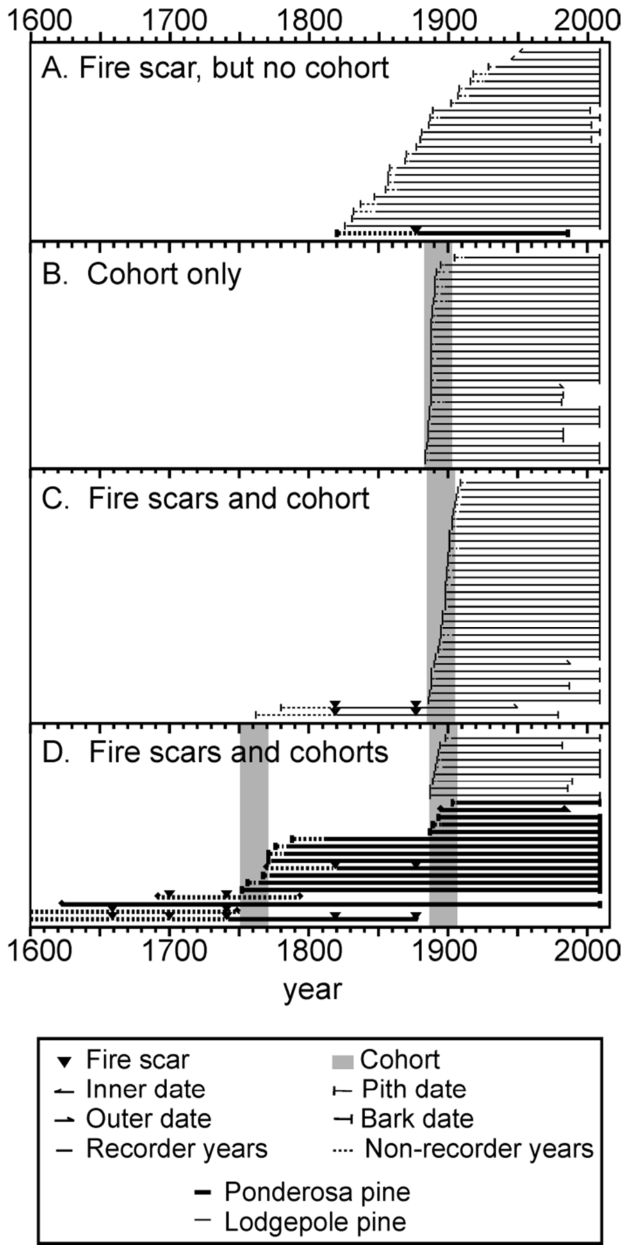

Figure 2. Examples of the dendrochronological evidence of tree demography and fire history used to infer fire severity. Life spans are indicated by horizontal lines that connect the recruitment and death dates of individual trees. Recruitment dates are the dates at sampling height.

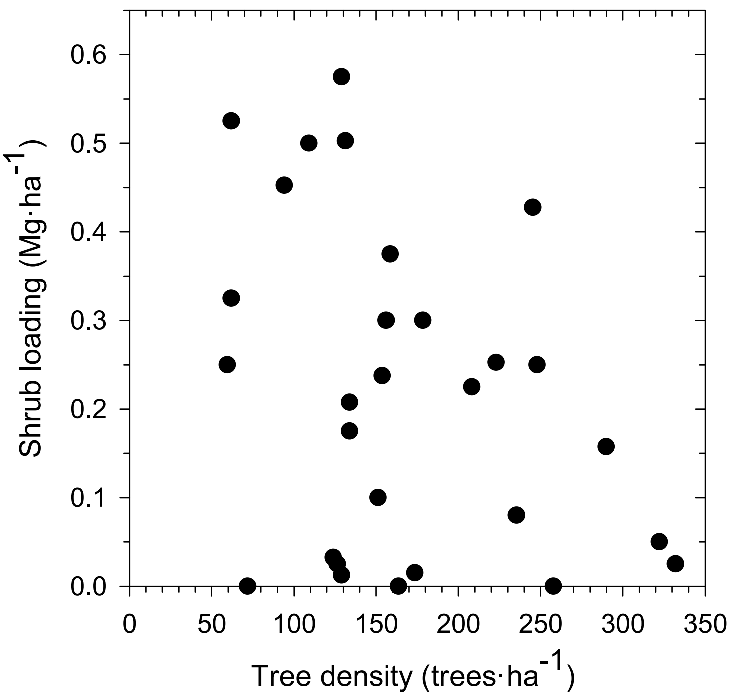

Figure 3. The highest shrub loadings occurred in plots with the lowest tree densities. Shrubs were dominated by antelope bitterbrush, but big sagebrush, wax currant, and rabbitbrush also occurred in some plots.

