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ARTICLE

Vegetation Ecology

Diverse historical fire disturbance and successional dynamics in Douglas-fir forests of the western Oregon Cascades, USA

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Abstract

We created the first annually resolved records of historical fire occurrence coupled with precise estimates of tree establishment for the northern half of the west slope of the Oregon Cascades, a region that is home to some of the most productive forests on earth. Our reconstructions at 36 randomly located sites document exceptional diversity in historical fire disturbance and successional dynamics. Most stands where we collected data appear to have initiated following stand-replacing fire between 200 and 750 years ago, although many sites exhibited evidence of moderate-severity fire that created multi-aged stands. More than two-thirds of sites experienced multiple non-stand-replacing fires following stand initiation. A spatial generalized linear mixed model demonstrated that historical fire occurrence was negatively associated with average snow disappearance day and time since last fire and positively associated with drought. Significant variability in the number of fires, length of fire return intervals, and sample depth across sites made calculation of informative mean fire return intervals (MFRIs) difficult. Site-level annual probability of fire from our mixed model ranged from 0.039 to 0.003, equivalent to MFRIs of 26–389 years. We used fire and tree establishment records to infer the general location of several large historical fire events that likely burned as much or more area as the >50,000 ha fires that burned across our study region in 2020. We also identified periods of extensive burning and subsequent tree establishment that occurred across seven centuries within six large river drainages that made up our study region. Although tree establishment occurred for up to a century following stand-replacing fire at some sites, we show that these apparent long periods of establishment were relatively short pulses of regeneration separated by reburns. This study demonstrates that many highly productive Douglas-fir-dominated stands in western Oregon are significantly departed from historical fire disturbance regimes. Management that emphasizes rapid re-establishment of closed canopy forest conditions following fire and development of old-growth forest conditions in the absence of fire may fail to provide for the unique and highly valued ecosystem services associated with these forests.

KEYWORDS
dendroecology, Douglas-fir, moderate-severity fire, non-stand-replacing fire, North American Fire-Scar Network (NAFSN), stand-replacing fire, succession, tree ring fire history, western Oregon Cascades, wildfire

INTRODUCTION

Fire is a key influence on forest structure, composition, and provision of ecosystem services (e.g., Bowman et al., 2009; Driscoll et al., 2010; Hurteau & Brooks, 2011; Lee et al., 2015). Understanding the range of variability in the historical fire regime of different forest communities over long time periods informs adaptation to the rapid environmental change expected this century (Bergeron et al., 2002; Morgan et al., 1994; Mote et al., 2003). Extensive tree ring-based reconstructions of fire occurrence have provided scientists and managers with reliable knowledge of the historical range of variability of fire in dry interior forests of the American West (Falk et al., 2010; Harley et al., 2018). But there remain important gaps in our knowledge of historical fire regimes (Margolis et al., 2022). In particular, there are no annually resolved reconstructions of historical fire occurrence in the moistest and most productive coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*)-dominated forests in the north portion of the west slope of the Cascades Mountains of Oregon.

Western Oregon Cascades forests (hereafter, "westside forests") are nationally and globally significant resources that serve as models for conservation of late successional habitat (Thomas et al., 2006). They store more carbon than any other terrestrial system and are the most productive softwood timberlands in the United States (Adams & Latta, 2007; Hudiburg et al., 2009; Smithwick et al., 2002). They are key components of water supply and storage systems, provide critical habitat for threatened, endangered, and sensitive species, and are iconic cultural legacies (Murphy et al., 2018; Ruggiero et al., 1991). An older model of stand development attributes the complexity of westside forests to stand-replacing fire that resets succession at coarse (10^3–10^4 ha) spatial scales followed by a long fire-free period with stand development driven primarily by competition and fine-scale disease and windthrow disturbance (Agee, 1996; Franklin et al., 1981, 2002; Franklin & Hemstrom, 1981).

The central role of large stochastic fire events in models of westside forest dynamics owes much to scientists' and managers' experience with a series of large wind-driven fires (e.g., Cowlitz, Yacolt, and Tillamook fires) that burned a total of ~100,000 ha across southwestern Washington and northwestern Oregon between 1886 and 1951 (Agee, 1996; Tepley, 2010). Recent fire events in northwestern Oregon may have tended to reinforce the view that infrequent fires resulting in extensive mortality over large areas are a distinguishing feature of westside Douglas-fir systems (Reilly et al., 2022). In late summer 2020, almost 300,000 ha—three-quarters of the total area burned in the last 70 years in this region—burned in just 72 h by fires driven by sustained winds from the east with speeds in excess of 9 m s^{-1} and gusts up to 27 m s^{-1} (Abatzoglou et al., 2021; Higuera & Abatzoglou, 2021; Mass et al., 2021).

Although large high-severity fires are clearly an important feature of westside Douglas-fir forests over the last ~150 years, low- and moderate-severity fire makes up the largest portion of contemporary fire perimeters (Dunn et al., 2020; Johnston et al., 2019; Reilly et al., 2017). And the handful of studies of historical fire disturbance undertaken in westside forests in recent decades report complex fire dynamics during earlier time periods. Morrison and Swanson (1990) and Weisberg (2004) noted multiple nonlethal fire injuries in Douglas-fir stands in study sites in western Oregon and western Washington that were formed 150–600 years BP. Tepley et al. (2013, 2014) inferred multiple non-stand-replacing fires from analysis of tree establishment in the central Oregon Cascades. Merschel et al. (2024) and Johnston et al. (2023) created annually resolved fire histories and records of tree establishment in the central-southern portions of the Oregon Cascades and reported mean fire return intervals (MFRIs) in Douglas-fir-dominated stands ranging from 19 to 150 years. Many older Douglas-fir-dominated forest stands in these study areas exhibited multiple fire-initiated tree cohorts.

Several studies suggest periods of widespread burning followed by extensive tree regeneration resulted in distinctive tree cohorts present in today's old-growth forest stands across the western Oregon Cascades. These hypothesized periods of widespread fire and tree establishment include the 1800s, the late 1400s through the

1500s, and potentially also the period between 1100 and 1300 (Tepley, 2010; Weisberg & Swanson, 2003). Tepley (2010) suggests relatively fire quiescent periods from the mid-1300s through the mid-1400s CE and during the early to mid-1700s CE. A better understanding of the historical extent and tempo of fire and tree establishment will inform adaptation to recent increases in area burned in western Oregon (Reilly et al., 2022).

Studies of succession following historical fire in westside forests report equivocal and sometimes contradictory findings. Early studies of regeneration following large stand-replacing events in the early 20th century (e.g., Munger, 1940) reported re-establishment of forest cover across burned areas within a decade after fire. Winter et al. (2002) reported overstory establishment that lasted just two decades and development of high-density closed canopy forest conditions in just 40 years following stand-replacing fire approximately 500 years ago at a study site in southwestern Washington state. But another study in 180- to 330-year-old stands in western Oregon and Washington reported establishment periods of 50–70 years (Freund et al., 2014). Field counts of stumps in western Oregon clearcuts found that overstory trees often established over more than 100 years, suggesting low-density stands that established slowly over time from distant seed sources or as the result of multiple disturbance events during stand initiation (Poage & Tappeiner, 2002). The somewhat ambiguous conclusions about the nature of stand initiation in westside Douglas-fir forests from previous research may result from the failure of previous studies to cross-date wood samples and integrate both fire scar and tree establishment lines of evidence (see Johnston et al., 2023; Merschel et al., 2024).

Different interpretations of the relative influence of stand-replacing and non-stand-replacing fire and succession following fire may also reflect considerable biophysical variability across westside forests. Both topography and climate influence fire by modulating the amount, type, arrangement, continuity, and moisture of fuels available to fire, as well as the potential for convection and radiation transfer of heat energy during fire events (Parisien & Moritz, 2009; Rothermel, 1983). Stand history, including stand age and past history of fire, may also influence wildfire by selecting for particular types and arrangements of vegetative fuel (Heinselman, 1981; Romme & Knight, 1981; Tepley et al., 2018). Finally, the tempo of lightning ignitions and the weather conditions associated with ignitions may influence the frequency and extent of fire (Rorig & Ferguson, 1999).

Our previous work developing long-term records of fire and tree establishment in the western Cascades to the south of the landscape investigated here showed that several strongly correlated variables that modulate fuel moisture were highly explanatory of variability in fire frequency between data collection sites, including elevation, average maximum vapor pressure deficit (VPD), average maximum summer temperature, and average snow disappearance day (Johnston et al., 2023). Fire occurrence at most of these sites was also associated with increased drought severity as measured by reconstructed Palmer Drought Severity Index (PDSI). But fire at some sites was not related to drought severity, one of several lines of evidence that suggests an important role for Indigenous use of fire in the historical period (Coughlan et al., 2024; Johnston et al., 2023).

The goal of the present study was to build annually resolved records of fire and tree establishment throughout the moistest and most productive Douglas-fir forests of the western Oregon Cascades. Specific research objectives include (1) quantifying variability in historical fire occurrence across a high biomass forested region; (2) quantifying the biophysical, climatic, stand history, and lightning ignition drivers of historical fire occurrence; (3) identifying the location and extent of past large stand-replacing fire events and/or periods of heightened burning that synchronized tree establishment over large areas; and (4) characterizing temporal patterns of post-fire Douglas-fir establishment.

METHODS

Study region

We reconstructed historical fire occurrence on national forest land managed by the U.S. Forest Service across those portions of the Mt. Hood National Forest found west of the crest of the Cascades and the Willamette National Forest south to the upper Middle Fork Willamette River drainage (Figure 1), a total area of approximately 922,000 ha. This landscape is strongly associated with extensive old, structurally complex, high biomass Douglas-fir forests (Franklin & Waring, 1980). Wildfires in these forests have tremendous impacts on wildlife habitat, timber supplies, recreational opportunities, and water quality (Flitcroft et al., 2023; Hulse et al., 2016; Johnson et al., 2023).

The climate of this region is maritime influenced with cool wet winters and warm dry summers. Thirty-year average annual precipitation ranges from 1600 to more than 4000 mm per annum (mean for study region = 2144 mm), 86% of which falls from October to April. Thirty-year normal monthly mean temperatures range from 17.0 and 17.1°C during the hottest months of July and August, respectively, and 1.3 and 1.8°C during the coldest months of January and February, respectively. Elevations across our

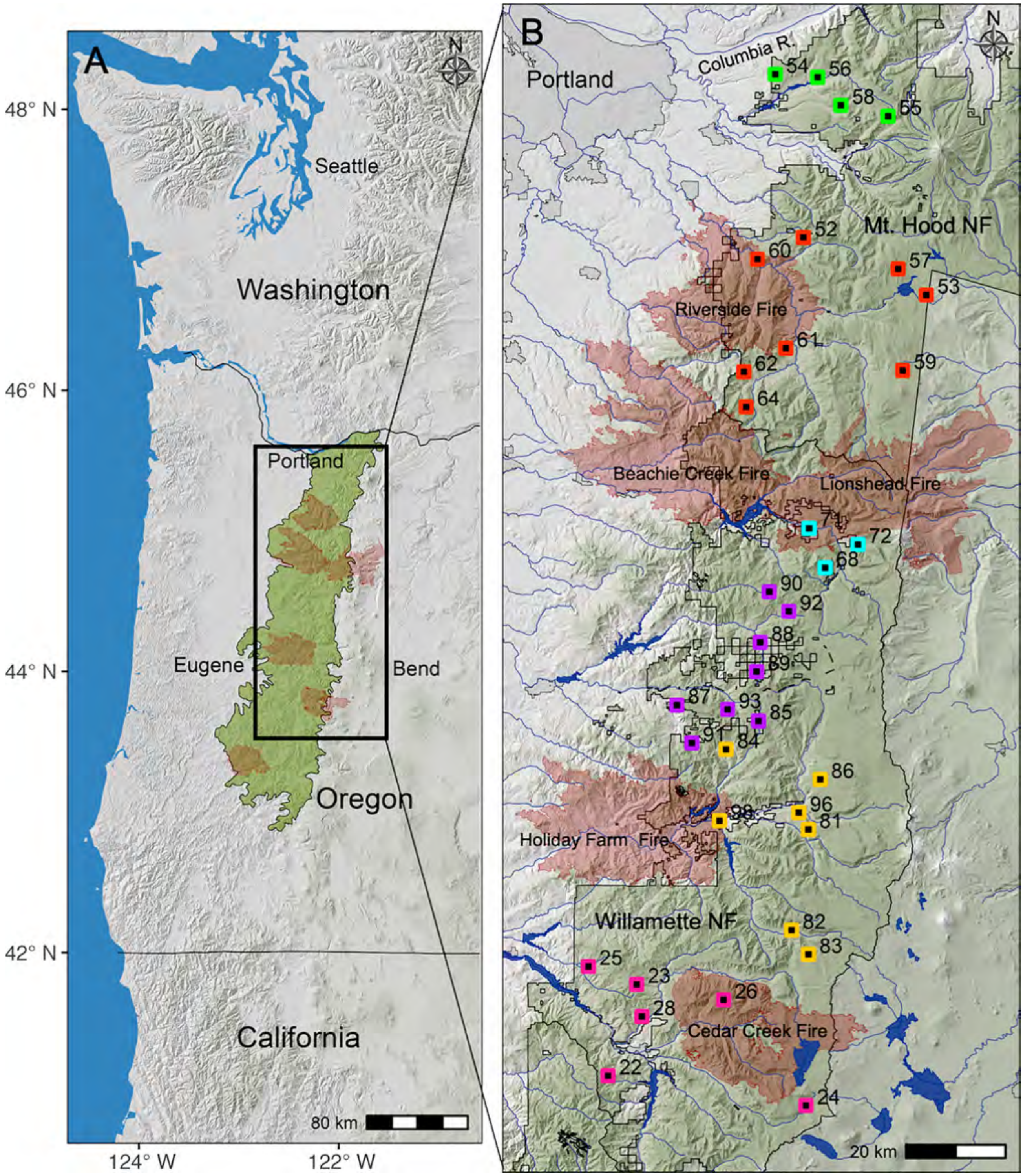


FIGURE 1 (A) Map showing the Pacific Northwest with the western Oregon Cascades shaded in green and all fires ≥25,000 ha that burned between 1984 and 2024. From north to south: Riverside (2020; 53,378 ha), Beachie Creek (2020; 73,896 ha), Lionshead (2020; 78,064 ha), Holiday Farm (2020; 67,097 ha), Cedar Creek (2022; 45,441 ha), and Archie Creek (2020; 50,788 ha) fires. (B) Study region map showing the Mt. Hood and Willamette National Forests and randomly located study sites ($n = 36$) color coded by large river drainages. From north to south: the Lower Columbia-Sandy, Clackamas, North Santiam, South Santiam, McKenzie, and Middle Fork Willamette River drainages.

study region range from 60 m near the Columbia River to 3429 m at the top of Mt. Hood, although most of the study region lies between 500 and 2000 m. The majority of precipitation that occurs below 450 m falls as rain, while most precipitation above 1200 m falls as snow, which can persist through the end of June at upper elevations. Between 450 and 1200 m lies the transient snow zone where snow level fluctuates throughout the winter as warm and cold fronts transit the Cascades and rain on snow events occasionally result in significant flooding in western Oregon (Perkins & Jones, 2008).

