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ARTICLE

A multi-century history of fire regimes along a transect of mixed-conifer forests in central Oregon, U.S.A.

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Abstract: Dry mixed-conifer forests are widespread in the interior Pacific Northwest, but their historical fire regimes are poorly characterized, in particular the relative mix of low- and high-severity fire. We reconstructed a multi-century history of fire from tree rings in dry mixed-conifer forests in central Oregon. These forests are dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.). Across four, 30-plot grids of ~800 ha covering a mosaic of dry mixed-conifer forest types, we sampled 4065 trees for evidence of both high- and low-severity fire. From 1650 to ~1900, all four sites sustained frequent, often extensive, low-severity fires that sometimes included small patches of severe fire (50–150 ha during 18%–28% of fire years). Fire intervals were similar among sites and also among forest types within sites (mean intervals of 14–32 years). To characterize the continuous nature of the variation in fire severity, we computed a plot-based index that captures the relative occurrence of low- and high-severity fire. Our work contributes to the growing understanding of variation in past fire regimes in the complex and dynamic forests of North America's Interior West.

Key words: dendrochronology, fire scars, fire severity, postfire cohorts, severity index.

Résumé : Les forêts sèches mélangées de conifères sont très répandues dans la zone intérieure du Pacific Northwest mais leur régimes de feu passés sont mal définis, en particulier le mélange relatif de feux de faible et forte gravité. Nous avons reconstruit l'historique des feux sur une période de plusieurs siècles à partir des cernes annuels des arbres dans les forêts sèches mélangées du centre de l'Oregon. Ces forêts sont dominées par le pin ponderosa (*Pinus ponderosa* Lawson & C. Lawson), le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et le sapin grandissime (*Abies grandis* (Douglas ex D. Don) Lindl.). Parmi quatre grilles de 30 places échantillons de ~800 ha couvrant une mosaïque de types de forêts sèches mélangées de conifères, nous avons échantillonné 4065 tiges pour mettre en évidence le feux de faible et forte gravité. De 1650 à ~1900, les quatre sites ont fréquemment subi des feux de faible gravité, souvent vastes, qui incluaient dans certains cas des parcelles (50–150 ha) ayant subi un feu de forte gravité lors de 18–28 % des années où il y a eu des feux. Les intervalles entre les feux étaient similaires parmi les sites et aussi parmi les types de forêts dans ces sites (intervalles moyens de 14–32 ans). Pour caractériser la nature continue de la variation de la gravité des feux, nous avons calculé un indice fondé sur les places échantillons qui détecte l'occurrence relative de feux de faible et forte gravité. Nos travaux contribuent à approfondir la compréhension de la variation des régimes de feu passés dans les forêts complexes et dynamiques de la zone intérieure de l'ouest de l'Amérique du Nord. [Traduit par la Rédaction]

Mots-clés : dendrochronologie, cicatrice de feu, gravité du feu, cohorte d'après feu, indice de gravité.

Introduction

Mixed-conifer forests are widely distributed in the interior Pacific Northwest and continue to change rapidly as a consequence of land-use change and climate (Turner et al. 2013; Hessburg et al. 2016). Snowpack, which is declining more rapidly in the Pacific Northwest than elsewhere in the western United States (Mote et al. 2018), has been linked to an increase in the incidence of wildfires (Westerling et al. 2006). Fires in the region have been excluded for over a century by livestock grazing, logging, and suppression. This has led to an increase in tree density and the proportion of shade-tolerant tree species and a reduction in structural and spatial heterogeneity, especially in forests that historically sustained fires every few decades (Hagmann et al. 2014; Merschel et al. 2014). These changes are significant for numerous species of plants and animals such as the threatened Northern Spotted Owl (*Strix occidentalis* (Xántus de Vésey, 1860)) and the White-headed Woodpecker (*Picoides albolarvatus* (Cassin, 1850); Hessburg et al. 2016).

Fire severity sets the stage for postfire recovery and succession and thus relates to key dynamic properties of ecosystems (Lentile et al. 2005; Keyser et al. 2008; Collins and Roller 2013). Most fires in mixed-conifer forests create complex landscape mosaics of severity that affect subsequent fire behavior and postfire recovery (Hessburg et al. 2016). The size of high-severity patches influences postfire erosion, soil loss, and recovery of the plant community (Haire and McGarigal 2010). For example, if the size of high-severity patches exceeds effective dispersal distances of surviving trees or if multiple fires occur before newly established trees reach reproductive maturity, postfire recovery can be delayed (Stevens-Rumann et al. 2018). In addition, the mix of low- and high-severity fire effects can vary continuously over space and time, complicating attempts to place these complex systems into simple fire-severity categories.