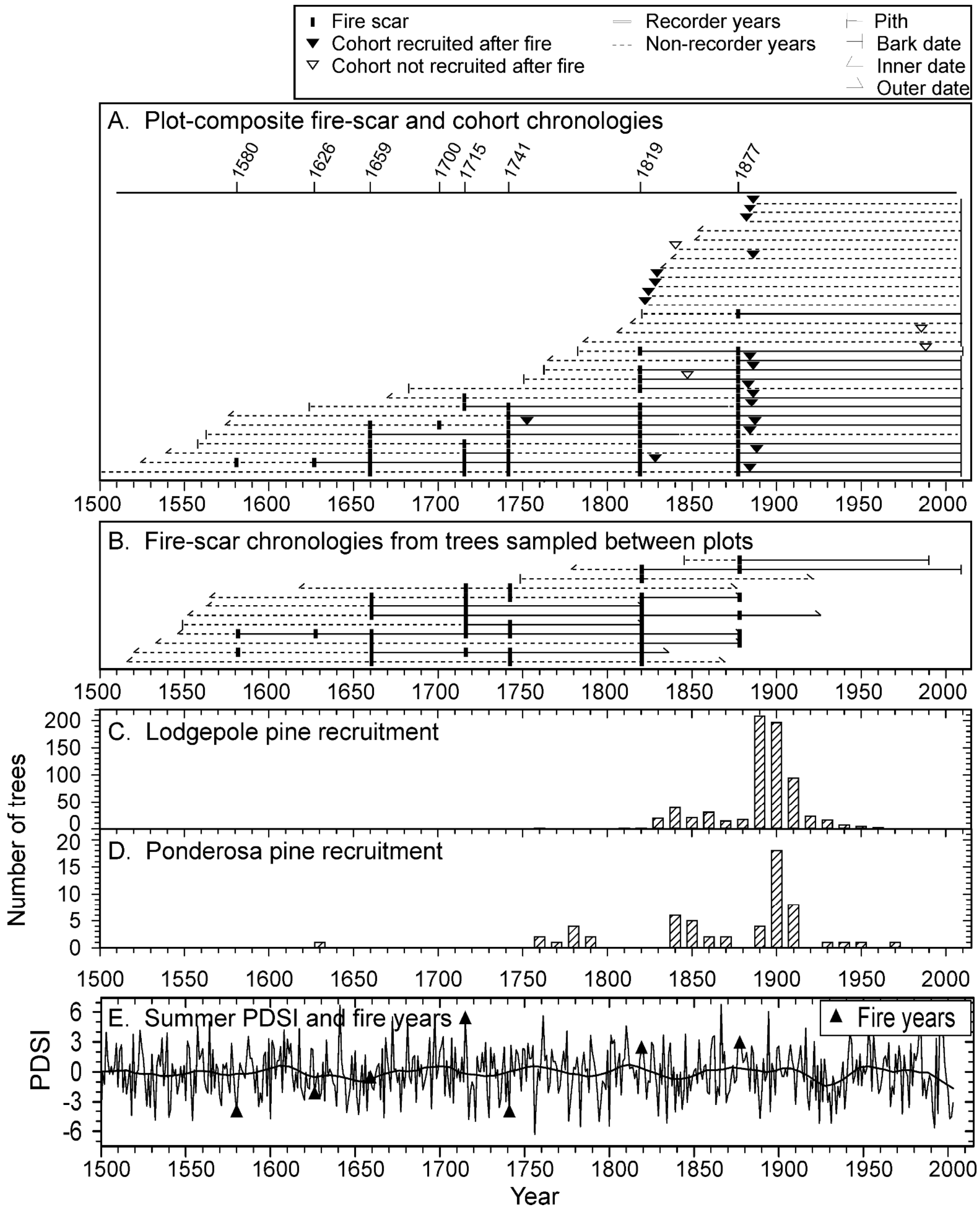

Figure 4. Chronologies of fire and tree recruitment. Each horizontal line in (a) shows tree life spans composited in one of 30 2-ha plots through time. Vertical lines indicate fires recorded on 2 or more trees at the site. Horizontal lines in (b) show the life spans of individual fire-scarred trees we encountered between plots. Non-recorder years precede the first scar; whereas recorder