Historical and ethnographic information about Indigenous use of our study region is limited. Standard accounts (e.g., Zenk & Rigsby, 1998) refer to this region as the ancestral homeland of the Molalla people, who are thought to have wintered in the lower elevation portions of western Cascades river valleys and engaged in extensive harvest of plant and animal resources in the uplands from the spring through the fall. Sources suggest that both the Kalapuya who resided in the Willamette Valley and a number of people living in eastern Oregon, including but not limited to the Tenino, Wasco, Klamath, Paiute, and Cayuse people, occupied the western Cascades on a seasonal basis (Baxter, 1986). Native peoples were forcibly removed to reservations in the 1850s through the 1860s, although traditional uses of national forests by people traveling from reservations were documented well into the 1940s and continue to this day (Bergland, 1992; Lewis, 2014, 2023).

Field data collection and data processing

We randomly located a total of 36 study sites to collect data (Figure 1B). We constrained random location procedures so that these sites fell outside of wilderness areas where the use of chainsaws is prohibited. We also constrained random location procedures so that sites fell within every ranger district of both national forests roughly in proportion to the non-wilderness area of each district to ensure that study sites were widely distributed across the study region. We visited each point and relocated most sites to the nearest clearcut harvested between 30 and 60 years ago because our past research on national forests in the western Cascades demonstrated that stumps in clearcuts of that age often held multiple fire scars and pith dates preserved by resin (Johnston et al., 2023). We do not believe that relocating points to the nearest clearcut relatively close to a road biased fire history reconstruction since roads are ubiquitous across all landforms and clearcuts are typically staggered along roads in a non-biased patchwork fashion across the non-wilderness portion of our study region (Figure 2).

Our goal at each study site was to collect partial cross sections from stumps that contained cambial scars that allowed us to create annually resolved fire records. Whenever possible, partial cross sections included the pith of the tree from close to the root collar to allow us to estimate the dates when trees established. We constrained the area we searched for dead wood at each site so that samples were taken from a relatively small area with homogenous slope and aspect and no major barriers to fire spread to ensure that the composite fire histories we created for each site did not overestimate fire occurrence by including fires that did not spatially overlap (Baker & Ehle, 2001; Johnston et al., 2023). Most data collection sites were small (mean = 1.8 ha), although data collection at a few relatively flat sites with no barriers to fire spread were as large as 11 ha (Table 1). Between 2021 and 2022, we used chainsaws to remove 1–3 partial cross sections from 9 to 24 (mean = 17.2) stumps from each site.

We applied glue as necessary, surfaced wood samples with a 30-cm jointer or 51-cm planer, and sanded samples to a high polish. Between 2021 and 2023, we cross-dated all tree rings present on each sample and assigned a calendar year to cambial injuries and to the pith, when present. In cases where the pith was not present but the last ring present was within 10 years of the pith, we estimated the pith year by overlaying wood samples with transparent concentric circles that matched wood sample growth patterns. Cambial injuries determined to be caused by fire were retained for subsequent analysis (Figure 3). When possible, we noted the season when fire occurred based on the position of the scar within each tree ring. Detailed descriptions of methods for diagnosing fire damage within wood samples from large and old Douglas-fir are found in Merschel et al. (2024) and Johnston et al. (2023).

Comparison with other regions and fire histories

An important objective of this study was to quantify variability in historical fire occurrence across some of the moistest and most productive forests found in North America. To contextualize the biophysical setting of our study sites relative to other forested areas and past dendroecology research, we compared net primary productivity (NPP), 30-year average annual precipitation, and 30-year average maximum monthly temperature among the 36 different sites where we collected data and: (1) a total of ~932,000 points systematically located 1 km apart across forested regions of the western United States; and (2) the location of 1666 western US fire history reconstruction sites from the North American Fire-Scar Network (NAFSN). NAFSN is the most comprehensive existing database of tree ring-based fire history research (Margolis et al., 2022). We

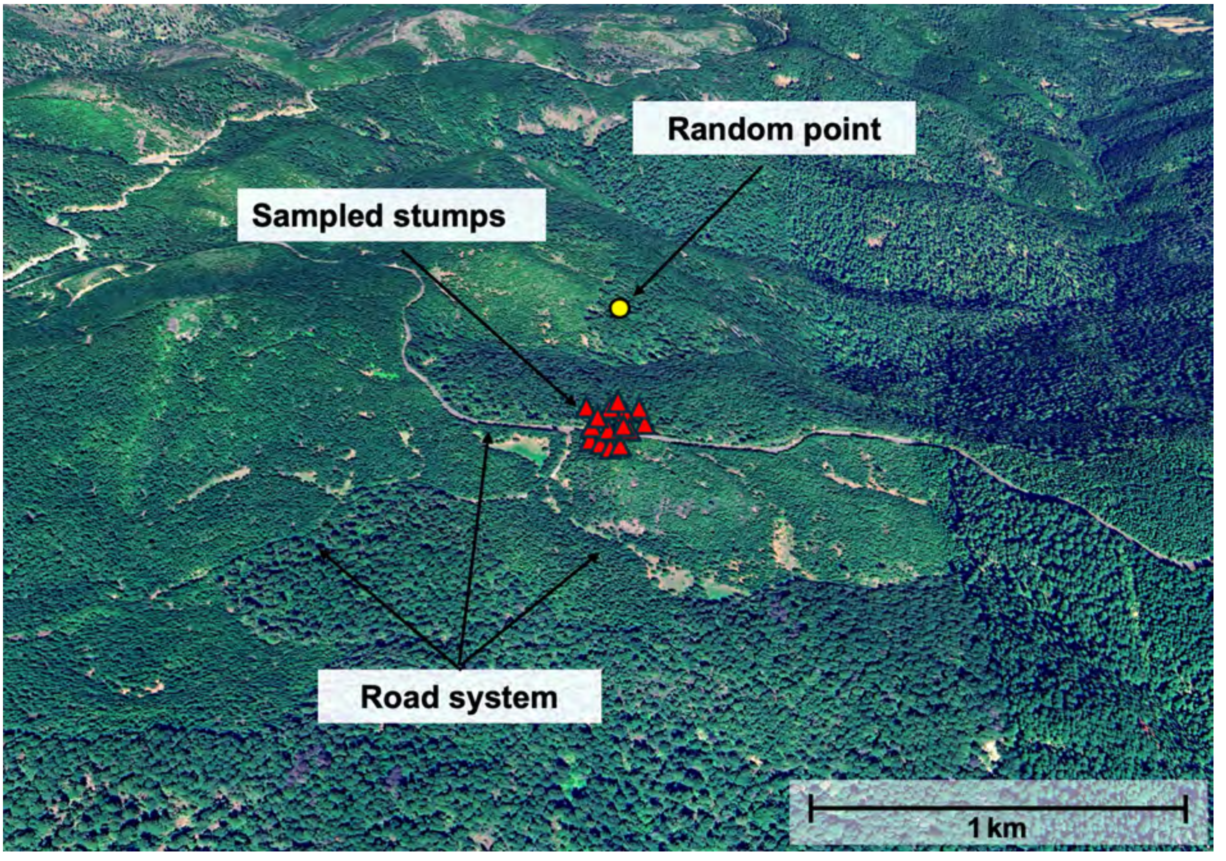


FIGURE 2 Overhead view of a typical data collection site (site 22) consisting of 15 sampled stumps within a 0.4 ha area (image: Google Earth). At most sites, data collection was relocated a short distance from a randomly located point to the nearest clearcut near a road to be able to more conveniently sample large partial cross sections. In this example, we moved site 22 data collection from an unlogged stand approximately 400 m to the south to be closer to a road and within a recent clearcut.

identified forested regions using the National Land Cover Database (Homer et al., 2015). Average annual precipitation and maximum temperature (obtained from the PRISM Climate Group; https://prism.oregonstate.edu) are strongly correlated with contemporary fire occurrence (Westerling, 2008). NPP, the difference between total carbon synthesized during photosynthesis and total carbon released during respiration, represents the inherent productivity of vegetation (Pan et al., 2014).

We tested for differences between NPP, precipitation, and maximum temperature between our systematic grid across the western US forested landscape, past fire studies collected in the NAFSN, and the present study using spatial permutation tests. Our custom R code (R Core Team, 2023) first calculated the observed mean for each of the three environmental variables across all 36 of our study sites. We then randomly sampled 36 points from the forested western US grid and 36 points from the NAFSN fire history sites without replacement and computed the mean of sampled values. We repeated this resampling 10,000 times to generate a null distribution of permuted means. Then we calculated a two-tailed empirical p value as the proportion of permuted means that were greater than or the same as the study site mean relative to the permutation distribution.

Fire history metrics

We began our analysis of fire history data by calculating a variety of statistics of fire occurrence for each site, including a site-level composite MFRI and the coefficient of variation (CV) of fire return intervals for each site (SD of intervals divided by mean of intervals). We limited this analysis to years prior to 1900 because we were interested in influences on fire prior to the establishment of the national forests and adoption of fire exclusion policies in the late 1800s through the early 1900s. The Mt. Hood and Willamette National Forests were originally established as forest reserves in 1893 and became national forests between 1905 and 1908 (Clary, 1986; Rakestraw & Rakestraw, 1991).

A composite site MFRI (calculated by dividing the length of the tree ring record for each site by one less

TABLE 1 Site characteristics and fire history metrics for the western Oregon Cascades study region.

Site	Site area (ha)	Elevation (m)	Slope (%)	Aspect	Years recording	No. fires	First fire	Last fire	Fire interval		MFRI	MFRI CV	Annual prob. fire	Model-based MFRI	Model-based MFRI CIs
									Min	Max					
55	0.45	1286	26	SW	246	4	1695	1874	44	78	59.7	0.29	0.011	92	60–141.4
58	0.83	1159	23	S	408	7	1499	1882	4	144	63.8	0.96	0.013	79.4	57.2–110.4
54	1.71	740	9	SW	384	7	1499	1784	6	132	47.5	1.06	0.017	59.3	41.1–85.8
56	1.51	488	20	SW	395	3	1546	1725	77	102	89.5	0.2	0.012	80.1	54.6–117.6
57	0.51	1327	13	W	226	3	1690	1714	10	14	12	0.24	0.01	103.5	65.5–164
62	1.35	1148	27	NE	235	1	1709	1709	...	...	...	...	0.006	160.9	107.7–240.8
53	1.98	1071	0	N	636	10	1320	1782	8	123	51.3	0.95	0.014	73.2	41.5–129.8
59	1.33	1162	16	E	556	1	1653	1653	...	...	...	...	0.007	149.3	91.1–245.2
64	1.22	1142	31	E	196	...	...	...	...	...	...	...	0.006	175.4	115.1–267.7
52	2.22	1206	19	S	476	8	1438	1896	8	168	65.4	0.83	0.014	72.6	55.8–94.7
61	1.3	877	28	SE	187	2	1723	1860	137	137	137	...	0.011	87.1	61.3–124.1
60	1.61	295	44	W	201	2	1765	1836	71	71	71	...	0.013	75	38.2–148.1
68	0.87	1240	29	SW	414	2	1522	1530	8	8	8	...	0.005	185.4	112.8–305.1
71	5.19	582	29	SE	261	10	1689	1883	4	49	21.6	0.69	0.023	43.3	29.6–63.5
72	0.75	900	31	SE	730	3	1467	1682	12	203	107.5	1.26	0.009	110.4	66.1–185.1
85	0.13	1393	61	NE	196	1	1812	1812	...	...	...	...	0.003	389.2	71.4–2141.3
90	0.31	1228	28	SW	376	1	1560	1560	...	...	...	...	0.004	243	145.8–405.4
89	0.83	1125	20	SE	355	3	1619	1730	16	95	55.5	1.01	0.007	133.7	84.2–212.6
92	0.56	1042	18	W	616	1	1496	1496	...	...	...	...	0.005	204.1	130.2–320.4
93	1.55	980	31	W	704	6	1617	1895	8	142	55.6	1	0.009	106.9	65.2–175.5
88	0.43	838	24	SE	327	1	1849	1849	...	...	...	...	0.007	149.8	103.3–217.5
87	1.15	845	19	NW	375	3	1536	1868	20	312	166	1.24	0.011	91.2	59.4–140.3
91	5.41	828	7	NE	724	7	1508	1700	14	73	32	0.71	0.013	76	47.8–121.3
83	0.9	1382	27	W	393	10	1522	1896	1	125	41.6	0.97	0.02	49.6	33.3–74.1
86	3.12	1001	17	NW	188	4	1733	1835	11	52	34	0.62	0.015	66.1	47.9–91.3
84	0.32	1025	28	SE	455	2	1552	1892	340	340	340	...	0.009	107.9	58.7–199.3
81	2.7	916	18	SW	262	1	1704	1704	...	...	...	...	0.012	82.1	60.2–112.1
82	1.13	826	19	S	274	15	1633	1889	1	85	18.3	1.2	0.039	26	18.7–36.3
96	11	527	5	SE	385	9	1741	1836	4	38	11.9	0.95	0.018	56.2	36.2–87.6
98	1.06	361	2	NW	305	5	1706	1877	5	93	42.8	0.86	0.019	52.7	31.4–88.8
26	0.83	1427	30	W	407	3	1740	1812	29	43	36	0.27	0.008	125.8	71–223.6
24	5.4	1541	29	SE	453	3	1648	1712	10	54	32	0.97	0.007	136.2	94.3–196.7
22	0.35	1158	9	NE	119	1	1807	1807	...	...	...	...	0.011	94.4	58.7–152.2
23	4.61	1012	17	SE	336	5	1615	1846	11	149	57.8	1.07	0.013	78.1	57.3–106.5
25	0.66	553	18	NE	338	4	1690	1870	13	141	60	1.17	0.012	81.4	52.8–125.9
28	0.34	530	28	SE	386	9	1568	1875	5	168	38.4	1.39	0.021	47.2	28.9–77.7
Mean	1.82	976.7	22.2	...	375.7	4.48	1625	1788	32.5	116.3	65.0	0.87	0.012	109.6	...
Range	0.13–11	295–1541	0–61	...	119–730	0–15	1320–1849	1496–1896	1–340	8–340	8–340	0.2–1.39	0.003–0.039	26.0–389.2	...