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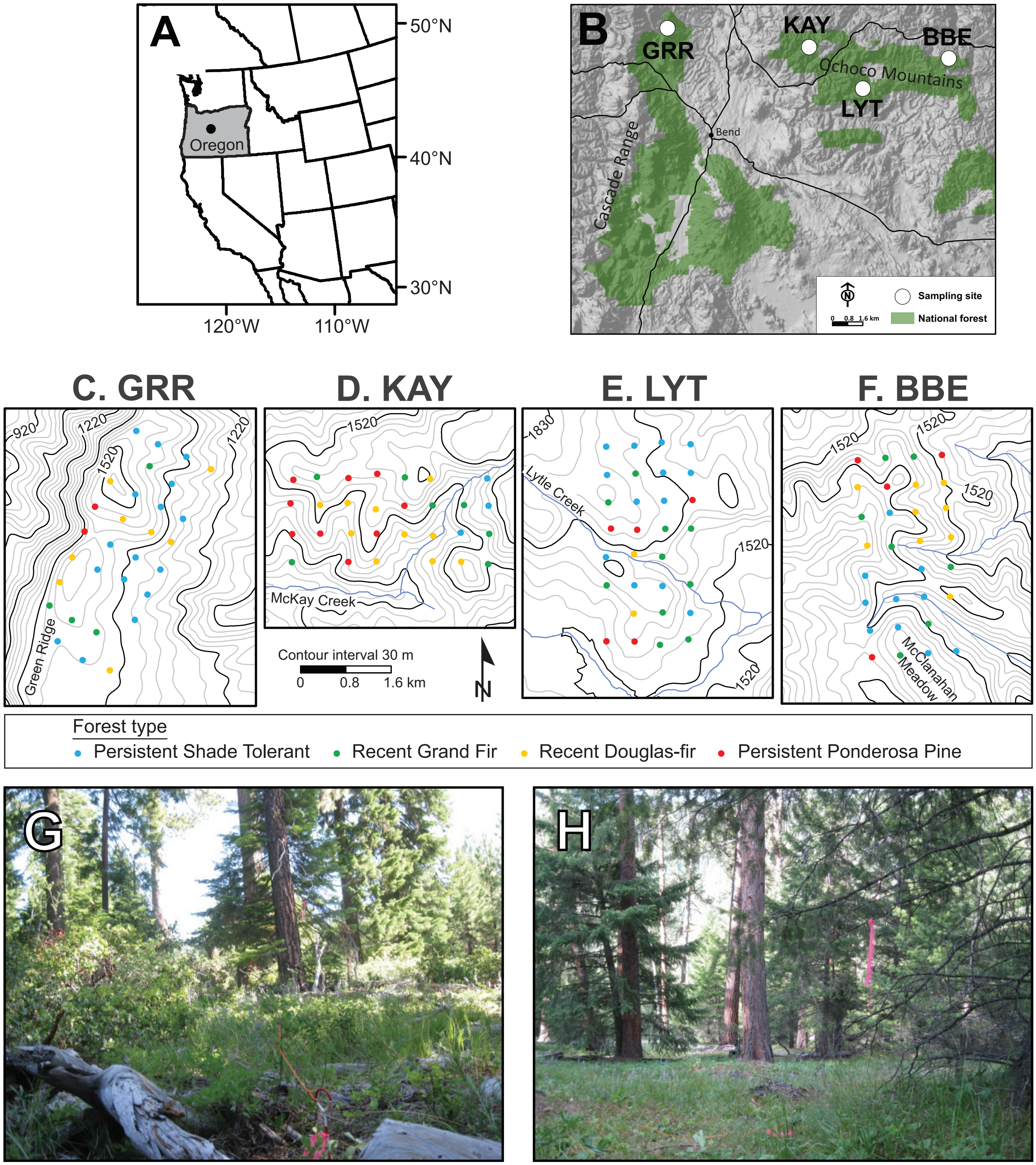
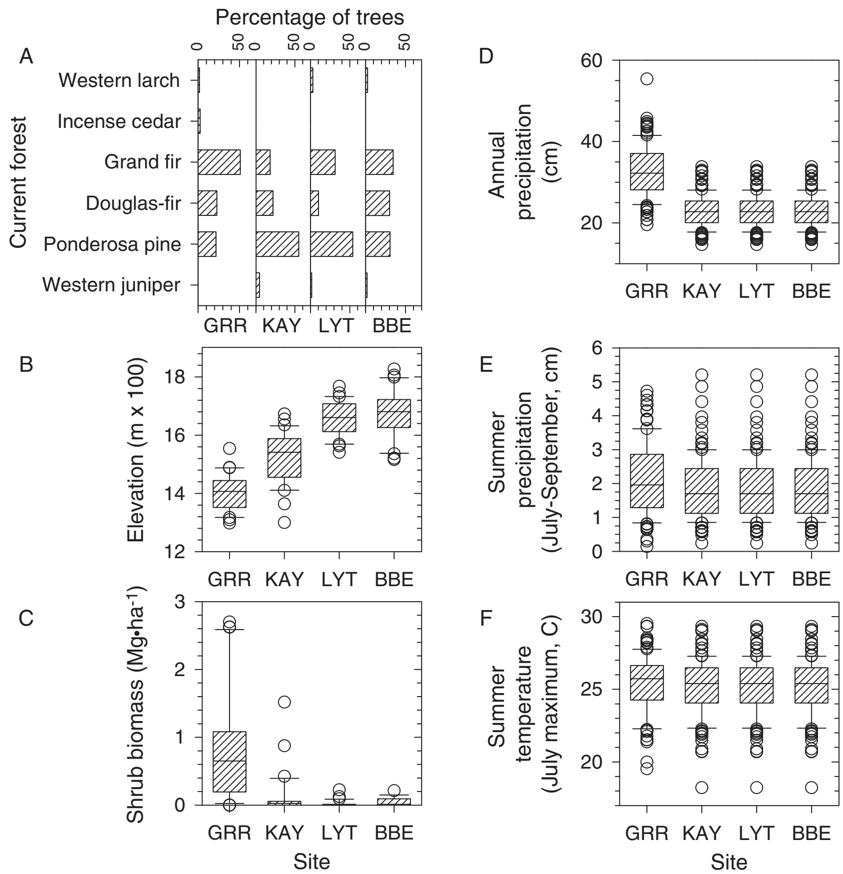
Fig. 1. (A and B) Location of study sites in central Oregon, USA. (C–F) Location and forest type (Merschel et al. 2014) of plots at each site. Shrub understories are common at the (G) eastern Cascades site (GRR) but not at the sites in the (H) Ochoco Mountains (e.g., BBE).



Mixed-conifer forests are distributed broadly in the interior Pacific Northwest, including central Oregon where they occur on both the eastern slopes of the Cascade Range (hereafter Cascades) and in the Ochoco Mountains (hereafter Ochocos; Fig. 1). They include a variety of tree species, but dry mixed-conifer forests in this region generally include a mix of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and (or) grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.). They occur in fine-grained, topographically driven mosaics (Ohmann and Spies 1998) and have recently been reclassified into four broad types (Merschel et al. 2014). The historical fire regime of this forest type is assumed to have been mixed severity that cre-

Fig. 2. Modern forest overstory and understory and climate at sampled plots. (A) Distribution of live trees at least 20 cm dbh. Distribution of plots by (B) elevation, (C) modern live shrub loadings, and (D–F) annual and seasonal climate (1895–2012; PRISM Climate Group 2012). Boxes enclose the 25th to 75th percentiles; whiskers enclose the 10th to 90th percentiles, and the horizontal line is the median. Plot values falling outside the 10th to 90th percentiles are indicated by circles.



ated a mosaic of forest patches in which varying amounts of tree mortality occurred (Perry et al. 2011; Hessburg et al. 2016; Reilly et al. 2017), but little quantitative data are available regarding this mosaic for individual fires before widespread fire exclusion. Managers are using landscape-scale approaches to restoring fire-dependent forests, but a lack information on landscape-scale variation in historical fire regimes and how they may have varied among forest types and across the region has led to controversy (Spies et al. 2010; Hessburg et al. 2016).

Multi-century histories of variation in mixed-severity fire regimes can be reconstructed by combining multiple tree-ring proxies (Tepley and Veblen 2015). Tree rings retain a record of low-severity fire as fire scars that form on individual trees through heat exposure (Falk et al. 2011), whereas the main measurable legacy of the high-severity component of mixed-severity fire regimes is the initiation dates of postfire cohorts. Both proxies can be sampled from multiple trees at a point and composited into a record of the relative mix in severities for the fires that occurred and, where multiple points are sampled, across landscapes or regions. Several fire histories have been reconstructed from tree rings in mixed-conifer forests in central Oregon, but the objectives of most of these studies did not include sampling across landscapes or attempting to reconstruct the full range of fire severities (Supplementary Table S1[1], but see Merschel et al. 2018). Furthermore, dry mixed-conifer forest types in the region vary in composition and environmental setting, and it is not known whether fire regimes varied among them in response to this variation (Merschel et al. 2014).