years generally follow it, but non-recorder years can also occur when the catface margin is consumed by subsequent fires or rot or in plots lacking fire-scarred trees. Recruitment dates are summed across all plots for lodgepole (c) and ponderosa (d); the more recent part of the age distribution is underestimated because we only sampled trees ≥20 cm DBH. The oldest lodgepole recruited in 1759. (e) Smoothed, tree-ring reconstructed Palmer Drought Severity Index (Cook et al. 2004) with fire years indicated.

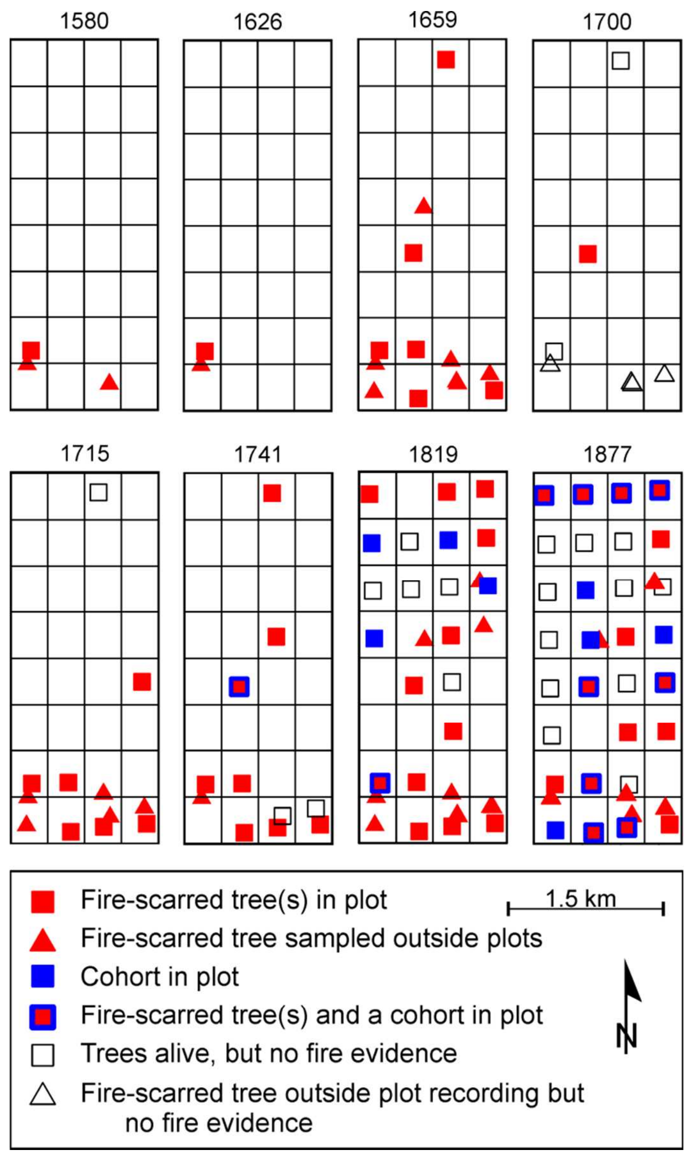

Figure 5. Schematic maps for each of the eight years (dates given above each map) with tree-ring evidence of fire we collected inside and outside our 30 plots. "Trees alive, but no evidence of fire" indicates that at least one tree was alive and in recording status (i.e., had scarred at least once) at that location during that year but lacked evidence of fire. Trees that were not alive during a given map year, or plots lacking such trees, are not mapped for that year.