Note: Fire history metrics are based on all years prior to 1900. Mean fire return interval (MFRI) was calculated from the intervals between cross-dated fires when at least two such intervals were available. Model-based MFRI was derived as the reciprocal of the site-level annual probability of fire estimated from our spatial binomial model. CIs were calculated as reciprocals of the upper and lower bounds of that estimate (see main text and Appendix S2). Sites are ordered by large river drainage. Within each drainage, they are arranged by snow disappearance day consistent with Figures 1, 5, and 6.

FIGURE 3 A cross-dated fire scar in an old-growth Douglas-fir partial cross section removed from a stump in a clearcut in the western Oregon Cascades. Note the presence of the pith in this sample, which was cut within 30 cm of the root collar, facilitating reconstruction of a precise establishment date. Photo credit: J. Johnston.

than the number of unique reconstructed fire events) is unlikely to be a meaningful descriptor of variability in fire frequency across our study sites for at least four reasons. First, the length of our fire history chronologies varied significantly, which potentially artificially deflates or inflates the denominator of the MFRI calculation. Second, no intervals could be calculated for one site for which we reconstructed no fires prior to 1900, or for eight sites for which we reconstructed only one fire prior to 1900. Third, four sites only recorded two fires, and the single interval between these fires was potentially highly misleading as to fire frequency. For instance, site 68 experienced two fires 8 years apart in the early 1500s, but no other fires for almost 400 years. Finally, most sites likely experienced a stand-replacing fire event that left no cross-dated fire scar evidence of that fire, and as we describe below, tree establishment following stand-replacing fire was often protracted. As a result, we do not have reliable information about the length of the first fire interval at most sites. We describe an alternative to conventional MFRI calculations below.

Environmental influences on fire occurrence

To evaluate influences on historical fire occurrence, we built a binomial mixed model that predicted fire occurrence (1 = fire; 0 = no fire) at each site in each year for which we had a cross-dated tree ring chronology that potentially recorded fire. Our model included variables that previous research (e.g., Johnston et al., 2023; Tepley et al., 2013, 2014, 2018) indicated potentially influenced fire occurrence, including historical climate, stand history, topography, variables associated with topographic-atmospheric controls on site fuel moisture, and lightning ignition density. We included site as a random effect in all models.

The historical climate variable evaluated for each year in our site-level chronologies was PDSI, a well-validated tree ring-based reconstruction of summer plant moisture availability (Cook et al., 2010; grid point 33). Stand history variables evaluated were time since last fire, calculated as the years elapsed since the last fire burned at each site, and stand age, calculated as the age in years between establishment of the oldest tree and year when fire was reconstructed at each site. Topographic variables modeled were slope steepness and landform curvature (an index that describes the potential for sites to hold moisture). Both topographic variables were calculated from a 10-m digital elevation model (DEM) and averaged across the location of all wood samples from each site.

We evaluated five different strongly correlated variables that potentially influenced fuel moisture: elevation, 30-year normal maximum temperature, 30-year normal precipitation, 30-year maximum VPD, and average snow disappearance day. Elevation was calculated from a 10-m DEM and averaged across the location of all wood samples from each site. Thirty-year normal maximum temperature, precipitation, and VPD were obtained at 800-m resolution from PRISM Climate Group (2023; https://prism.oregonstate.edu) and averaged across the location of all wood samples from each site. Snow disappearance data were obtained for the period 2001–2019 from the SnowCloudMetrics site (https://www.snowcloudmetrics.app) at 500-m resolution and averaged across all wood samples at each site. Average snow disappearance day is calculated by SnowCloudMetrics as the average day (from the beginning of the water year on October 1) at which snow was no longer detected from satellite imagery (Crumley et al., 2020).

Our modeling proceeded in three steps: First, we built candidate models with PDSI, both stand history variables (time since fire and stand age), both topographic variables (slope and curvature), and either elevation, maximum temperature, precipitation, VPD, or snow disappearance day. We used marginal Akaike information criterion (mAIC) to select from among these models with different strongly correlated fuel moisture variables the most explanatory of fuel moisture variables for use in a final model. Second, we tested the final model for temporal autocorrelation by examining graphs of residuals over time, examining autocorrelation function and partial autocorrelation function plots for each site, and by calculating a p value for a linear regression of model residuals and year for each site. We also tested the final model for spatial autocorrelation by plotting variograms of residuals for each year and by calculating Moran's I for each year. We detected no temporal autocorrelation. We detected modest spatial autocorrelation in residuals and so we fit the final model with a spatially correlated random effect using a Matérn covariance structure on easting and northing (in meters) site spatial coordinates using R's spaMM package (Rousset & Ferdy, 2014).

Model outputs from the spaMM specification included the spatial correlation parameters *nu* and *rho*, representing the strength and the speed of decay in spatial dependence. We plotted the distance between pairs of sites and the estimated correlation in fire occurrence at that distance to illustrate spatial dependence of fire occurrence across our study region, that is, the distances at which fire at one site was likely to predict fire at other sites. Given information about the likely distances at which the same fire events occurred, as a third step we fit an additional model that included density of lightning ignitions km^2 as a predictor of fire occurrence. We calculated lightning ignition density for each site by summing the total number of natural ignitions recorded by the Fire Occurrence Database (Short, 2017) within a distance from each site at which correlation in fire occurrence between sites was ≥0.5, and dividing total ignitions by total area contained within that buffer around each site.

We limited our binary response to fires that occurred between 1400 and 1900 since sample depth prior to 1400 was limited (only three cross-dated fire scars were formed prior to 1400) and we were interested in the historical period before modern fire exclusion policies which were adopted from the late 1800s through early 1900s. We confirmed that model assumptions were met by re-running our tests for temporal and spatial dependence on final models and performing diagnostic tests of normality and constant variance on the final model using R's Dharma package (Hartig, 2022). To estimate the influence of fixed effects on fire probability, we generated prediction grids for each focal variable while holding all other predictors constant at their mean values. Predictions were averaged across sites to produce smoothed trend lines representing marginal effects. We calculated 95% CIs for each prediction based on the variance of the fixed effects and plotted those estimates with CIs across the observed range of each variable. We calculated site-level annual fire probability by averaging all predictor values across years within each site and generating model-based predictions from these site-level summaries. A comprehensive description of our modeling strategy, final model structure, and parameter estimates is provided in Appendix S1.

As noted above, we do not believe that traditional MFRI calculations provide realistic representations of historical fire frequency, and so we calculated model-based MFRIs as the reciprocal of the site-level annual probability of fire from our final binomial model, with CIs for model-based MFRIs calculated as the inverse of the upper and lower bounds of the annual fire probability estimate. We provide a detailed account of this methodology in Appendix S2.

Evaluation of tree establishment

As in previous work in the western Cascades, we were able to obtain relatively precise estimates of tree establishment dates by removing wood samples that included the pith very low to the ground (mean distance from sample height to root collar = 39.7 cm, range = 0–185 cm). Most samples contained the pith or had just a few rings missing between the innermost ring and the pith (mean number of rings to pith for samples with missing pith = 2.9 rings, range = 1–7 rings). We used a simple linear regression model to predict establishment year as a function of pith year, species, sample height, and radial growth of the 10 rings closest to the pith (Johnston et al., 2023). Predicted years from the pith at sample height to tree establishment at the root collar ranged from 0 to 18.4 years (mean = 3.7).

Previous research south of our study region made use of precise estimates of tree establishment and a simulation procedure to identify discrete tree cohorts (Johnston et al., 2023; Merschel et al., 2024). These cohorts most likely represent extensive tree regeneration following fire that killed enough of the overstory to regenerate Douglas-fir, a shade-intolerant tree species that germinates best on exposed mineral soil (Isaac, 1943). Our simulation procedure compares the kernel density estimate of actual tree establishment dates to the kernel density estimate of randomly generated tree establishment dates equal to the number of actual establishment dates. When the kernel density estimate of actual tree establishment dates is greater than 99% of 10,000 simulated tree establishment dates, we consider those trees to belong to a discrete tree cohort. We applied this method at two spatial scales in the present study. First, we used all tree establishment data obtained from each of 36 different data collection sites to identify tree cohorts that likely originated after a fire at each site. We summarized the number of cohorts per site and length in years of these tree cohorts. Second, we used all tree establishment data aggregated at the scale of six large river drainages across our study region (Figure 1B) to identify periods of extensive tree establishment that likely resulted from widespread burning.

Detection of large historical fire events

Individual large fires that occurred across the westside in the early to mid-20th century and recent fires that occurred between 2020 and 2022 burned between 50,000 and 75,000 ha. These fires often traveled linear distances greater than 30 km and sometimes greater than 40 km, a distance that is significantly larger than the grain of our study site network (Figure 1B). We hypothesized that large stand-replacing fires burning during the historical period would have left fire scars from the same year and/or synchronized tree establishment across our study sites, which were a minimum of 3.9 km and a maximum of 27.1 km apart. We tested this hypothesis using two complementary approaches. First, we examined maps of sites that experienced fire in the same year within a distance that our binomial model for fire occurrence indicated that fire was potentially spatially autocorrelated (see "Environmental influences on fire occurrence" and Appendix S1). Second, we developed a permutation procedure to identify sites with fires burning in the same year that were closer together than expected by chance and potentially part of the same fire event.

Our custom fire year permutation function written in R first calculated the distance between sites where we reconstructed a fire in the same year. Then the function randomly assigned those fire years to sites 10,000 times and calculated distances between sites for each permutation. We considered sites that were located within the first quartile of the distances calculated for random assignment of fire years to sites to be fires that occurred closer together in space than expected by chance and examined those sites on a map. We also overlaid the range of years of tree establishment cohorts identified by our cohort detection procedures for each site. We examined sites with cohort years that overlapped and were found within the same distances that our fire year permutation procedure identified as potentially indicating a single fire event.

RESULTS

Comparison with other regions and fire histories

Our spatial permutation tests indicated that our randomly located data collection sites were exceptionally moist and productive relative to the rest of the forested western United States and almost all past western US fire history studies (Figure 4). Our 36 study sites were significantly moister ($p < 0.01$) than the rest of the western United States—mean annual precipitation across our study sites was 2183 mm compared to a mean of 882 mm across 10,000 random permutations of western states forests. Mean NPP at our sites was 9221 g C m^{-2} year^{-1}, significantly greater ($p < 0.01$) than the western US permuted mean of 5329 g C m^{-2} year^{-1}. There was no significant difference ($p = 0.38$) between mean maximum temperature of our sites (13.4°C) and the permuted mean maximum temperature of forested portions of the western United States (14.0°C).

Our study sites were significantly moister ($p < 0.01$) than the 1666 previous cross-dated fire history studies undertaken in the western United States found in the NAFSN database—2183 mm of precipitation a year at our study sites versus a permuted mean of 695 mm a year at NAFSN sites. Our sites were significantly more productive ($p < 0.01$) than previous fire histories—9221 g C m^{-2} year^{-1} versus a permuted mean of 6311 g C m^{-2} year^{-1}. There was modest evidence ($p = 0.04$) that our study sites were slightly cooler than previous fire histories—13.4°C versus a permuted mean of 14.4°C.

Fire history metrics

We cross-dated a total of 667 wood samples removed from 619 dead trees (primarily stumps, but occasionally logs) at 36 sites. Most cross-dated samples (87%) were

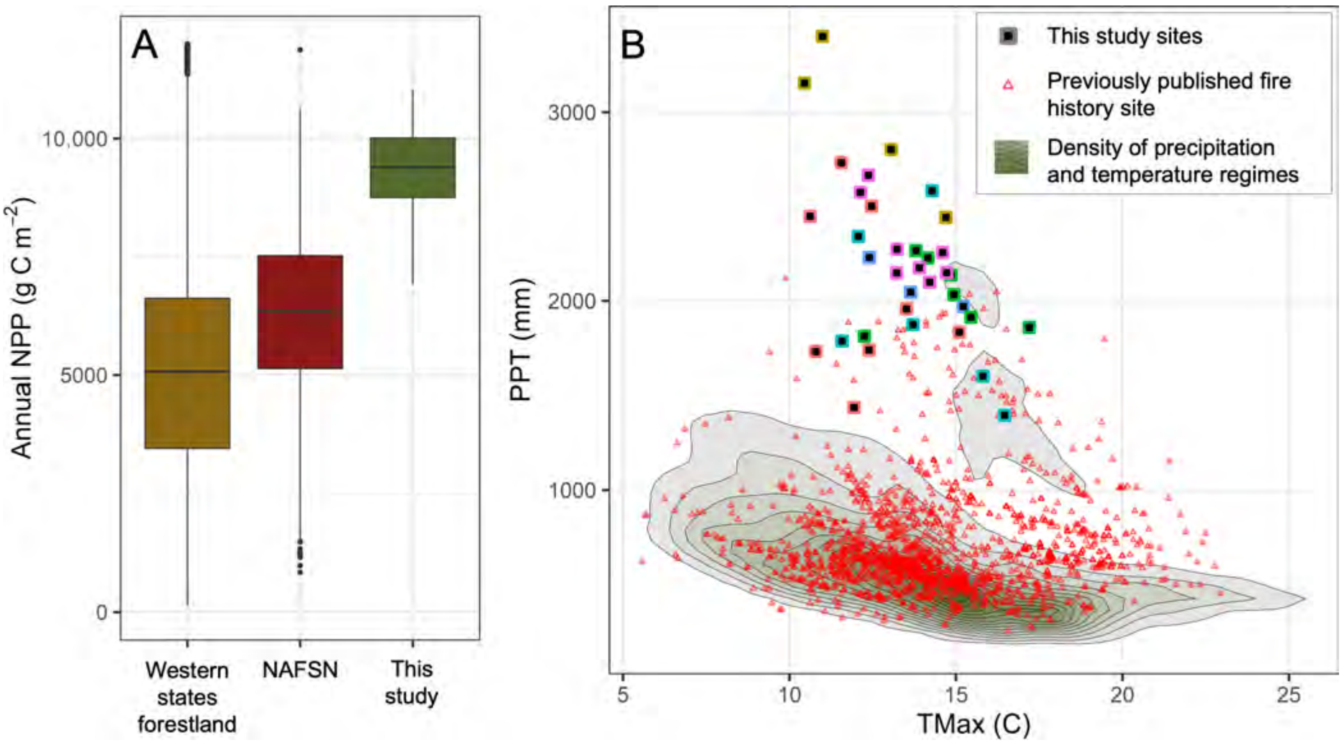


FIGURE 4 (A) Comparison of net primary productivity (NPP) between all western US forested areas, other western US fire history studies (from the North American Fire Scar Network), and the present study. (B) Comparison of temperature and precipitation regimes between all western US forested areas, other western US fire history studies, and the present study. Average maximum monthly temperature and annual precipitation for all forested areas in the western United States (~932,000 systematically located points) are shown as shaded contours—the denser the color and contour lines, the more area of western US forest falls in that temperature and precipitation regime. Small open triangles indicate the temperature and precipitation values for 1666 previously published fire history studies located within forest lands of the western United States. Large, filled boxes indicate temperature and precipitation values of new fire histories reported in the present study (colors correspond to large river drainages; see Figure 1).