Our objective was to characterize variation in historical fire regimes in dry mixed-conifer forests in central Oregon. We sampled four sites along a 140 km longitudinal transect from the eastern slope of the Cascades to the Ochocos. At each site, we established grids of plots and sampled tree-ring evidence (fire scars and tree recruitment and death dates) to determine the frequency and severity of wildfires over the past few centuries.

Methods

Study area

We sampled four mixed-conifer sites in the Deschutes and Ochoco National Forests (Fig. 1), one in the eastern Cascades and three in the Ochocos. Plots ranged in elevation from 1298 to 1827 m (Fig. 2B). Summers are hot and dry and winters are cold. Monthly temperature ranges 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). Mean annual precipitation averages 29 cm in Bend (elevation 1108 m), of which only 12% falls during the fire season (July–September, 1914– 2012; Western Regional Climate Center 2013). Although annual precipitation is highest at the Cascades site (Fig. 2D), fire-season climate is similar at all four sites (Figs. 2E and 2F).

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0193.

Table 1. Evidence used to reconstruct fire and forest histories.

Site code	Area (ha)	Recruitment-date trees: Number sampled	Recruitment-date trees: Number crossdated	Fire-scarred trees: Number sampled	Fire-scarred trees: Number crossdated	End of analysis period	Latitude (°N)	Longitude (°W)
Eastern Cascade Range								
GRR	866	902	745	101	90	1890	44.586	121.576
Ochoco Mountains								
KAY	782	899	766	118	108	1871	44.485	120.645
LYT	779	901	770	134	116	1890	44.278	120.291
BBE	795	900	768	110	99	1847	44.401	119.706
Total	3222	3602	3049	463	413			

Note: The 463 crossdated fire-scarred trees include 72 trees that we also sampled for tree recruitment dates. The analysis period for all sites began in 1650. We sampled 30 plots at each site.

Land use changed dramatically in central Oregon in the late 1800s. Native Americans have occupied central Oregon for millennia but were largely confined to reservations beginning in the late 19th century (Hessburg and Agee 2003). Sheep and cattle became abundant in the forests of the Ochocos and eastern Cascades shortly after Euro-Americans settled the region in the 1860s (Wentworth 1948; Oliphant 1968). Ponderosa pine forests were logged heavily from 1925 to 1946, and some logging continued into the late 20th century (Hessburg and Agee 2003).

Tree recruitment and death dates

Before conducting fieldwork, we used local databases and consulted with local land managers to identify four sites dominated by mixed-conifer forest that had road access but no evidence of 20th-century fires or extensive logging. In the Ochocos, we mapped three grids of 32 plots on 500 m spacing over ~800 ha (KAY, LYT, and BBE; Fig. 1; Table 1). We did not sample two of the plots at each site because they lacked trees larger than our diameter cutoff for sampling, 20 cm in diameter at a breast height of 1.4 m (dbh). In the eastern Cascades, we could not identify an unlogged area of similar size so we mapped a grid of 36 plots with the same 500 m spacing over an area about 10% larger (866 ha) and sampled the 30 plots that lay between clear-cut patches (GRR). In the field, we relocated 37 plots 50 m along random azimuths to avoid hazardous areas and areas lacking trees greater than 20 cm dbh, e.g., roads and logged areas.

At each plot, we sampled the 29 to 31 live or dead trees that (*a*) were closest to plot center, (*b*) appeared to have intact wood, and (*c*) were at least 20 cm dbh, the diameter of trees that likely recruited before the mid-20th century, which we determined from pilot sampling. We identified trees to species; however, grand fir and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) hybridize throughout central Oregon (Ott et al. 2015), but we refer only to grand fir for simplicity. From live trees, we removed increment cores at ~15 cm height, striving to sample within 10 rings of the pith, but removed no more than four cores per tree and retained the one closest to the pith. From dead trees (both standing and down), we removed one to three partial cross sections, generally including the pith, from ~15 cm stem height using a chainsaw. Plots ranged from 0.1 to 0.4 ha (0.2 ± 0.1 ha, mean ± standard deviation; plot size = π × (distance from plot center to farthest tree sampled)^2). We tallied dead trees that were at least 20 cm dbh but lacked intact wood, recording char, species, and dbh where possible.

We sanded all wood samples until we could see the cell structure with a binocular microscope. We assigned calendar years to tree rings by visually crossdating ring widths using chronologies that we developed from trees in our plots combined with existing nearby chronologies (Brubaker 1980; A.G. Merschel, personal communication), occasionally assisted by cross-correlation of measured ring-width series (Grissino-Mayer 2001*a*).

We estimated tree recruitment dates from pith dates at sampling height, geometrically estimating the years to pith for samples that did not intersect pith (5 ± 4 years for 61% of trees). We determined the death dates of logs and snags with intact outer rings, which we identified by the presence of bark and (or) intact outer sapwood (Margolis and Malevich 2016).

Forest composition

Data from some of our sites (trees species and density at GRR, KAY, and LYT) were combined with an extensive collection of similar data to reclassify mixed-conifer forests in central Oregon based on historical structure and composition plus successional trajectories following recent changes in land use (Merschel et al. 2014). The four types occur in significantly different microclimates and all historically contained ponderosa pine but currently vary in the proportion and age distribution of shade-tolerant trees (grand fir and Douglas-fir). The Persistent Ponderosa Pine and Recent Douglas-fir types occupy relatively hot–dry sites compared with the Recent Grand Fir and Persistent Shade Tolerant types, which occupy warm–moist and cold–wet sites, respectively. We classified the plots at BBE into these same four categories and eliminated one plot at KAY from further analyses because it was dominated by western juniper and thus lies beyond the dry end of this mixed-conifer forest classification (KAY18D; Supplementary Fig. S3[1]).

To quantify visual differences in modern understory among sites, we recorded the shrub species that occurred within 5.6 m of plot center. We estimated total shrub biomass by visually comparing the vegetation at each plot with reference photographs of known shrub loadings (Keane and Dickinson 2007), averaging the estimates from four 1 m^2 microplots placed 4.5 m in the cardinal directions from plot center.

Evidence of past fire

We sampled fire scars to reconstruct low-severity fire effects within and across each plot. We used a chainsaw to remove partial cross sections with fire scars from up to 10 live or dead trees (average four) across ~2 ha at each plot. We sanded and crossdated as described above and identified the calendar year of fire occurrence as the date of the tree ring in which a fire scar formed. We assigned scars that formed on the boundary between two rings to the preceding calendar year, assuming that historical fires burned during the same season as modern fires in central Oregon, i.e., the late summer or fall (Bartlein et al. 2008) so that ring-boundary scars formed after cambial growth had ceased during the preceding year.