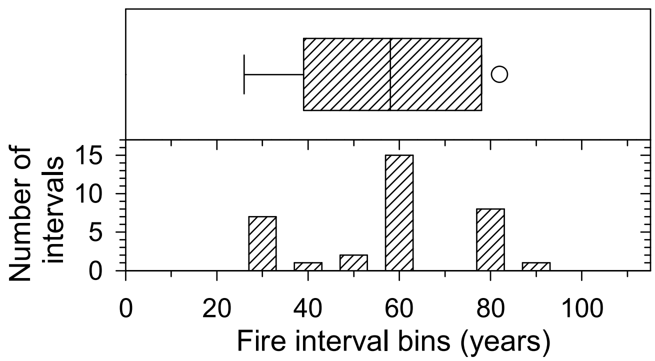

Figure 6. Distribution of 34 plot-composite fire intervals reconstructed from fire-scar and cohort dates occurring between 1650 and 1900 in 12 of our 30 2-ha plots for which we could compute intervals (i.e., more than one fire was reconstructed). The box (top panel) encloses the 25th to 75th percentiles and the whisker is the 10th percentile of the distribution of intervals. The vertical line is the median fire interval and the circles are all values falling outside the 10th to 90th percentiles.

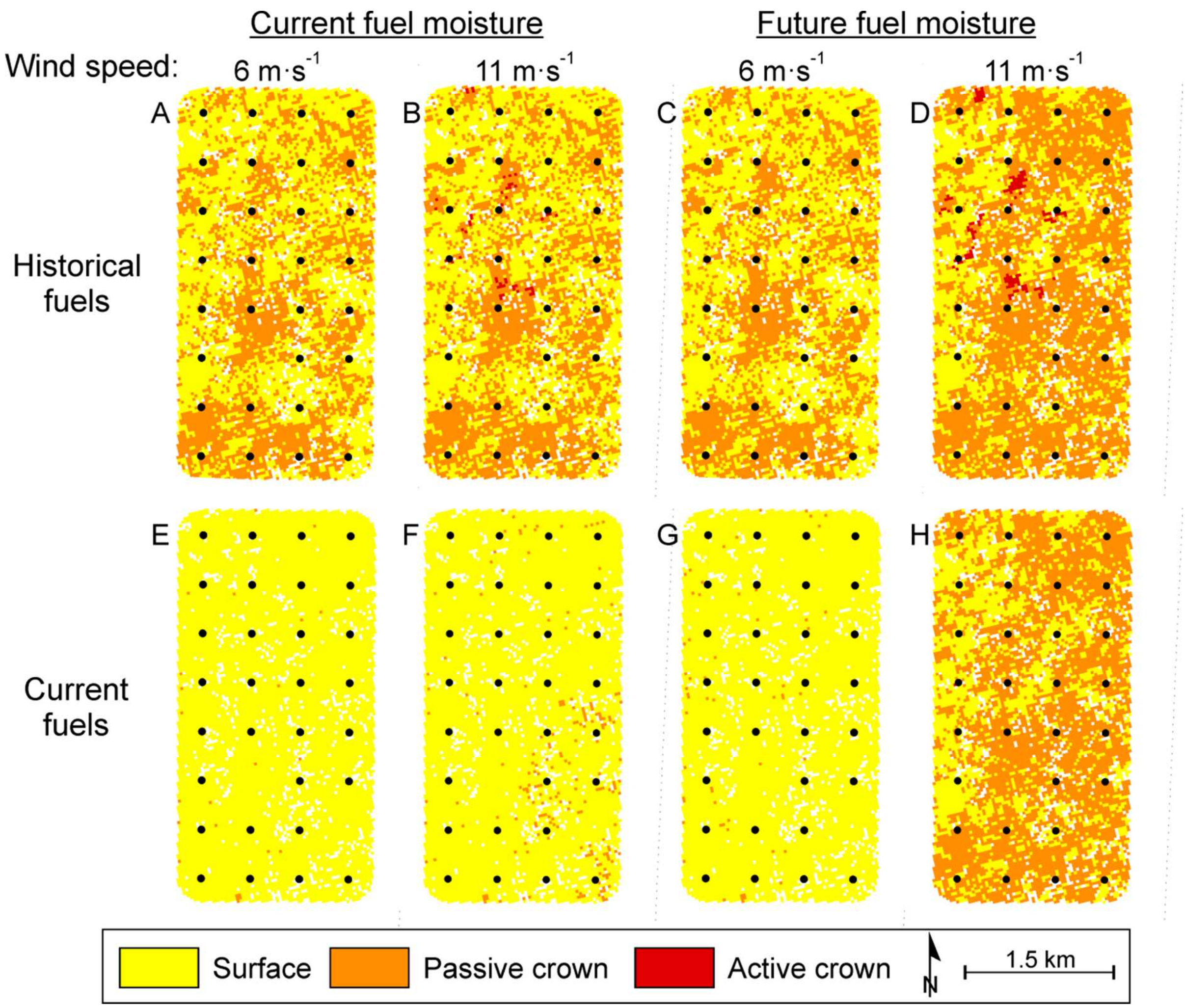

Figure 7. Maps of simulated fire behavior (FlamMap, Finney 2006) at Potholes using historical and current fuel loading and four different fire weather scenarios that vary in fuel moisture and wind speed (Table 1). Wind speeds of 6 and 11 $m \cdot s^{-1}$ at 6 m are equivalent to 14 and 25 miles per hour at 20 feet, respectively.