Douglas-fir. Approximately 8% of samples were from western hemlock (*Tsuga heterophylla*) or mountain hemlock (*Tsuga mertensiana*), which hybridize at middle to high elevations in our study region. Approximately 2% of samples were noble fir (*Abies procera*) and another 2% were other species including western red cedar (*Thuja plicata*), silver fir (*Abies amabilis*), and grand fir (*Abies grandis*). All but two of our 36 sites were dominated by large overstory Douglas-fir prior to clearcutting, almost all of which proved to be in excess of 200 years of age at the time they were cut. Most of the trees available for sampling at sites 55 and 85 were 250–300-year-old mountain hemlock or true fir.

Results of our fire history and tree establishment reconstructions are shown in Figure 5. There was significant variability in forest age structure between stands, with dominant overstory cohorts that established anywhere from 850 to 200 years ago. We cross-dated a total of 412 cambial injuries caused by fire, which documented fire that occurred in 129 different years. We cross-dated between 1 and 15 different fire years within our 36 data collection sites (mean = 4.5 fire years per site; Table 1). We were able to reliably determine seasonality of 64% of fire scars. A total of 92% of these scars were formed during the period of dormant ring growth. Our experience observing the initiation of early wood and late wood growth when coring live Douglas-fir suggests this scar position in tree rings was the result of a fire burning sometime between the middle of summer and late fall. The remainder of scars were found in the latewood, indicating a fire burning sometime between early summer and late summer.

The number of sampled trees potentially recording fire began to decline in the period between 1500 and 1600. Just 7% of total reconstructed fire years occurred prior to 1500, 10% of fire years occurred between 1500 and 1600, 18% between 1600 and 1700, 30% between 1700 and 1800, 26% between 1800 and 1900, and 8% after 1900. Most of the fire scars that we dated after 1900 were evaluated to be the result of slash treatments in adjacent clearcuts that occurred before sampled trees were cut.

We were unable to reconstruct any fires that occurred prior to 1900 from cross-dated fire scars at one (site 64). We

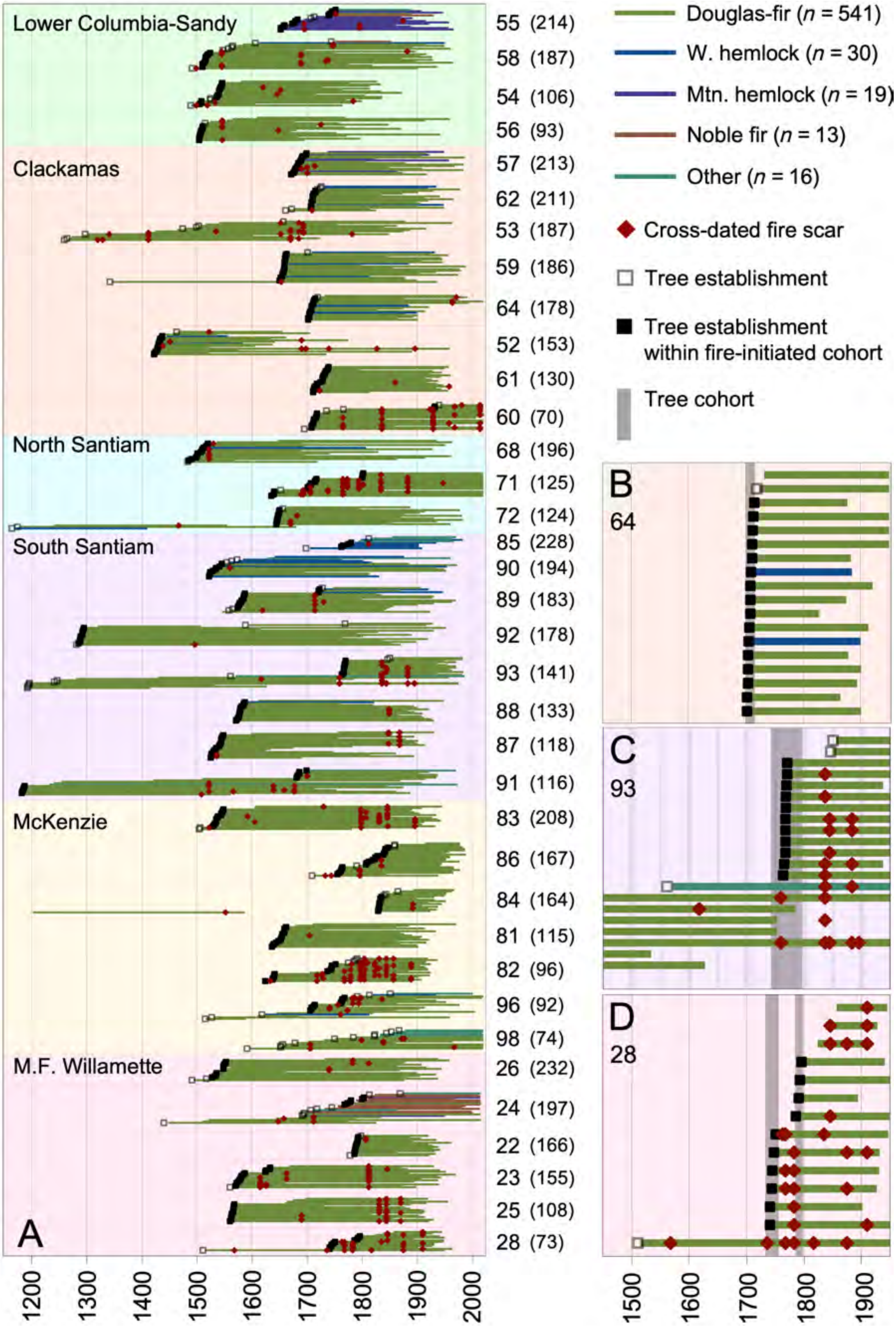


FIGURE 5 Legend on next page.

were unable to reconstruct more than one fire prior to 1900 at eight sites. Intervals between fires at sites that experienced more than one fire prior to 1900 ranged from 1 year to 340 years. MFRIs calculated from available intervals ranged from 8 to 340 years, although this statistic is misleading because it was often based on just one or two intervals.

Only four sites had fire return interval CVs < 0.3, indicating regular, evenly spaced intervals suggestive of relatively predictable historical fire frequency. Notably, three sites (sites 71, 82, and 28) experienced fires every ~15–25 years over multiple centuries, a tempo of fire similar to the historical tempo of fire we have reconstructed in dry ponderosa pine-dominated stands in eastern Oregon (see Johnston et al., 2017; Merschel et al., 2018). Most sites had fire return interval CVs > 0.7, indicating both long and short gaps between fires. Six sites had fire return intervals <13 years as well as intervals >130 years. Table 1 displays site-level summaries of environmental characteristics and fire history metrics.

Environmental influences on fire occurrence

Average snow disappearance day proved to be the most explanatory of a suite of strongly correlated variables (elevation, temperature, precipitation, VPD) that exert a strong control on live and dead fuel moisture. Plotting the distance between pairs of sites and the estimated correlation in fire occurrence at that distance to illustrate spatial dependence of fire occurrence indicated strong autocorrelation over lag distances $\leq$5 km, suggesting a potential for the same fire to burn sites found within these relatively short distances. Autocorrelation of fire occurrence declined sharply as distance between sites increased, suggesting that the same fire event rarely burned across sites separated by more than 10 km (see Appendix S1). Based on this analysis of spatial autocorrelation of fire occurrence, we calculated lightning ignition density for a 10 km buffer surrounding each site. Probability of fire increased as lightning ignition density increased, although this effect was modest and CIs for the estimate of the effect of lightning ignition density were very wide and had significant overlap with zero. Inclusion of the lightning ignition density variable did not improve model explanatory power as measured by mAIC, and so our final model consisted of the PDSI, stand history (stand age and time since fire), topography (slope and slope curvature), and average snow disappearance day variables as well as site and spatial random effects.

Annual probability of fire for individual sites from this final model ranged from 0.039 to 0.003 a year (Figure 6A), approximating MFRIs of 26–389 years (Table 1). Probability of historical fire occurrence estimated by this final model decreased as average snow disappearance day increased—a 30-day earlier snow disappearance day was associated with a 13% relative increase in the probability of fire (Figure 6B). Probability of historical fire increased with drought severity as measured by PDSI (Figure 6C). Although CIs for the estimated effect of PDSI slightly overlapped zero, summer drying was clearly associated with a meaningful increase in the likelihood of fire. A 0.75-unit decrease in PDSI—representing a shift toward moderately drier-than-average conditions—was associated with a 6% relative increase in the modeled probability of fire. During significantly dry conditions, that is, PDSI values 1.5 units below the median, the probability of fire increased by 12%. Probability of fire decreased significantly with time since fire (Figure 6D). A 30-year shorter time since fire—that is, more recent fire activity—was associated with a 9% relative increase in the probability of subsequent fire. There was no evidence for an effect of slope, curvature, or stand age on fire occurrence.

Patterns of tree establishment

Our simulation procedure for detecting coherent tree establishment identified a total of 50 tree cohorts at 34 of our 36 study sites. Fourteen sites exhibited two different

FIGURE 5 (A) Annually resolved reconstructions of fire occurrence and tree establishment from 1150 to 2020 at 36 sites in the western Oregon Cascades. Horizontal lines show the length of individual tree ring chronologies within each site, color coded by species. Red diamonds indicate the year in which a fire scar was formed on individual trees, open boxes indicate the year in which individual trees established, and solid boxes indicate the year in which individual trees that belong to a fire-initiated cohort established. Sites are grouped by six large river drainages lying north to south across the study area (Figure 1). Within those large river drainages, sites are arranged from latest to earliest snow disappearance day (in days from October 1, noted in parentheses next to site number). (B) Site 64 likely experienced a stand-replacing fire in the late 1600s followed by rapid regeneration of Douglas-fir within 10–15 years and no evidence of additional fire activity for several centuries. (C) Site 93 experienced periodic moderate-severity fire, including a fire in the mid-1700s that regenerated a Douglas-fir cohort, although many trees that established 500 years previously survived until the site was clearcut in the late 20th century. (D) Site 28 experienced chronic fire for hundreds of years prior to the establishment of the national forests in the early 1900s, including at least four fires in the 1700s associated with at least two distinct cohorts of Douglas-fir establishment.

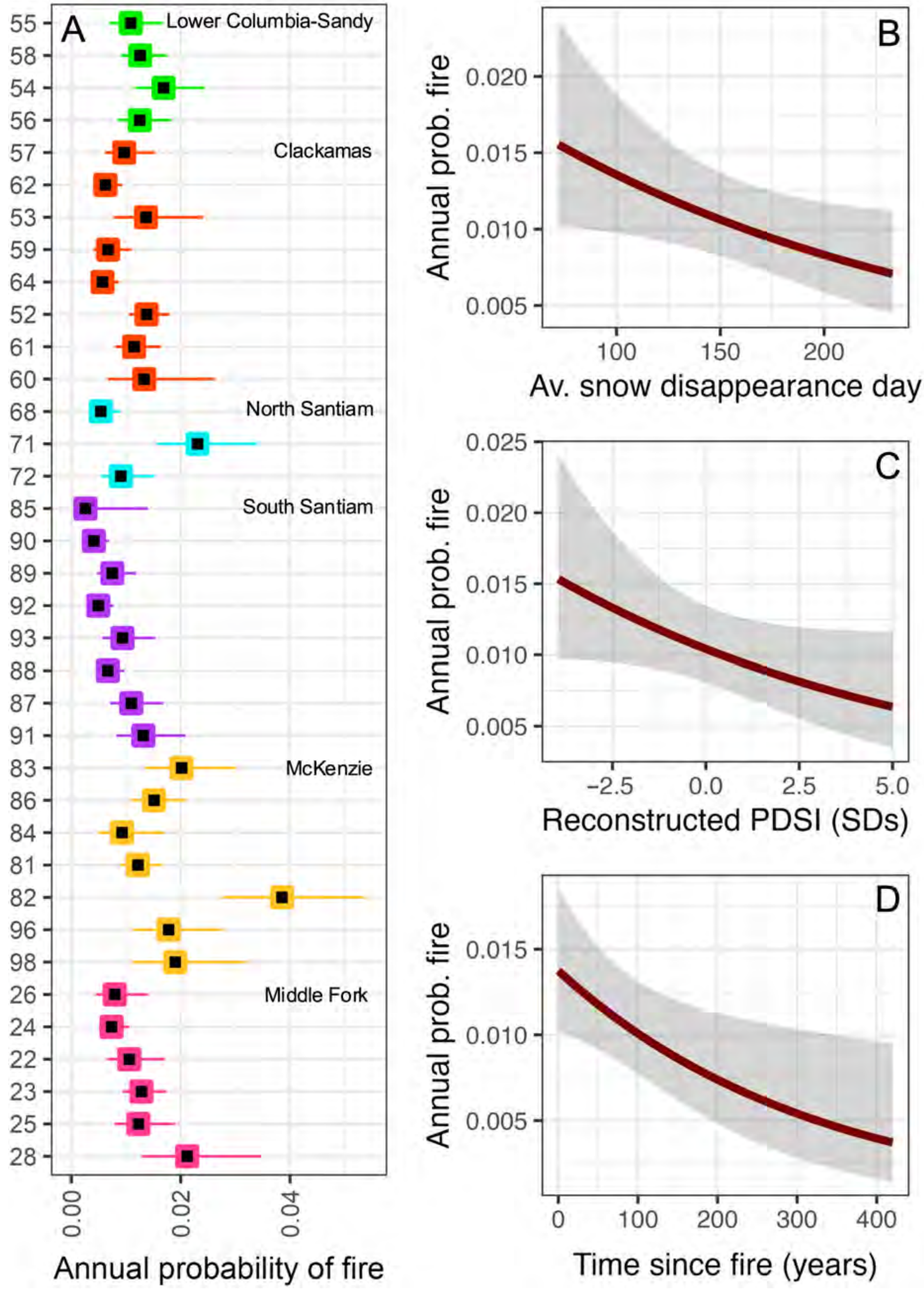


FIGURE 6 (A) Estimated annual probability of historical (1400–1900) fire occurrence at each of 36 sites. Sites are arranged from top to bottom by large river drainage and within drainages by latest to earliest snow disappearance day as in Figure 5. Horizontal lines indicate 95% CIs. (B–D) Marginal effects of modeled variables with significant or marginally significant influence on annual probability of historical fire occurrence. Estimates are shown as red lines and 95% CIs as a gray ribbon.

tree cohorts, and one site (site 71) exhibited three different cohorts. The first cohort initiated at approximately two-thirds of our sites was consistent with regeneration in the immediate aftermath of a stand-replacing fire because we reconstructed little or no tree establishment prior to cohort initiation (e.g., Figure 5B). Regeneration of trees within at least eight sites was more consistent with moderate-severity fire because at least a quarter of wood samples from that site were from trees that established several hundred years before cohort initiation (e.g., Figure 5C). Although some sites experienced tree establishment that lasted a hundred or more years, our annually resolved fire records and simulation procedure using precise estimates of tree establishment demonstrated that these long periods of tree establishment usually consisted of several short-duration periods of tree establishment separated by fires (e.g., Figure 5D). Continuous tree establishment in 82% of tree cohorts we identified occurred over a period less than 20 years.