We inferred high-severity fire effects from the initiation dates of tree cohorts. Unlike fire scars, tree recruitment dates do not yield exact fire dates so we applied a rule set that identified a cohort when five or more trees recruited within 20 years after a gap of at least 30 years during which no trees recruited. We have shown elsewhere that our overall conclusions about historical fire regimes are insensitive to variations in this rule set (Heyerdahl et al. 2012), and recent work in mixed-conifer forests elsewhere has shown that recruitment may not begin for 10 to 20 years after fire (Naficy 2017). We also looked for death cohorts (five or more trees dying in the same year, excluding the 15 death dates that we obtained from the stumps of logged trees) but did not find any.

Historical fire regimes

We combined fire-scar and cohort-initiation dates from each plot into a plot-composite fire chronology that included both low- and high-severity fire effects, excluding scar dates recorded by only one tree across a site (22 scars or 1% of all scars eliminated). We assumed that cohorts and scars were created by the same fire when the cohort initiated less than 30 years after (*a*) a fire scar in the same plot or (*b*) a widespread fire at the same site, i.e., one that scarred at least 25% of recording plots. We computed plot-composite fire intervals (hereafter fire intervals) as the number of years between fires, eliminating intervals when no trees were recording. Fire intervals were positively skewed, as such distributions commonly are (Falk and Swetnam 2003), so we report fire frequency as the percentiles of two-parameter Weibull distributions fit to our fire-interval distributions (SAS PROC UNIVARIATE, SAS Institute, Inc. 2011). We assessed the fit of the Weibull distributions to our interval data using probability plots because the number of intervals per site was large (148 to 296 fire intervals per site).

Although all four sites had some fire scars in the 1400s and 1500s, we analyzed fires only from 1650, when at least 25% of fire-scar plots were recording at each site, through one year after the last widespread fire, including any cohorts that established within 30 years following this last fire. This fire occurred in the late 1800s at most sites (GRR 1890, KAY 1871, and LYT 1890) but several decades earlier at BBE (1847). Recording plots had trees with at least one fire scar and thus were more likely to record fires than plots lacking such trees (Lentile et al. 2005).

We assessed whether fire intervals were related to site or forest type by modeling these as fixed effects in generalized linear mixed models. In these models, we also assessed the effect of spatial autocorrelation in intervals among the plots at each site by modeling plot as a random effect (Bolker et al. 2009). We fit models by maximum likelihood (Laplace approximation) assuming a Gamma error distribution and log scale (lme4 package in the R statistical programming environment; Bates and Maechler 2009; R Core Team 2017). Residuals graphs indicated good model fit with no overdispersion and Laplace estimation methods converged easily. We tested for significant differences in modeled mean fire interval across sites (i.e., regardless of forest type) and within sites (i.e., all combinations of forest type within each site) using adjusted post hoc multiple comparisons (Tukey's honestly significant difference, $\alpha = 0.05$; Multcomp package in R; Hothorn et al. 2008).

We assessed the relative mix of fire severities at two scales: across space for each fire and through time for each plot. For each fire, we estimated the relative size of patches of low versus high severity as a percentage of recording plots. For each plot, we computed an index of the severity of the fire regime as the sum of the severities of all fires during the analysis period (Heyerdahl et al. 2012; Margolis and Malevich 2016). To compute the index, we identified low-severity fires as those with scars only and assigned a value of 0. We identified mixed-severity fires as those with (*a*) both scars and cohorts or (*b*) a single cohort plus at least two trees that survived the fire. We assigned these fires a value of 50. We identified high-severity fires as those with a single cohort and no surviving trees and assigned them a value of 100. The index is the sum of these values divided by the number of fires and is the mean severity value over time.

Results

Tree recruitment and death dates

We sampled 3602 trees; most were alive (89%), but some were snags, logs, or stumps. We removed wood samples from most of these trees (3235 trees, 90%) and were able to crossdate most of those (3049 trees, 94%). These included sampling intact wood from 153 of the 257 large logs and snags in our plots. Only 29 of these had intact outer rings from which we obtained death dates; one died in 1850 and the remaining trees died between 1973 and 2009.

We tallied an additional 1213 dead trees in our plots that were at least 20 cm dbh but lacked intact wood. Their species distribution was similar to that of the trees with intact wood. They were mostly small (70% were less than 50 cm in diameter), mostly logs or snags (84%), and mostly not charred (78%).

Forest composition

Modern overstory composition was similar among sites. All were dominated by grand fir, Douglas-fir, and ponderosa pine and included minor but varying amounts of western larch (*Larix occidentalis* Nutt.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), or western juniper (*Juniperus occidentalis* Hook.; Fig. 2A). All four sites were mosaics of the four forest types at our sampling scale of one plot per 25 ha (Figs. 1C–1F).

Shrub biomass was generally higher and more diverse at the eastern Cascades site than the Ochocos sites (Figs. 1G, 1H, and 2C), averaging 0.73 $Mg \cdot ha^{-1}$ versus 0.04 to 0.08 $Mg \cdot ha^{-1}$, respectively. In the eastern Cascades, Oregon boxleaf (*Pachistima myrsinites* (Pursh) Raf.), snowbrush ceanothus (*Ceanothus velutinus* Douglas ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), common snowberry (*Symphoricarpos albus* (L.) S.F. Blake), and oceanspray (*Holodiscus discolor* (Pursh) Maxim.) occurred in more than one-third of the plots. In the Ochocos, in contrast, only creeping barberry (*Mahonia repens* (Lindl.) G. Don) and common snowberry occurred in more than one-third of the plots.

Evidence of past fire

Fire scars were widespread; fire-scarred trees occurred in 95% of all plots (Fig. 3). Of the 463 trees from which we removed fire-scarred partial cross sections, we were able to crossdate 485 sections from 413 of them (Table 1). The crossdated trees were mostly ponderosa pine (98%) but included a few western larch and Douglas-fir. Most of the trees were dead when sampled (92%). Collectively, these samples yielded 2408 fire scars during the analysis period (436 to 828 scars per site).

Cohorts were not as widespread as fire scars; they occurred in 43% of all plots (Fig. 3). From the 2846 pith dates that we obtained, we identified 74 cohorts. Of these, we analyzed the 53 cohorts that occurred during the analysis period. Two-thirds of these cohorts were associated with fire scars or trees that survived the fire in the same plot, so we assigned them a value of 50 for computing the severity index. The remaining third had only evidence of high-severity fire so we assigned them a value of 100. Cohorts began recruiting during every century from 1600 to 1900, but most began in the 1800s (75%). We assigned all 53 analysis-period cohorts to a fire date. Most began recruiting within 30 years of a fire-scar date in the same plot (40 cohorts, 16 ± 8 years); the remaining 13 cohorts recruited within 30 years of widespread fire-scar dates at the same site but in different plots (9 ± 7 years). Most plots with cohorts had a single cohort, but two plots had two (KAY16D and KAY17C; Supplementary Fig. S3[1]). Three plots had old trees but neither fire scars nor cohorts: GRR20C (Supplementary Fig. S2[1]), LYT16C (Supplementary Fig. S4[1]), and BBE20E (Supplementary Fig. S1[1]). We did not find evidence of extensive high-severity fire at the site scale. Rather, old living trees were widespread. More than half of the plots (53%) had living trees that were at least 300 years old, and 24% had living trees that were 400 to 631 years old.