Supplementary material

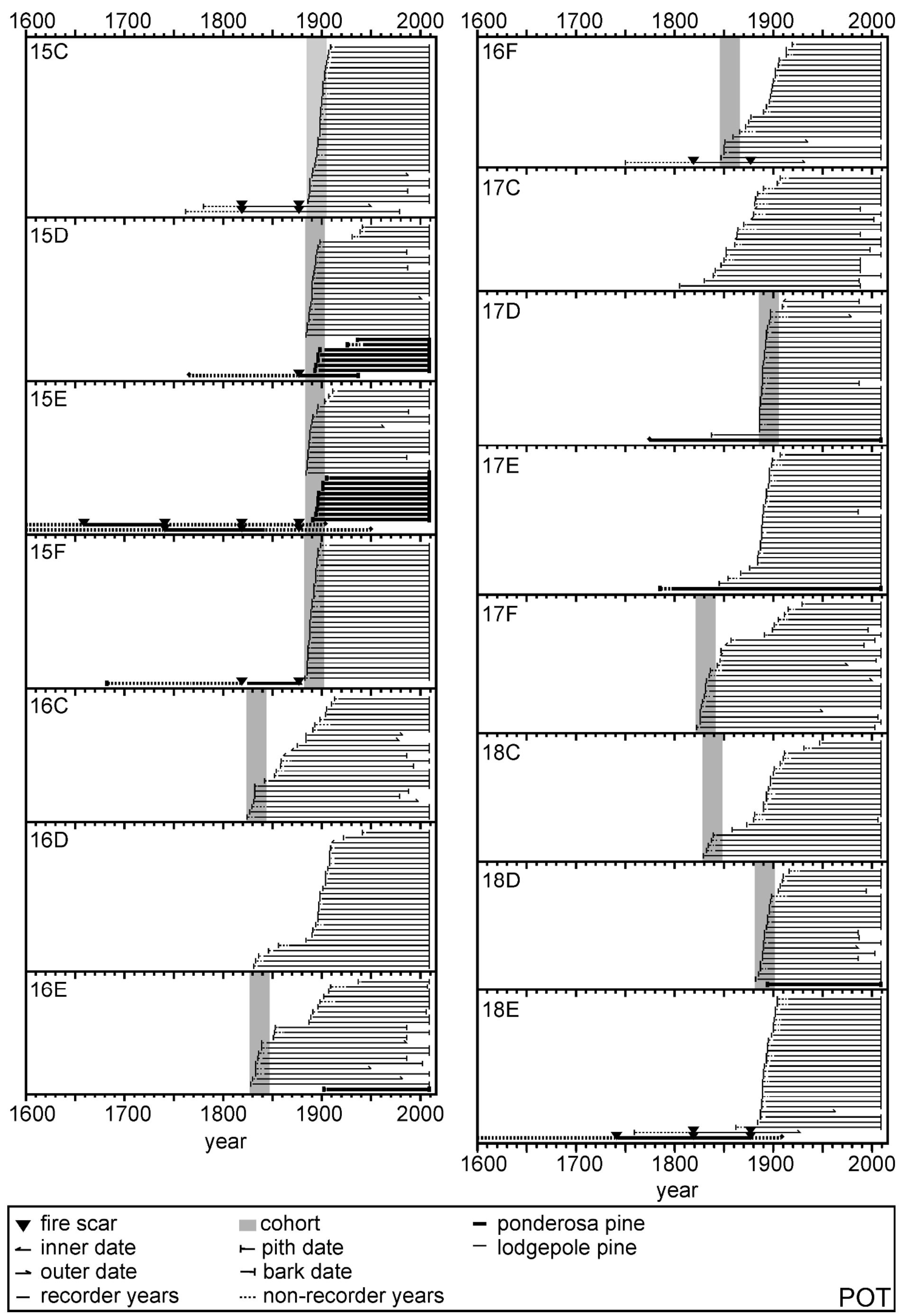

Figure S1. Tree life spans and evidence of fire by plot. Each panel includes the chronologies of tree demography (recruitment and death dates), fire scar dates, and cohort dates for a single plot.