Our simulation procedures detected two to four periods of significant tree establishment that was probably related to heightened burning within each of the six large river drainages that made up our study region. The earliest period of heightened burning we were able to detect occurred in the South Santiam drainage in the late 1100s. The latest was in the McKenzie drainage in the mid-1800s (Figure 7). Sites in four of the six large drainages that made up our study region experienced significant regeneration following fire in the late 1400s through the 1500s. Sites in three of six drainages experienced significant regeneration following fire in the 1600s.

Detection of large stand-replacing fire events

There was surprisingly little synchrony in fire occurrence across our study sites relative to the synchrony in fire noted between widely spaced study sites in previously published fire history research in other parts of Oregon (e.g., Heyerdahl et al., 2008; Johnston et al., 2017; Merschel et al., 2018). Twenty-one fire years that occurred prior to 1900 (18% of total fire years occurring before 1900) were reconstructed at two of our sites. Seven fire years (6% of fire years occurring before 1900; the years 1690, 1783, 1812, 1831, 1836, 1844, and 1846) were reconstructed at three different sites. One fire year (1522) was reconstructed at four sites. No fire year was reconstructed at more than four of our 36 study sites.

Of the 29 fire years that occurred before 1900 that were reconstructed at more than one site, our permutation procedures suggested that six of these fires occurred closer in space than expected by chance and were potentially part of the same fire event. The remaining fire years were reconstructed at distances consistent with multiple fire events burning across the study region in the same year. Of those six fires that occurred relatively close together, one fire year (1499) was consistent with a large wind-driven event occurring in the Bull Run watershed within the larger Lower Columbia–Sandy River drainage (see below and Agee & Krusemark, 2001). The remaining fire years (1768, 1783, 1798, 1831, and 1846) all burned along the northern portion of the Middle Fork Willamette River drainage and the southern portion of the McKenzie River drainage and were consistent either with large fires that were roughly the same size as fires that burned in our study region circa 2020–2022, or a series of relatively smaller fires burning in the same year.

Our evaluation of temporally synchronous tree establishment cohorts provided evidence that several large historical fires may have occurred in our study area. Sites 88 and 89 (located 6 km apart) had cohorts that initiated at nearly the same time in the late 1560s through the early 1570s, possibly following the same stand-replacing fire event. Site 90, located 10 km to the north, recorded a fire in 1560 that may have been the same fire that initiated tree cohorts at sites 88 and 89. Sites 83 and 26 (located 20 km apart) had cohorts that initiated in the late 1520s through the early 1530s, possibly because of the same fire event. Sites 23 and 25 (located 11 km apart) had cohorts that established in the late 1550s through the early 1560s. Temporally synchronous cohorts at sites 23 and 25 are suggestive of a large patch or patches of stand-replacing fire driven by east winds given the close proximity of these sites along an east–west axis within the Winberry Creek watershed of the Middle Fork Willamette drainage, and the paucity of tree establishment or fire scar data found before this time at any sites across the Middle Fork drainage (Figure 5A). Sites 22 and 28 (located 14 km apart) both had cohorts initiated in the mid-1780s. A 1783 fire reconstructed at site 28 initiated a second Douglas-fir cohort, although more than half of the trees sampled at this site survived that fire. The same fire may have initiated the only cohort detected at site 22.

The most compelling evidence of potentially very large fire events associated with extensive patches of stand-replacing fire was found at the north end of our study region. The 1499 fire event recorded at sites 54 and 58 in the Bull Run watershed was followed by significant tree establishment at sites 54, 56, and 58, which span 15 km along an east–west axis. Tree establishment at two of these sites appears to have been protracted by reburns (Figure 8). Sites 60, 61, 62, and 64 spanning 30 km north to south along the upper Clackamas River drainage all had significant tree establishment that began during the same 10-year period in the early 1700s. Synchronous tree establishment in this area is most likely attributable to a very large fire or series of fires occurring within a relatively short period of

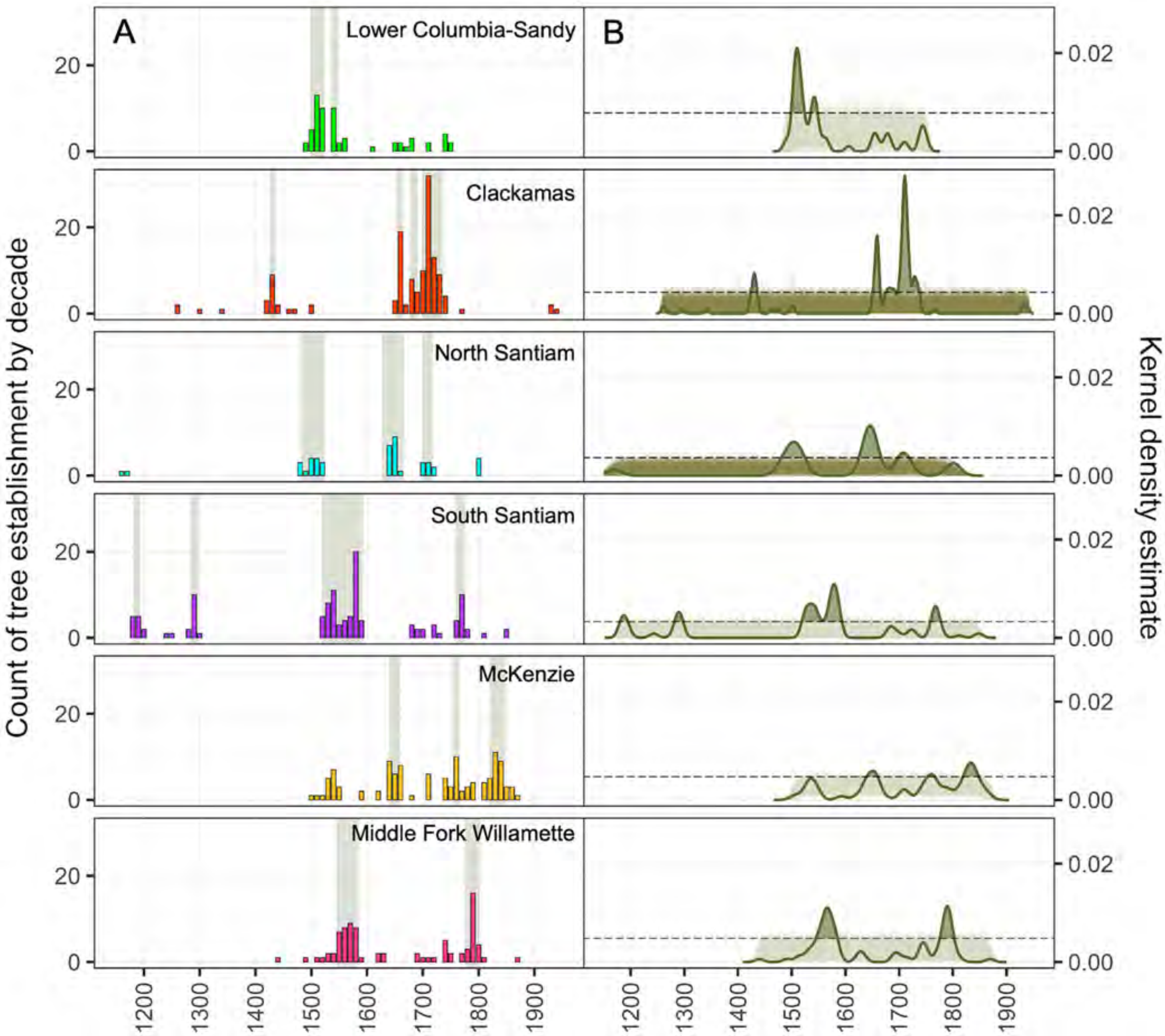


FIGURE 7 (A) Counts of tree establishment binned by decade between 1150 and 1950 CE for all sites within six large river drainages across the study area. Periods of significant tree establishment are indicated by shaded polygons. (B) Kernel density estimates of reconstructed tree establishment (solid green line) and 10,000 tree establishment simulations (thin khaki lines). We considered significant tree establishment to have occurred during periods when the kernel density estimate of reconstructed tree establishment exceeds the kernel density estimate of 99% of tree establishment simulations (the 99% critical value is identified by a gray dashed line and green shading).

time in the late 1600s or early 1700s that involved significant stand-replacing fire effects (Figure 9).

DISCUSSION

Diverse fire histories across the western Oregon Cascades

The extravagant complexity and stupendous accumulation of biomass in coast Douglas-fir-dominated forests of the western Cascades have fascinated scientists for hundreds of years. Explanations for these characteristics typically focus on the annual climate pattern of the Pacific Northwest, where exceptionally moist but mild winters and warm and dry summers favor long-lived conifers (Waring & Franklin, 1979). This study suggests that fire and fire adaptations may be overlooked as an explanation for the dominance of Douglas-fir forests in our region. The results of this study may provide an answer to the riddle posed by Stevens et al. (2020), who note that forests of western Oregon and Washington have the most

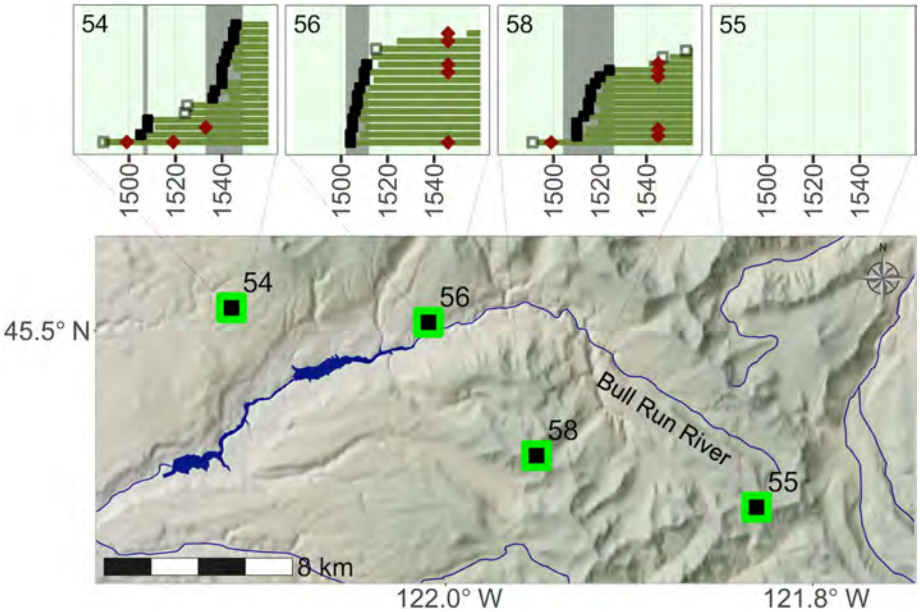


FIGURE 8 Reconstruction of a large fire with significant stand-replacing fire effects inferred from tree establishment and fire scar evidence within the Bull Run watershed (Lower Columbia–Sandy River drainage). As in Figure 5, horizontal segments indicate the length of individual tree ring chronologies, red diamonds indicate cross-dated fire scars, open boxes indicate tree establishment, solid boxes indicate trees that are part of a distinct cohort, and gray shaded polygons indicate the length of individual tree cohorts. Sites 54 and 58 both recorded a fire scar in the year 1499. An overstory tree cohort did not establish for another 20 years at site 58 following the 1499 fire, most likely because of reburns, several of which were recorded at site 54. The dominant overstory cohort at site 56 established relatively quickly after the 1499 fire. No tree establishment or fire scars were reconstructed during the 1500s at site 55, a high-elevation site dominated by mountain hemlock and *Abies* species. It is unclear whether this site was affected by the late 1400s fire(s).

fire-resistant tree species of any fire regime currently mapped as infrequent. We show that in fact many Douglas-fir forests experienced relatively frequent fire and are well adapted to a wide range of fire frequencies and severities.

Although forests in our study region are among the moistest and most productive forests in North America (Figure 4), exceptional biomass accumulation does not necessarily imply long periods without fire. It is possible that other moist and highly productive forest ecosystems also experienced more frequent historical fire than anticipated by current theory. Our research suggests that fire ecologists still have much to learn about historical fire regimes and the influence of environmental gradients on fire occurrence, particularly in moist and productive forest settings.

Although it is unlikely that we reconstructed all fires that occurred at our sites, the number of fires we reconstructed is probably well in excess of what many scientists and managers working in highly productive coast Douglas-fir forests anticipated. Only a handful of our 36 sites (e.g., sites 57, 62, 59, and 64) plausibly conform to the expectation of a long fire-free period following a stand-replacing fire. Our findings are consistent with previous work that indicates an important role for non-stand-replacing fire in Douglas-fir-dominated stands of the western Cascades (e.g., Weisberg, 2004). In particular, Tepley et al. (2013) found that only a quarter of sampled stands in the McKenzie River and Middle Fork Willamette drainages had tree establishment dynamics consistent with long fire-free intervals. Tree establishment dynamics in approximately two-thirds of Tepley et al.'s study stands were consistent with episodic non-stand-replacing fires that regenerated multiple tree cohorts. Tree establishment dynamics in approximately 10% of their study stands were consistent with relatively frequent fire occurring for multiple centuries.