Fig. 3. Chronologies of fire and tree recruitment at study sites. We analyzed fire regimes starting in 1650 at each site (Table 1). Horizontal lines in the top box of each panel show the length of the composite fire-scar record in each plot (2 ha). Non-recorder years precede the first scar, whereas recorder years generally follow (Grissino-Mayer 2001*b*). However, non-recorder years can also occur when the scarred margin is consumed by subsequent fires or rot. End dates of the lines indicate the last dated ring for fire-scarred trees; most recruitment trees were live when sampled. Recruitment dates are tree ages at 15 cm stem height and are summed across all plots at a site in the bottom two boxes of each panel. We did not capture the recent chronology of tree recruitment because we sampled only trees at least 20 cm dbh.

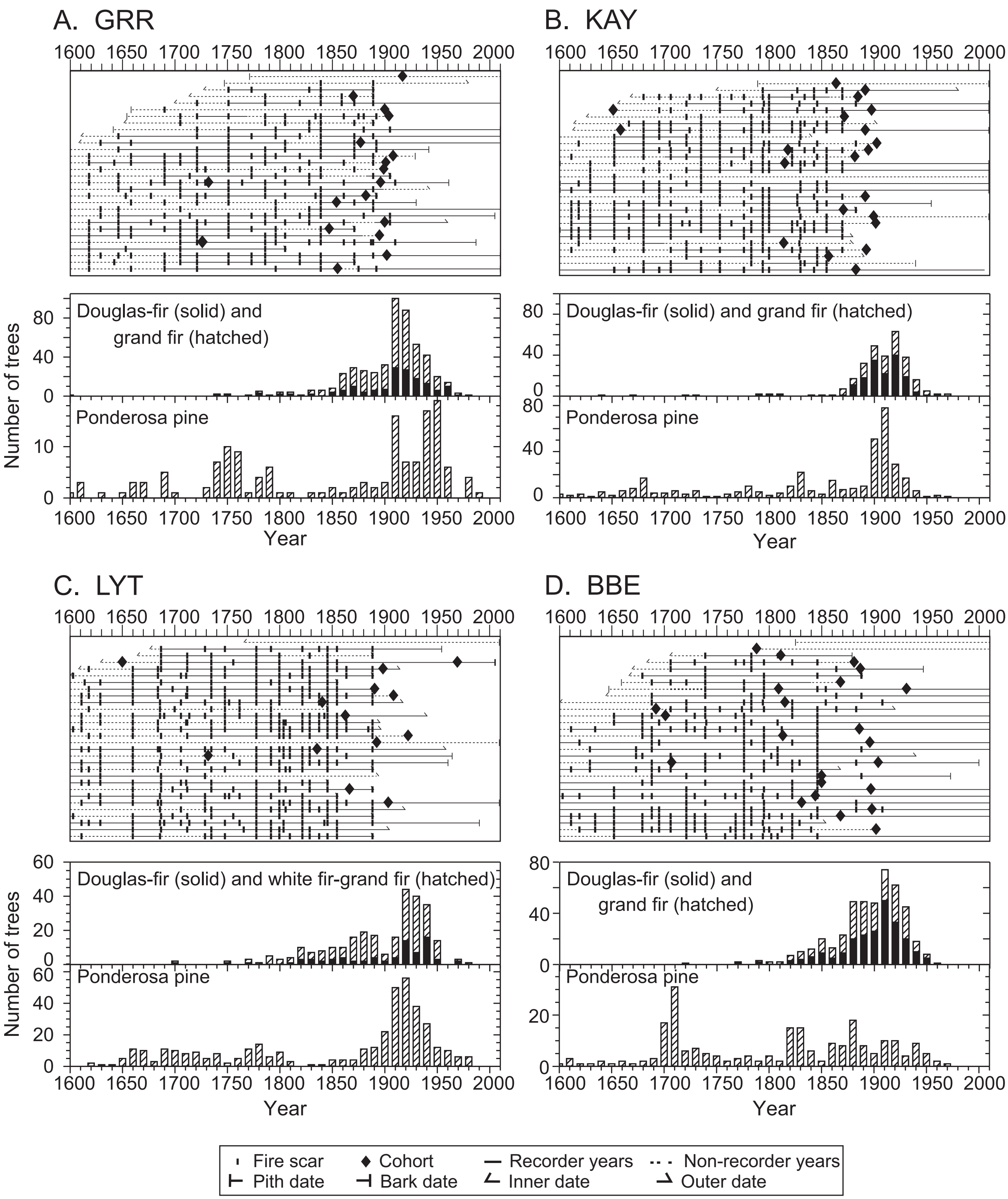


Table 2. Effect of site and forest type on fire frequency: results of generalized linear mixed modeling.

			Generalized linear mixed model results				
Site	Number of intervals	WMI (years)	Mean fire interval (years)	Lower 95% confidence level (years)	Upper 95% confidence level (years)	SE	Group
Did fire intervals vary among sites?							
GRR	148	25	27	22	32	0.1	b
KAY	222	16	18	15	21	0.1	a
LYT	296	16	18	15	21	0.1	a
BBE	160	18	22	18	26	0.1	a b
Did fire intervals vary among forest types at GRR?							
Persistent Shade Tolerant	53	32	33	26	41	0.1	b
Recent Grand fir	28	20	21	15	29	0.1	a
Recent Douglas-fir	58	23	24	18	30	0.1	a b
Persistent Ponderosa Pine	9	16	20	11	40	0.3	a b
Did fire intervals vary among forest types at KAY?							
Persistent Shade Tolerant	6	20	21	10	42	0.3	a
Recent Grand fir	49	17	19	14	25	0.1	a
Recent Douglas-fir	79	17	18	15	23	0.1	a
Persistent Ponderosa Pine	88	15	15	12	19	0.1	a
Did fire intervals vary among forest types at LYT?							
Persistent Shade Tolerant	97	19	20	17	25	0.1	a
Recent Grand fir	130	15	16	14	20	0.1	a
Recent Douglas-fir	28	14	15	10	23	0.2	a
Persistent Ponderosa Pine	41	14	15	11	20	0.1	a
Did fire intervals vary among forest types at BBE?							
Persistent Shade Tolerant	22	25	27	17	42	0.2	a
Recent Grand fir	54	19	25	16	38	0.2	a
Recent Douglas-fir	46	18	20	14	30	0.2	a
Persistent Ponderosa Pine	38	15	17	9	30	0.2	a

Note: WMI is the Weibull median interval, i.e., the 50th percentile of the fitted Weibull distribution. Groups sharing a letter are not significantly different ($p \le 0.05$). SE, standard error.