Bark dates for stumps are shown as outer dates.

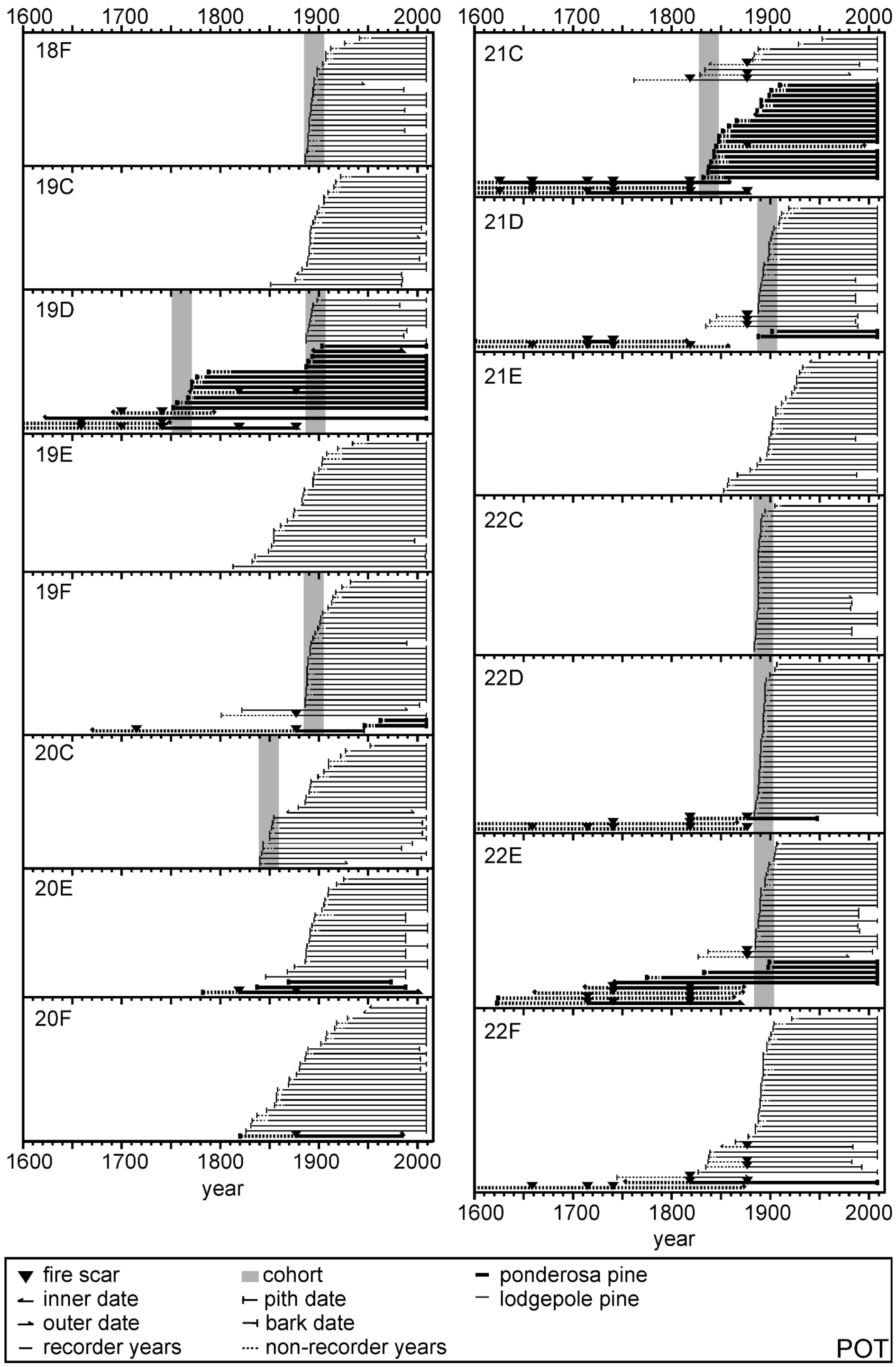

Figure S1. *Continued.*