Our spatial binomial mixed model demonstrated that interannual climate variability (PDSI) and broad-scale controls on fuel moisture (average snow disappearance day) explained much of the variability in historical fire occurrence across our study sites. Snow disappearance day was the most predictive of several correlated variables that modulate fuel moisture, probably because observed snow disappearance day is influenced by elevation, precipitation, and the shading effects of aspect and topography. These influences are not as well integrated by the other fuel moisture variables we tested in candidate models. Snow cover itself did not impede fire because snow had melted from all of our sites by mid-summer or fall when historical fires

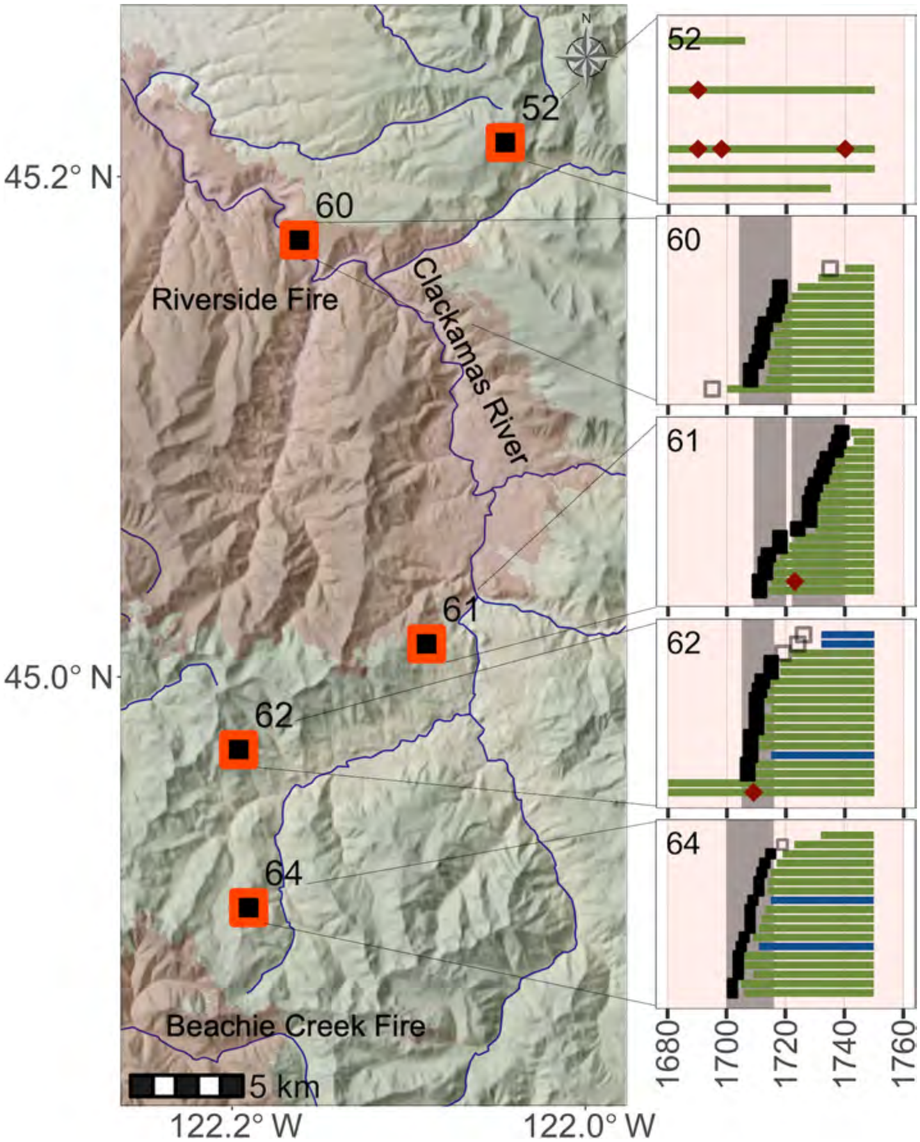


FIGURE 9 Reconstruction of a large stand-replacing fire inferred from tree establishment along the upper Clackamas River. As in Figure 5, horizontal segments indicate the length of individual tree ring chronologies, red diamonds indicate cross-dated fire scars, open boxes indicate tree establishment, solid boxes indicate tree establishment that are part of a distinct cohort, and gray shaded polygons indicate the length of individual tree establishment cohorts. Sites 60, 61, 62, and 64 initiated at approximately the same time, most likely following a large stand-replacing fire or series of stand-replacing fires in quick succession. Site 52 recorded a non-stand-replacing fire in 1690, which may indicate the northern edge of the large stand-replacing event that initiated other stands in the upper Clackamas River watershed.

occurred. Snow cover was associated with variability in historical fire occurrence because shadier and cooler landscape settings that hold snow longer are also associated with moister fuels throughout the fire season.

Although finer-scale variability in topography may influence historical patterns of fire (Tepley et al., 2013), we found no evidence that differences in slope or landform curvature between our study sites influenced probability of fire occurrence. Reconstructing historical fire over larger study sites than we attempted may reveal variability in fire occurrence associated with fine-scale topography. Density of lightning was associated with a higher probability of fire, but ignition density did not appear to be a decisive influence on historical fire, possibly because lightning is more common at higher elevations which have higher fuel moistures during the fire season. We modeled lightning ignition density using contemporary data, and it is possible that the spatial pattern of lightning ignitions differed in the historical past. Variability in fire occurrence may also reflect variability in human management over time and space in the western Cascades. Several of our sites (e.g., sites 71, 83, and 82) seemed to depart from an otherwise relatively strong relationship between average snow disappearance day and fire occurrence (Figure 6A,B). It is possible that fire history at these sites and other areas in the western Oregon Cascades reflects anthropogenic ignition subsidies (Coughlan et al., 2024).

Time since fire also exerted a significant influence on historical fire occurrence in our western Cascades study region (Figure 6D). Previous research demonstrates that the successional stage of forest communities can influence flammability of fuels (Gray & Franklin, 1997; Tepley et al., 2018; Zald & Dunn, 2018). Mature, closed canopy forests can reduce wind speeds and maintain higher fuel moisture which tends to limit fire spread (Krawchuk et al., 2009; Nowacki & Abrams, 2008). Early seral stands without significant overstory canopy cover in our study region can be more fire prone because of higher solar radiation and surface temperatures, better aerated fuels, and more continuous fine fuels (Agee & Huff, 1987; Neiland, 1956). But we found no evidence that stand age influenced probability of fire occurrence. On the contrary, our data show that fire was relatively common in young, mature, and old-growth forests (Figure 5A).

The explanatory power of the time since fire variable appears to reflect a tendency of many of our study sites to experience periods of chronic fire over 2–5 decades bracketed by fire quiescent periods that often lasted a century or more (Figure 5A). Historical fire likely created abundant activity fuels and dried these fuels via increased solar radiation associated with removal of some or all of the overstory by fire. In a few of our sites, a lack of ignitions and/or anomalously cool or moist conditions may have prevented reburns and resulted in relatively rapid re-establishment of closed-canopy conditions. In most of our stands, ignition dynamics and climate appear to have been conducive to one or more reburns over multiple decades until changes in fuel loading, overstory cover, climate, and/or ignition dynamics initiated a fire quiescent period. Although these alternating periods of heightened fire activity and fire quiescence may have had important implications for stand development, wildlife habitat, and other ecosystem functions, there is little evidence that the highly variable fire activity we document resulted in state changes in high biomass forest stands with significant successional inertia (Iglesias & Whitlock, 2020). An overstory of large and old Douglas-fir was the distinguishing characteristic of sites that experienced fire-free intervals lasting centuries and at sites where fire occurred every 15–20 years.

The role of fire in initiating and mediating forest succession

Although most of our sites appear to have originated after stand-replacing fire, succession at a number of our sites (e.g., sites 71, 82, 89, 91, 93, 96; see Figure 5) was mediated primarily by moderate-severity fire that resulted in only partial removal of overstory trees followed by regeneration of new cohorts that complemented an existing template of older overstory trees. Moderate-severity successional pathways for Douglas-fir-dominated forests deserve more attention from scientists and managers, particularly since this pathway is fairly common within many contemporary fire perimeters across our study region (see Dunn et al., 2020; Reilly et al., 2017, and Figure 10).

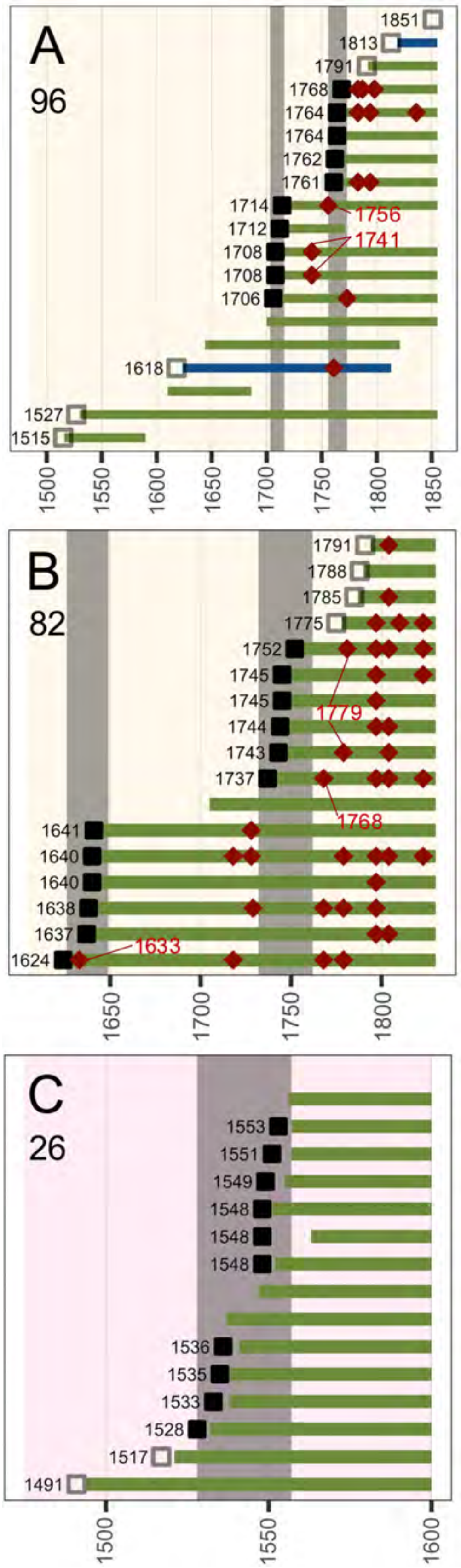
Our research may resolve discrepancies between direct observations of rapid regeneration following stand-replacing fire in Douglas-fir forests and previous historical reconstructions that observe establishment ranging from multiple decades to a century or more. Most forest stands in the western Cascades experience extensive regeneration immediately following contemporary fire (Laughlin et al., 2023). Our study sites also likely experienced rapid regeneration following fire, but succession to closed-canopy conditions was often interrupted by reburns, which prolonged early seral forest conditions. Tree cohort establishment occurring over several decades to a century observed in earlier studies (e.g., Freund et al., 2014; Poage & Tappeiner, 2002) was likely the result of undocumented fires. Even our rather limited tree establishment data provide ample evidence that reburns influenced early stand development processes at most sites. For instance, sites 54 and 58 appear to have experienced a high-severity fire in the late 1400s, but approximately 6% of the trees we sampled at these sites survived that fire. Establishment of trees that ultimately recruited to the overstory at this site may not have been completed for 30–50 years following the fire that reset succession (Figure 8).

Our cohort detection procedure appeared to be highly skillful at accurately identifying multiple fire-initiated tree cohorts at some of our study sites. For instance, tree establishment at site 28 occurred for almost 60 years between 1741 and 1796. But our cohort detection procedure was able to parse this apparent long period of tree establishment into two very short-duration regeneration events: a cohort initiated between 1741 and 1751 and a second cohort initiated between 1786 and 1796. Three fires (in 1763, 1768, and 1783) occurred during a 35-year tree establishment interregnum at this site (Figure 5D). Similarly, our procedure identified two distinctive periods of tree establishment in the 1700s at site 96 that each lasted less than a decade separated by at least two fires in the mid-1700s (Figure 11A).

In many cases, however, our limited tree establishment data likely prevented our procedure from providing a complete account of fire-mediated tree establishment and a comprehensive understanding of stand

FIGURE 10 Moderate-severity successional pathway within a 1996 fire perimeter in the Middle Fork Willamette watershed. Unpublished data (not part of the present study) indicate at least two distinctive overstory tree cohorts established more than 150 years apart, many of which were killed by the 1996 fire. A new cohort of Douglas-fir, along with western hemlock and western red cedar, regenerated rapidly after the 1996 fire. This site will likely support at least three fire-mediated age classes of Douglas-fir spanning the last 300 years. Photo credit: J. Johnston.

development. Additional data collection at site 96, for example, may reveal several tree cohorts established in the 1500s, 1600s, or 1800s in addition to the two distinct cohorts identified in the 1700s (Figure 11A). We reconstructed two cohorts at site 82, although our data suggest that there may have been as many as four cohorts initiated by fire (Figure 11B). It is likely that larger, systematic tree establishment data collection efforts would paint an even more complex picture of disturbance and succession in westside Douglas-fir forests than we report here.



In some cases, even extensive additional data collection may not clarify the origin of westside Douglas-fir forests because multiple fires during early stages of stand development may not leave wood evidence available for sampling. For instance, approximately half of the overstory trees we sampled at site 26 dated to a cohort initiated between 1548 and 1553. But the other half of the trees we sampled at this site established in the 60 years prior to initiation of this cohort. It may be impossible to determine if this stand originated following one large stand-replacing fire and a series of reburns or if it experienced one or several moderate-severity fires over many centuries that ultimately gave rise to the overstory that was removed by clearcutting in the mid-to-late 1900s (Figure 11C).