Historical fire regimes

Fires were frequent at all four sites; Weibull median intervals (i.e., the 50th percentile of the Weibull distribution fit to our fire intervals) ranged from 16 to 25 years per site (Table 2). Fires burned with a range of intervals at all sites, with most intervals (80%) from 6 to 46 years. At each site, fires were most frequent in the driest forest type (Persistent Ponderosa Pine, Weibull median interval 14–16 years) and least frequent in the most mesic type (Persistent Shade Tolerant, 19–32 years).

Plot, modeled as a random effect in our generalized linear mixed models, explained relatively little of the variation in fire intervals among sites (0.04301 ± 0.2074), suggesting that spatial autocorrelation among plots did not influence model outcomes. Modeled mean fire intervals were shortest at KAY and LYT (18 years) and significantly longer ($p \le 0.05$) at BBE (22 years) and GRR (27 years) (Table 2; Fig. 4). Within sites, fire intervals differed among forest types only at GRR, where Persistent Shade Tolerant plots had significantly longer intervals than Recent Grand Fir (33 years vs. 21 years, $p \le 0.05$; Table 2; Fig. 4).

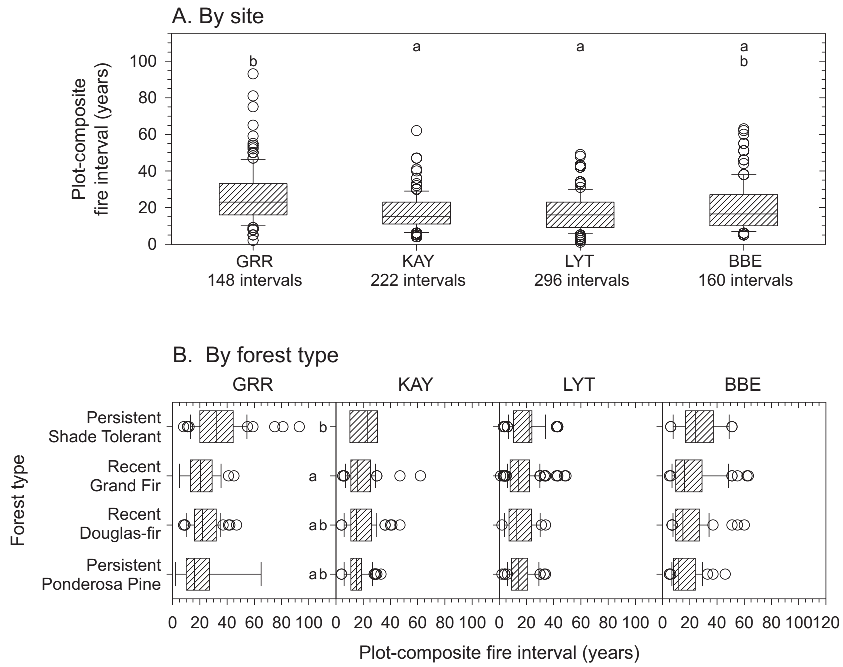
All four sites frequently sustained extensive low-severity fires that occasionally included small patches in which some or all of the trees were killed (Fig. 5A). For 111 fire years (25 to 33 fire years per site), we found evidence of fire at 1 to 26 plots, equivalent to 3% to 87% of the ~800 ha grids; however, most of these fires burned at least one margin of the grid and so may have been more extensive. Most of the 111 fire years were recorded only by fire scars (72%–82% of fire years per site; Fig. 5A). During the remaining fire years, cohorts occurred in 1 to 8 plots per year, or 3% to 27% of the ~800 ha grids. Plots with cohorts were almost always embedded in a more extensive fire recorded by fire scars, comprising 4% to 57% of the plots recording fire in a given year. For example, the 1688 fire at BBE was recorded in 17 plots; 14 of these had only fire scars, two had fire scars plus cohorts, and one had a single cohort. Only the 1870 fire at KAY had high-severity fire in a majority (57%) of the 14 plots in which it was recorded.

Patches of mixed- and high-severity fire were relatively small. Cohorts occurred in two or three adjacent plots (roughly 50–75 ha) during four fire years and in six adjacent plots (roughly 150 ha) during another fire year. In addition, most of the fires reconstructed from cohorts were not completely stand replacing in our plots; instead, some trees survived (4 ± 6 trees per plot). Only 34% of cohorts had no surviving trees, although more than half of these were survived by large trees within 80 m of the plot (i.e., those that we sampled for fire scars).

At most plots, although the fire regime was mixed in severity when considered over the analysis period, individual fires were more commonly low than high in severity. The severity index at most plots (91%) was less than 20, with only one plot having an index greater than 50 (Fig. 5B). This plot was classified into the Persistent Shade Tolerant forest type and had a single cohort (BBE21C; Supplementary Fig. S1[1]). It lies in a valley bottom and was dominated by grand fir that began recruiting into a cohort in the late 1700s. Most of the other plots with cohorts did not have only high-severity fires. For example, in plot BBE20F, all but one tree was killed during a widespread fire that burned across the site in 1688. Subsequently, 11 low-severity fires burned this plot over the next two centuries with no further evidence of high-severity fire. Neither cohorts nor severity indices occurred preferentially in any of the forest types (Figs. 5B and 5C).

The tree recruitment dates, fire-scar dates, and associated metadata that we collected for this study 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 (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/fire-history).

Fig. 4. Historical fire frequency at mixed-conifer sites in central Oregon (1650 to 1847–1890). (A) Intervals between fires of all severities, computed at each plot and then pooled by site (plot size 0.2 ± 0.1 ha for recruitment dates and 2 ha for fire scars). (B) The same fire intervals pooled by site and forest type (Merschel et al. 2014). The site–forest type categories include 52 ± 33 intervals, although two categories had only a few intervals (six in KAY Persistent Shade Tolerant and nine in GRR Persistent Ponderosa Pine; Table 1). Boxes enclose the 25th to 75th percentiles of the distribution of fire intervals, whiskers enclose the 10th to 90th percentiles, circles are all intervals outside these percentiles, and the line across each box is the median. In both panels, lowercase letters a and b indicate groups with similar fire intervals, identified by generalized linear mixed models. This modeling did not find significant differences in fire intervals among forest types at KAY, LYT, or BBE.