Our data suggest that large fires of the sort that resulted in more than 300,000 ha burned across our study region between 2020 and 2022 (Figure 1) also likely occurred in the distant past. Legacies in the form of coherent forest age structure that are still evident today over relatively large areas provide evidence of these fires (Figures 8 and 9). Our network of randomly located sites had very diverse origin dates (Figure 5A), and synchronous establishment of trees in adjacent sites is almost certainly not a coincidence. But it is possible that coherent age structure across nearby sites (Figures 8 and 9) represents a series of fires close together in time and space rather than one very large fire event. It is notable that we only detected two or three compelling examples of fire events occurring between 1400 and 1900 that were

FIGURE 11 Examples of the results of the cohort detection procedure illustrating both the accuracy and limitations of this approach given sample sizes. (A) Site 96 exhibits significant tree establishment for almost 60 years in the early to mid-1700s. But our simulation procedure shows that this long period of establishment is actually two relatively short-duration pulses of regeneration separated by two fires occurring in 1741 and 1756. (B) At site 82, our simulation procedure considered all trees to be established between 1624 and 1641 as one cohort. Additional samples might allow us to detect tree establishment prior to a 1633 fire as a separate cohort, or the 1633 fire may have eliminated most evidence of this cohort. It is also possible that a larger sampling effort would have shown one or more additional tree establishment cohorts following fires in 1768 and 1779. (C) At site 26, it is unclear if additional data collection would have distinguished multiple establishment cohorts in the early to mid-1500s separated by fires, or shown this stand to have originated following a stand-replacing fire, a large stand-replacing fire and multiple reburns, or moderate-severity fire.

comparable in size to the half dozen large fires that burned in 2020 or 2022 (see Figure 1 and "Patterns of tree establishment"). Either the recent tempo and extent of large stand-replacing fires is anomalous, or extensive small patches of stand-replacing fire occurring over the intervening years since past large fires confound detection of those events. The frequency of fire we document, the diversity of age structure across the landscape, the relatively short-distance spatial correlation of fire occurrence, and lack of synchrony between tree cohorts at most sites that are in close proximity to one another all suggest that relatively small patches of high-severity and moderate-severity fire were the most important drivers of stand initiation in our study region.

Management implications

Current management of Douglas-fir forests across most of our study region emphasizes rapid regeneration of forest following disturbance and succession uninterrupted by fire until another major stand-replacing disturbance (Kroll et al., 2020). But early seral habitats dominated by shrubs, herbs, and forbs following stand-replacing wildfire are increasingly recognized as a critical source of landscape-scale biodiversity and resilience to changing climate regimes (Hutto et al., 2016; Prichard et al., 2018; Swanson et al., 2011; Tepley et al., 2018). Between a quarter and one-third of federally managed forests in the westside are young stands (<80 years old) that were replanted at very high densities following clearcut harvest between 1950 and 1990. This research questions the potential for these stands to develop into structurally complex forest in the absence of disturbance.

Previous studies noted significant Douglas-fir establishment 400–550 years ago (Poage et al., 2009; Tepley et al., 2013, 2014). Weisberg and Swanson (2003) suggest that fire in the western Oregon Cascades was widespread from the 1400s through the mid-1600s and quiescent from the mid-1600s until the early 1800s. In contrast, this study documents periods of tree establishment that likely followed stand-replacing fire throughout the western Cascades from the late 1100s through the mid-1850s (Figure 7). Our findings are suggestive of a shifting mosaic of tree age classes that was highly variable over time at the scale of individual river drainages but relatively stable over time at regional scales. The extensive non-stand-replacing fire we reconstructed may play a role in stabilizing landscape-scale old-growth structure (Koontz et al., 2020; Steel et al., 2021).

This study calls into question the assumption that succession in the absence of disturbance is critical to the conservation of late-successional associated wildlife species. Studies of both California spotted owls (*Strix occidentalis occidentalis*) and northern spotted owls (*S. occidentalis caurina*) suggest that these species are adapted to the extensive low- and moderate-severity fire and small patches of high-severity fire that we believe were typical of the historical landscape within our study region (Jones et al., 2024; Jones, Kramer, et al., 2020; McGinn et al., 2025; Rockweit et al., 2024). Relatively frequent fire in westside Douglas-fir forests was likely to have been an important driver of forest complexity upon which endangered species like the northern spotted owl depend. At stand scales, historical fire likely helped create complex habitat including broken tops, epicormic branching, platforms, bole cavities, etc. that owls and other species utilize (Johnston et al., 2019). At landscape scales, historical fire likely helped create a rich mosaic of structural and compositional configurations alternately suitable for nesting, roosting, and foraging (Comfort et al., 2016; Jones, Kramer, et al., 2020). Understanding the tempo and severity of future fire in the westside will be critical to adapting conservation strategies for threatened, endangered, and sensitive species (Jones, Gutiérrez, et al., 2020; Spies et al., 2006). An important question for future research is the degree to which habitat for late-successional dependent species was created by the relatively frequent historical fire we document, and if so, whether this habitat can be perpetuated through time in the absence of fire.

Future warming that melts snow earlier will also likely dry fuels earlier, potentially making some or all landforms in the western Oregon Cascades inherently more prone to fire. At many of our study sites, historical fire occurrence initiated a period of heightened fire activity that lasted decades. There has been a significant increase in area burned across our study region in the last 5 years (Figure 1), and it is likely that forest stands within these fire perimeters are at heightened risk of future fire relative to stands that have not burned in 100+ years. However, historical fire occurrence likely reflected complex interactions between drought, topography, ignitions, and time since last fire. We caution that projecting future fire occurrence in the western Oregon Cascades based on historical fire occurrence data is problematic given changes in forest structure and composition (i.e., extensive clearcut harvesting) as well as exigencies in contemporary fire ignitions and suppression operations. Contemporary fire ignitions are strongly influenced by novel socioeconomic spatial patterns (Balch et al., 2017; Jenkins et al., 2023; Reilley et al., 2023). Contemporary fire spread is strongly influenced by suppression efforts, which in turn are contingent on access and land management designations (Barros et al., 2021; Downing et al., 2022; Johnston et al., 2021; Leonard et al., 2021).

CONCLUSIONS

Although we show that western Oregon Cascades forests are well adapted to extraordinary variability in tempo and severity of fire at both stand and landscape scales, today's forests are experiencing novel disturbances and successional processes that may have significant unintended consequences (Freeman et al., 2017; Sayedi et al., 2024; Thompson et al., 2009). Historically, stand initiation in westside Douglas-fir forests was often a complex process consisting of multiple regeneration episodes rather than a single discrete event. Today, managers most often emphasize rapid re-establishment of closed canopy conditions following a stand-replacing event (either fire or timber harvest). Historically, fire likely played an important role in creating and maintaining the complex structural and compositional characteristics associated with today's old-growth forests. Today, the majority of Douglas-fir forests across the west slope of the Cascades are managed for intensive timber production or set aside as protected reserves. Neither management regime anticipates or welcomes significant fire. Given profound changes to the landscape and human communities over the past 150 years, it may be difficult to re-establish the historical extent and severity of fire in westside Douglas-fir forests, creating considerable uncertainty about the long-term future of this resource.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code are available from Zenodo: https://doi.org/10.5281/zenodo.15809237.

REFERENCES

Abatzoglou, J. T., D. E. Rupp, L. W. O'Neill, and M. Sadegh. 2021. "Compound Extremes Drive the Western Oregon Wildfires of September 2020." *Geophysical Research Letters* 48(8): e2021GL092520.

Adams, D. M., and G. S. Latta. 2007. "Timber Trends on Private Lands in Western Oregon and Washington: A New Look." *Western Journal of Applied Forestry* 22(1): 8–14.

Agee, J. K. 1996. *Fire Ecology of Pacific Northwest Forests*. Washington, D.C: Island Press.

Agee, J. K., and M. H. Huff. 1987. "Fuel Succession in a Western Hemlock/Douglas-Fir Forest." *Canadian Journal of Forest Research* 17(7): 697–704.

Agee, J. K., and F. Krusemark. 2001. "Forest Fire Regime of the Bull Run Watershed, Oregon." *Northwest Science* 75(3): 292–306.

Baker, W. L., and D. Ehle. 2001. "Uncertainty in Surface-Fire History: The Case of Ponderosa Pine Forests in the Western United States." *Canadian Journal of Forest Research* 31(7): 1205–26.

Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. "Human-Started Wildfires Expand the Fire Niche across the United States." *Proceedings of the National Academy of Sciences* 114(11): 2946–51.

Barros, A. M., M. A. Day, T. A. Spies, and A. A. Ager. 2021. "Effects of Ownership Patterns on Cross-Boundary Wildfires." *Scientific Reports* 11(1): 19319.

Baxter, P. 1986. "Archaic Upland Adaptations in the Central Oregon Cascades." Dissertation, University of Oregon.

Bergeron, Y., A. Leduc, B. D. Harvey, and S. Gauthier. 2002. "Natural Fire Regime: A Guide for Sustainable Management of the Canadian Boreal Forest." *Silva Fennica* 36(1): 81–95.

Bergland, E. O. 1992. "Historic Period Plateau Culture Tree Peeling in the Western Cascades of Oregon." *Northwest Anthropological Research Notes* 25(2): 31–53.

Bowman, D., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio, et al. 2009. "Fire in the Earth System." *Science* 324: 481–84.

Clary, D. A. 1986. *Timber and the Forest Service*. Lawrence, KS: University Press of Kansas.

Comfort, E. J., D. A. Clark, R. G. Anthony, J. Bailey, and M. G. Betts. 2016. "Quantifying Edges as Gradients at Multiple Scales Improves Habitat Selection Models for Northern Spotted Owl." *Landscape Ecology* 31: 1227–40.

Cook, E. R., R. Seager, R. R. Heim, Jr., R. S. Vose, C. Herweijer, and C. Woodhouse. 2010. "Megadroughts in North America: Placing IPCC Projections of Hydroclimatic Change in a Long-Term Palaeoclimate Context." *Journal of Quaternary Science* 25: 48–61.

Coughlan, M. R., J. D. Johnston, K. M. Derr, D. G. Lewis, and B. R. Johnson. 2024. "Pre-Contact Indigenous Fire Stewardship: A Research Framework and Application to a Pacific Northwest Temperate Rainforest." *Frontiers in Environmental Archaeology* 3: 1347571.

Crumley, R. L., R. T. Palomaki, A. W. Nolin, E. A. Sproles, and E. J. Mar. 2020. "SnowCloudMetrics: Snow Information for Everyone." *Remote Sensing* 12(20): 3341.

Downing, W. M., C. J. Dunn, M. P. Thompson, M. D. Caggiano, and K. C. Short. 2022. "Human Ignitions on Private Lands Drive USFS Cross-Boundary Wildfire Transmission and Community Impacts in the Western US." *Scientific Reports* 12(1): 2624.

Driscoll, D. A., D. B. Lindenmayer, A. F. Bennett, M. Bode, R. A. Bradstock, G. J. Cary, M. F. Clarke, et al. 2010. "Fire Management for Biodiversity Conservation: Key Research Questions and our Capacity to Answer them." *Biological Conservation* 143: 1928–39.

Dunn, C. D., J. D. Johnston, M. J. Reilly, R. A. Miller, and J. D. Bailey. 2020. "How Does Tree Regeneration Respond to Mixed-Severity Fire in the Western Oregon Cascades, USA?" *Ecosphere* 11(1): e03003.

Falk, D. A., E. K. Heyerdahl, P. M. Brown, T. W. Swetnam, E. K. Sutherland, Z. Gedalof, and T. J. Brown. 2010. "Fire and Climate Variation in Western North America from Fire-Scar and Tree Ring Networks." *Pages News* 18(2): 70–72.

Flitcroft, R., L. Whitman, J. White, R. Wallick, L. S. Garvin, C. Smith, L. Stratton Garvin, et al. 2023. "Science to Support Conservation Action in a Large River System: The Willamette River, Oregon, USA." *Water Biology and Security* 2(4): 100203.

Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. "Ecological Characteristics of Old-Growth Douglas-Fir Forests." General Technical Report PNW-GTR-118. USDA Forest Service, Pacific Northwest Research Station.

Franklin, J. F., and M. A. Hemstrom. 1981. "Aspects of Succession in the Coniferous Forests of the Pacific Northwest." In *Forest Succession: Concepts and Application*, edited by D. C. West, H. H. Shugart, and D. B. Botkin, 211–230. New York: Springer-Verlag.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, R. Van Pelt, et al. 2002. "Disturbances and Structural Development of Natural Forest Ecosystems with Silvicultural Implications, Using Douglas-Fir Forests as an Example." *Forest Ecology and Management* 155(1–3): 399–423.

Franklin, J. F., and R. H. Waring. 1980. "Distinctive Features of the Northwestern Coniferous Forest: Development, Structure, and Function." In *Forests: Fresh Perspectives from Ecosystem Analysis* 59–86. Corvallis, OR: Oregon State University Press.

Freeman, J., L. Kobziar, E. W. Rose, and W. Cropper. 2017. "A Critique of the Historical-Fire-Regime Concept in Conservation." *Conservation Biology* 31(5): 976–985.

Freund, J. A., J. F. Franklin, A. J. Larson, and J. A. Lutz. 2014. "Multi-Decadal Establishment for Single-Cohort Douglas-Fir Forests." *Canadian Journal of Forest Research* 44(9): 1068–78.

Gray, A. N., and J. F. Franklin. 1997. "Effects of Multiple Fires on the Structure of Southwestern Washington Forests." *Northwest Science.* 71(3): 174–185.

Harley, G. L., C. H. Baisan, P. M. Brown, D. A. Falk, W. T. Flatley, H. D. Grissino-Mayer, A. Hessl, et al. 2018. "Advancing Dendrochronological Studies of Fire in the United States." *Fire* 1(1): 1–6.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models (Version 0.4.6) [R Package]." https://CRAN.R-project.org/package=DHARMa

Heinselman, M. L. 1981. "Fire and Succession in the Conifer Forests of Northern North America." In *Forest Succession: Concepts and Application* 374–405. New York: Springer.

Heyerdahl, E. K., D. McKenzie, L. D. Daniels, A. E. Hessl, J. S. Littell, and N. J. Mantua. 2008. "Climate Drivers of Regionally Synchronous Fires in the Inland Northwest (1651–1900)." *International Journal of Wildland Fire* 17(1): 40–49.

Higuera, P. E., and J. T. Abatzoglou. 2021. "Record-Setting Climate Enabled the Extraordinary 2020 Fire Season in the Western United States." *Global Change Biology* 27(1): 1–2.

Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, et al. 2015. "Completion of the 2011 National Land Cover Database for the Conterminous United States–Representing a Decade of Land Cover Change Information." *Photogrammetric Engineering and Remote Sensing* 81(5): 345–354.