Discussion

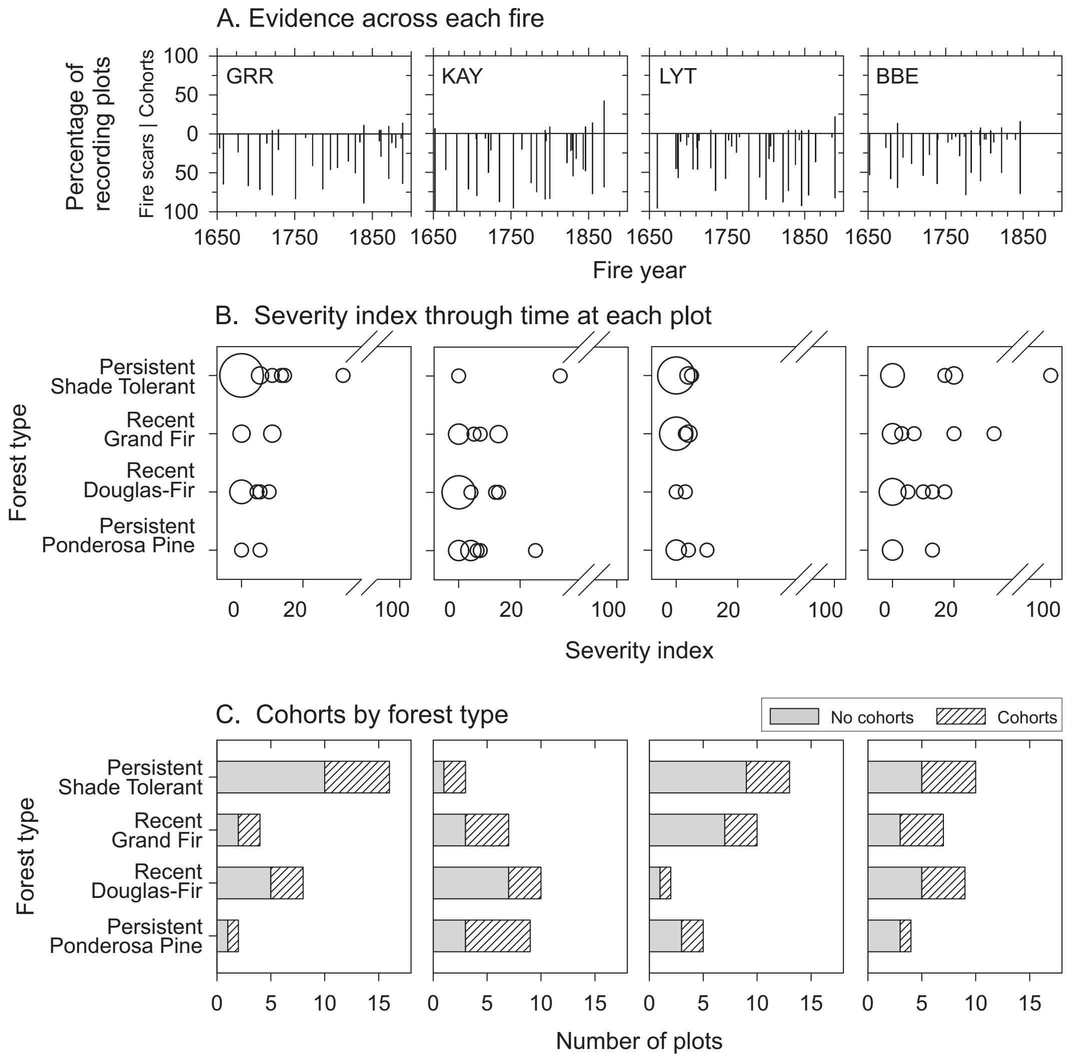
All four of our sites historically sustained frequent, often extensive fires with primarily low-severity effects and occasional patches of high- or mixed-severity effects, consistent with other landscape-scale tree-ring reconstructions in mixed-conifer forests elsewhere in eastern Oregon and Washington (Supplementary Table S1[1]; Merschel et al. 2018) and with modern fires (e.g., Lentile et al. 2005). We found little evidence for extensive high-severity fires. For example, at BBE 49, trees recruited between 1692 and 1710, the largest number of trees recruited during any 30-year period at any of our sites (Fig. 3). We identified cohorts in three plots from 28 of these recruitment dates; however, these cohorts likely did not establish in response to an extensive high-severity fire because some trees survived through this period at almost all of these plots (Supplementary Fig. S1[1]). Cohorts could have established locally in response to a small patch of high-severity fire or another disturbance, but we found no evidence of extensive high-severity fire.

Significant differences in fire frequency among some sites likely did not result from differences in natural ignition patterns but may have resulted from other environmental differences. At regional scales, the densities of lightning strikes and lightning-ignited fires are similar among all four sites (Rorig and Ferguson 1999); however, fires may have occurred less often at GRR in the Cascades because this site may have a shorter fire season, the period when weather and fuel conditions are favorable for fire spread (Riley and Loehman 2016). The median snow-off date at GRR is about one month later than in the Ochocos based on data from the four snow survey sites with elevations similar to our sampling sites (Derr, Ochoco Meadows, Hogg Pass, and McKenzie sites, 1981–2010; https://www.wcc.nrcs.usda.gov/snow/). Topographic position may have increased the pyric isolation of those sites, limiting fire spread from neighboring regions (Merschel et al. 2018); there is a steep canyon to the west of GRR, and BBE lies near the forest boundary in close proximity to an arid region. Alternatively, the effect sizes detected by the model may be statistically significant but not ecologically relevant (Martínez-Abraín 2008).

Although fire occurrence depends on locally dynamic conditions of weather and fuel moisture, regional ignition patterns, climate, and topography (Parisien and Moritz 2009; Holden and Jolly 2011), it is not surprising that fire regimes were similar among the forest types that we analyzed because they occur in a fine-grained mosaic lacking significant barriers to fire spread. This finding is consistent with a lack of variation in historical fire frequency among forest types elsewhere in the region where barriers to fire spread are absent (Heyerdahl et al. 2001; Johnston et al. 2016).

Computing an index of severity allowed us to quantify variation among mixed-severity fire regimes that are often lumped into a single broad class (Daniels et al. 2017). For example, the severity index in our mixed-conifer plots averaged 6 compared with an average of 42 in dry lodgepole pine (*Pinus contorta* Douglas ex Loudon) plots elsewhere in the region where fire intervals are longer (mean fire intervals of 26–82 years) and patches of torching fire were common (Heyerdahl et al. 2014). At most of our plots (91%), the severity index was less than 20; only one plot had a severity index greater than 50 (BBE21C; Supplementary Fig. S1[1]). In contrast, most plots at the lodgepole pine site (57%) had severity indices greater than 20 and seven plots had indices of 100. The highest severity indices that we reconstructed for the mixed-conifer forests in this study occurred in the most mesic forest type (Persistent Shade Tolerant) at all sites except LYT (Fig. 5B), and it is likely that mesic mixed-conifer and subalpine forest types at higher elevations in the region would also have higher severity indices. Our index of severity may be affected by the fading record in tree demography; however, most of the plots that lack demography trees early in the analysis period have fire-scarred trees that record low-severity fires during the entire analysis period. Adding

Fig. 5. Historical fire severity at four mixed-conifer sites in central Oregon during the analysis period (1650 to 1847–1890). (A) The distribution of plots by evidence type (fire scars versus cohorts) for each fire year. (B) Severity index, where 0 indicates a low-severity fire regime at a plot through time, 100 indicates a high-severity regimes, and values in between indicate mixed-severity regimes. Symbols are proportional in area to the number of plots (range 1 to 10 plots). (C) Distribution of plots by forest type, indicating number of plots with cohorts during the analysis period.



more trees in this early period might identify new cohorts, but it might also identify more trees with evidence of low-severity fire, so there is no a priori reason to expect that the index would be shifted one way or the other.

Shrubs are currently abundant at our Cascades site (Figs. 1G, 1H, 2C, and 2D) but may not have been in the past. Most of the plots at our Cascades site, but only a minority of plots at our Ochocos sites, are locally classified into wet mixed-conifer forest plant-association groups (93% and 25%, respectively; Simpson 2007). However, all four sites are similarly warm and dry during the fire season (Figs. 2E and 2F) and burned frequently in the past (Fig. 3). These fires are likely to have prevented long-term accumulation of high shrub biomass at any of the sites. Furthermore, all the common shrubs at the Cascades site are adapted to survive and, in some cases, thrive with frequent fire (Supplementary Table S2[1]). This site would likely have been classified as dry mixed-conifer before frequent fires were excluded in the late 1800s (Merschel et al. 2014). Finally, high shrub cover was associated with crown damage during modern fires in this area (Thompson and Spies 2009), suggesting that frequent, low-severity fires may have inhibited shrub ladder fuels and reduced the probability of extensive severe fires, consistent with the lack of such fires in the historical regime that we reconstructed there.

The historical fire frequencies assigned by a national mapping effort are consistent with our tree-ring reconstructions in the Ochocos but not in the eastern Cascades, likely because some forest types were misclassified on the national map. The LANDFIRE program has comprehensively mapped mean fire intervals across the United States (LANDFIRE 2001). In the Ochocos, mean fire intervals < 40 years dominated both our reconstructions and LANDFIRE (95% of tree-ring plots and 96% of pixels, respectively; LANDFIRE 2010). In the eastern Cascades, mean fire intervals < 40 years also dominated our reconstructions (79% of tree-ring plots) but were mapped on only 4% of LANDFIRE pixels. Mean fire intervals mapped by LANDFIRE are linked directly to the mapping of potential vegetation classes (biophysical settings). At our Ochocos sites, the biophysical settings and therefore mean fire intervals mapped by LANDFIRE are consistent with our tree-ring data in which 89% to 95% of land area at these sites is mapped as dry ponderosa pine or ponderosa pine – Douglas-fir biophysical settings. In contrast, our Cascades site is also dominated by dry forests, but about 66% of this site is mapped as more mesic biophysical settings dominated by Douglas-fir, grand fir, western hemlock, and silver fir, with corresponding mean fire intervals of 50 to 200 years. This misclassification may have resulted from the steep environmental gradients at this site. Our comparison suggests that the LANDFIRE vegetation and historical fire regimes may need to be adjusted for our eastern Cascades site before they are used for local projects. The need for such local adjustments is recognized by LANDFIRE, which was designed for use at regional and national scales (Rollins 2009).

The high-severity component of mixed-severity fire regimes becomes more difficult to detect further back in time as mortality from subsequent fires and other factors erodes the original cohort, termed the "fading record" problem in historical ecology. Tree demographic evidence is more prone to the fading record problem than the fire-scar record because young trees that are killed by fire decompose quickly in central Oregon and so are lost from the tree-ring record, whereas resinous, fire-scarred ponderosa pine are well preserved. However, two considerations bolster our confidence in the mixed-severity regimes that we inferred for our sites in central Oregon. First, although we assigned most cohorts to fire dates in the 1800s (77%), we did detect some older cohorts in the 1700s (15%) and 1600s (8%). Thus, either mixed-severity fires did not occur as often in the distant past or, more likely, we failed to identify some cohorts from the early part of the record because they were destroyed by subsequent fires or decay. However, even if we were to assume a constant rate of cohort recruitment, i.e., that the same number of cohorts recruited from 1650 to 1799 as recruited in the 1800s when our record is presumably more complete, the resulting 103 plot-level cohorts would still comprise only 13% of total fire dates and our inference of a mixed-severity regime dominated by low-severity fire would still hold. Second, a recent analysis of the fading record problem (Naficy 2017) used age structure and fire-scar dates from three of our sites (GRR, KAY, and LYT) with increasing numbers of fires, i.e., progressively further back in time, and inferred a relatively low rate of loss in stand density, supporting our inference of a primarily low-severity fire regime. New methods of sampling tree-ring data, including age structure, and interpreting fire severity from tree age structure have been developed to address some of the limitations in reconstructing historical fire regimes from post-fire cohorts that we have discussed here (Tepley and Veblen 2015; Naficy 2017).

On the other hand, we assumed that all cohorts recruited after fire, so we may have reconstructed more high-severity fire than actually occurred because cohorts can recruit following any disturbance that creates canopy gaps, e.g., insect outbreaks, wind, or drought, and cohorts elsewhere establish during periods of fire quiescence (e.g., Brown and Wu 2005), especially following the onset of fire exclusion in the past century (O'Connor et al. 2017). Our inferences of postfire recruitment could have been supported by the death dates of trees killed by fire, but the nonresinous portions of dead trees are poorly preserved in central Oregon, so we obtained few death dates.

Although we have confidence in the general fire regime characteristics that we inferred for our sites, inferring historical mixed-severity fire regimes from tree rings remains challenging, and much is left to learn in central Oregon. Our sampling was limited to mixed-conifer forests that historically included some component of ponderosa pine. In the Ochocos, we sampled 1.4% of the area in the two biophysical settings groups that dominate the Ochoco National Forest (Ponderosa Pine-1 and Ponderosa Pine – Douglas Fir-1; 86% of forested area; LANDFIRE 2010). In contrast to the smaller Ochoco Mountain range, which covers only ~1° of latitude, the eastern Cascades cover many degrees of latitude and include a steep longitudinal gradient in elevation and environment, but we sampled across only a small portion of this variation. We did not sample extensive areas of mesic mixed-conifer forest, which may have sustained more high-severity fire, nor did we sample very dry ponderosa pine that occurs in monospecific stands or with western juniper. Furthermore, the historical distribution of fire sizes is poorly known, especially for extensive fires. We sampled over ~800 ha per site but likely did not capture the full extent of most fires; elsewhere, more than a third of the historical low-severity fires in similar mixed-conifer forests burned at least 1500 ha at a site ~100 km to the south-southwest (Merschel et al. 2018).

Mixed conifer forests in the Pacific Northwest are an important component of regional ecosystem diversity (Hessburg et al. 2016), which must meet multiple management objectives, including timber, watershed resources, wildlife and botanical habitat, recreation, and cultural history. Fire regimes of these systems are intrinsically complex and defy simple categorization. Our study illustrates gradients of continuous variation in fire severity in space and time, which can present a formidable challenge to land managers, especially in the face of increasing climate pressure (Kitzberger et al. 2017). Recognition of this inherent variability can form the basis for management that avoids "one size fits all" approaches (Hessburg et al. 2016).

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