Hudiburg, T., B. Law, D. P. Turner, J. Campbell, D. C. Donato, and M. Duane. 2009. "Carbon Dynamics of Oregon and Northern California Forests and Potential Land-Based Carbon Storage." *Ecological Applications* 19(1): 163–180.

Hulse, D., A. Branscomb, C. Enright, B. Johnson, C. Evers, J. Bolte, and A. Ager. 2016. "Anticipating Surprise: Using Agent-Based Alternative Futures Simulation Modeling to Identify and Map Surprising Fires in the Willamette Valley, Oregon, USA." *Landscape and Urban Planning* 156: 26–43.

Hurteau, M. D., and M. L. Brooks. 2011. "Short- and Long-Term Effects of Fire on Carbon in U.S. Dry Temperate Forest Systems." *Bioscience* 61(2): 139–146.

Hutto, R. L., R. E. Keane, R. L. Sherriff, C. T. Rota, L. A. Eby, and V. A. Saab. 2016. "Toward a more Ecologically Informed View of Severe Forest Fires." *Ecosphere* 7(2): e01255.

Iglesias, V., and C. Whitlock. 2020. "If the Trees Burn, Is the Forest Lost? Past Dynamics in Temperate Forests Help Inform Management Strategies." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375(1794): 20190115.

Isaac, L. A. 1943. *Reproductive Habits of Douglas-Fir*. Washington, D.C: Charles Lathrop Pack Forestry Foundation.

Jenkins, J. S., J. T. Abatzoglou, D. E. Rupp, and E. Fleishman. 2023. "Human and Climatic Influences on Wildfires Ignited by Recreational Activities in National Forests in Washington, Oregon, and California." *Environmental Research Communications* 5(9): 095002.

Johnson, B. R., A. A. Ager, C. R. Evers, D. W. Hulse, M. Nielsen-Pincus, T. J. Sheehan, and J. P. Bolte. 2023. "Exploring and Testing Wildfire Risk Decision-Making in the Face of Deep Uncertainty." *Fire* 6(7): 276.

Johnston, J. D., J. D. Bailey, C. J. Dunn, and A. A. Lindsay. 2017. "Historical Fire-Climate Relationships in Contrasting Interior Pacific Northwest Forest Types." *Fire Ecology* 13(2): 18–36.

Johnston, J. D., C. J. Dunn, and M. J. Vernon. 2019. "Tree Traits Influence Response to Fire Severity in the Western Oregon Cascades, USA." *Forest Ecology and Management* 433: 690–98.

Johnston, J. D., J. B. Kilbride, G. W. Meigs, C. J. Dunn, and R. E. Kennedy. 2021. "Does Conserving Roadless Wildland Increase Wildfire Activity in Western U.S. National Forests?" *Environmental Research Letters* 16(8): 084040.

Johnston, J. D., M. R. Schmidt, A. G. Merschel, W. M. Downing, M. R. Coughlan, and D. G. Lewis. 2023. "Exceptional Variability in Historical Fire Regimes across a Western Cascades Landscape, Oregon, USA." *Ecosphere* 14(12): e4735.

Jones, G. M., R. J. Gutiérrez, W. M. Block, P. C. Carlson, E. J. Comfort, S. A. Cushman, R. J. Davis, et al. 2020. "Spotted Owls and Forest Fire: Comment." *Ecosphere* 11(12): e03312.

Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, et al. 2020. "Habitat Selection by Spotted Owls after a Megafire Reflects their

Adaptation to Historical Frequent-Fire Regimes." *Landscape Ecology* 35: 1199–1213.

Jones, G. M., C. K. Stanley, M. Z. Peery, C. Maxwell, and K. N. Wilson. 2024. "Accelerated Forest Restoration May Benefit Spotted Owls through Landscape Complementation." *Animal Conservation* 28: 236–248. https://doi.org/10.1111/acv.12976.

Koontz, M. J., M. P. North, C. M. Werner, S. E. Fick, and A. M. Latimer. 2020. "Local Forest Structure Variability Increases Resilience to Wildfire in Dry Western U.S. Coniferous Forests." *Ecology Letters* 23(3): 483–494.

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. "Global Pyrogeography: The Current and Future Distribution of Wildfire." *PLoS One* 4(4): e5102.

Kroll, A. J., J. D. Johnston, T. D. Stokely, and G. W. Meigs. 2020. "From the Ground Up: Managing Young Forests for a Range of Ecosystem Outcomes." *Forest Ecology and Management* 464: 118055.

Laughlin, M. M., L. K. Rangel-Parra, J. E. Morris, D. C. Donato, J. S. Halofsky, and B. J. Harvey. 2023. "Patterns and Drivers of Early Conifer Regeneration Following Stand-Replacing Wildfire in Pacific Northwest (USA) Temperate Maritime Forests." *Forest Ecology and Management* 549: 121491.

Lee, C., C. Schlemme, J. Murray, and R. Unsworth. 2015. "The Cost of Climate Change: Ecosystem Services and Wildland Fires." *Ecological Economics* 116: 261–69.

Leonard, B., A. J. Plantinga, and M. Wibbenmeyer. 2021. "Stranded Land Constrains Public Land Management and Contributes to Larger Fires." *Environmental Research Letters* 16(4): 045004.

Lewis, D. G. 2014. "Four Deaths: The Near Destruction of Western Oregon Tribes and Native Lifeways, Removal to the Reservation, and Erasure from History." *Oregon Historical Quarterly* 115(3): 414–437.

Lewis, D. G. 2023. *Tribal Histories of the Willamette Valley*. Portland, OR: Ooligan Press.

Margolis, E. Q., C. H. Guiterman, R. D. Chavardès, J. D. Coop, K. Copes-Gerbitz, D. A. Dawe, and P. J. Weisberg. 2022. "The North American Tree-Ring Fire-Scar Network." *Ecosphere* 13(7): e4159.

Mass, C. F., D. Ovens, R. Conrick, and J. Saltenberger. 2021. "The September 2020 Wildfires over the Pacific Northwest." *Weather and Forecasting* 36(5): 1843–65.

McGinn, K., B. Zuckerberg, G. M. Jones, C. M. Wood, S. Kahl, K. G. Kelly, S. A. Whitmore, et al. 2025. "Frequent, Heterogenous Fire Supports a Forest Owl Assemblage." *Ecological Applications* 35(1): e3080.

Merschel, A. G., E. K. Heyerdahl, T. A. Spies, and R. A. Loehman. 2018. "Influence of Landscape Structure, Topography, and Forest Type on Spatial Variation in Historical Fire Regimes, Central Oregon, USA." *Landscape Ecology* 33(7): 1195–1209.

Merschel, A. G., M. A. Krawchuk, J. D. Johnston, and T. A. Spies. 2024. "Historical Pyrodiversity in Douglas-Fir Forests of the Southern Cascades of Oregon, USA." *Forest Ecology and Management* 572: 122306.

Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. "Historical Range of Variability: A Useful Tool for Evaluating Ecosystem Change." *Journal of Sustainable Forestry* 2(1–2): 87–111.

Morrison, P. H., and F. J. Swanson. 1990. *Fire History and Pattern in a Cascade Range Landscape. Gen. Tech. Rep. PNW-GTR-254* 77. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Mote, P. W., E. A. Parson, A. F. Hamlet, W. S. Keeton, D. Lettenmaier, N. Mantua, E. L. Miles, et al. 2003. "Preparing for Climatic Change: The Water, Salmon, and Forests of the Pacific Northwest." *Climatic Change* 61(1–2): 45–88.

Munger, T. T. 1940. "The Cycle From Douglas Fir to Hemlock." *Ecology* 21(4): 451–59.

Murphy, B. P., L. L. Yocom, and P. Belmont. 2018. "Beyond the 1984 Perspective: Narrow Focus on Modern Wildfire Trends Underestimates Future Risks to Water Security." *Earth's Future* 6(11): 1492–97.

Neiland, B. J. 1956. "Forest and Adjacent Burn in the Tillamook Burn Area of Western Oregon." *Ecology* 39: 660–671.

Nowacki, G. J., and M. D. Abrams. 2008. "The Demise of Fire and 'Mesophication' of Forests in the Eastern United States." *Bioscience* 58(2): 123–138.

Pan, S., H. Tian, S. R. Dangal, Z. Ouyang, B. Tao, W. Ren, S. R. S. Dangal, C. Lu, and S. Running. 2014. "Modeling and Monitoring Terrestrial Primary Production in a Changing Global Environment: Toward a Multiscale Synthesis of Observation and Simulation." *Advances in Meteorology* 2014: 965936.

Parisien, M. A., and M. A. Moritz. 2009. "Environmental Controls on the Distribution of Wildfire at Multiple Spatial Scales." *Ecological Monographs* 79(1): 127–154.

Perkins, R. M., and J. A. Jones. 2008. "Climate Variability, Snow, and Physiographic Controls on Storm Hydrographs in Small Forested Basins, Western Cascades, Oregon." *Hydrological Processes* 22(25): 4949–64.

Poage, N. J., and J. C. Tappeiner, II. 2002. "Long-Term Patterns of Diameter and Basal Area Growth of Old-Growth Douglas-Fir Trees in Western Oregon." *Canadian Journal of Forest Research* 32(7): 1232–43.

Poage, N. J., P. J. Weisberg, P. C. Impara, J. C. Tappeiner, and T. S. Sensenig. 2009. "Influences of Climate, Fire, and Topography on Contemporary Age Structure Patterns of Douglas-Fir at 205 Old Forest Sites in Western Oregon." *Canadian Journal of Forest Research* 39(8): 1518–30.

Prichard, S., P. Hessburg, R. Gray, N. Povak, B. Solter, C. Stevens-Rumann, and P. Morgan. 2018. "Evaluating the Influence of Prior Burn Mosaics on Subsequent Wildfire Behavior, Severity, and Fire Management Options."

PRISM Climate Group. 2023. "Oregon State University." http://www.prism.oregonstate.edu

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Rakestraw, L., and M. Rakestraw. 1991. *History of the Willamette National Forest* 272. Portland, OR: USDA Forest Service Pacific Northwest Region.

Reilley, C., M. S. Crandall, J. D. Kline, J. B. Kim, and J. de Diego. 2023. "The Influence of Socioeconomic Factors on Human Wildfire Ignitions in the Pacific Northwest, USA." *Fire* 6(8): 300.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. "Contemporary Patterns of Fire Extent and Severity in Forests of the Pacific Northwest, USA (1985–2010)." *Ecosphere* 8(3): e01695.

Reilly, M. J., A. Zuspan, J. S. Halofsky, C. Raymond, A. McEvoy, A. W. Dye, D. C. Donato, et al. 2022. "Cascadia Burning: The

Historic, but Not Historically Unprecedented, 2020 Wildfires in the Pacific Northwest, USA." *Ecosphere* 13(6): e4070.
Rockweit, J. T., K. M. Dugger, D. B. Lesmeister, R. J. Davis, A. B. Franklin, and J. M. Higley. 2024. "Changing Fire Regimes and Nuanced Impacts on a Critically Imperiled Species." *Biological Conservation* 296: 110701.
Romme, W. H., and D. H. Knight. 1981. "Fire Frequency and Subalpine Forest Succession along a Topographic Gradient in Wyoming." *Ecology* 62(2): 319–326.
Rorig, M. L., and S. A. Ferguson. 1999. "Characteristics of Lightning and Wildland Fire Ignition in the Pacific Northwest." *Journal of Applied Meteorology and Climatology* 38(11): 1565–75.
Rothermel, R. C. 1983. *How to Predict the Spread and Intensity of Forest and Range Fires*, Vol. 143. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
Rousset, F., and J. B. Ferdy. 2014. "Testing Environmental and Genetic Effects in the Presence of Spatial Autocorrelation." *Ecography* 37(8): 781–790.
Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff. 1991. *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests (Gen. Tech. Rep. PNW-GTR-285)*. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
Sayedi, S. S., B. W. Abbott, B. Vannière, B. Leys, D. Colombaroli, G. G. Romera, et al. 2024. "Assessing Changes in Global Fire Regimes." *Fire Ecology* 20(1): 1–22.
Short, K. C. 2017. *Spatial Wildfire Occurrence Data for the United States, 1992–2015 [FPA_FOD_20170508]*, 4th ed. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2013-0009.4.
Smithwick, E. A., M. E. Harmon, S. M. Remillard, S. A. Acker, and J. F. Franklin. 2002. "Potential Upper Bounds of Carbon Stores in Forests of the Pacific Northwest." *Ecological Applications* 12(5): 1303–17.
Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. "Conserving Old-Growth Forest Diversity in Disturbance-Prone Landscapes." *Conservation Biology* 20(2): 351–362.
Steel, Z. L., D. Foster, M. Coppoletta, J. M. Lydersen, S. L. Stephens, A. Paudel, S. H. Markwith, K. Merriam, and B. M. Collins. 2021. "Ecological Resilience and Vegetation Transition in the Face of Two Successive Large Wildfires." *Journal of Ecology* 109(9): 3340–55.
Stevens, J. T., M. M. Kling, D. W. Schwilk, J. M. Varner, and J. M. Kane. 2020. "Biogeography of Fire Regimes in Western US Conifer Forests: A Trait-Based Approach." *Global Ecology and Biogeography* 29(5): 944–955.
Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. "The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites." *Frontiers in Ecology and the Environment* 9: 117–125. https://doi.org/10.1890/090157.
Tepley, A. J. 2010. *Age Structure, Developmental Pathways, and Fire Regime Characterization of Douglas-Fir/Western Hemlock Forests in the Central Western Cascades of Oregon*. Corvallis, OR: Oregon State University.
Tepley, A. J., F. J. Swanson, and T. A. Spies. 2013. "Fire-Mediated Pathways of Stand Development in Douglas-Fir/Western Hemlock Forests of the Pacific Northwest, USA." *Ecology* 94(8): 1729–43.
Tepley, A. J., F. J. Swanson, and T. A. Spies. 2014. "Post-Fire Tree Establishment and Early Cohort Development in Conifer Forests of the Western Cascades of Oregon, USA." *Ecosphere* 5(7): 1–23.
Tepley, A. J., E. Thomann, T. T. Veblen, G. L. Perry, A. Holz, J. Paritsis, et al. 2018. "Influences of Fire–Vegetation Feedbacks and Post-Fire Recovery Rates on Forest Landscape Vulnerability to Altered Fire Regimes." *Journal of Ecology* 106(5): 1925–40.
Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Johnson. 2006. "The Northwest Forest Plan: Origins, Components, Implementation Experience, and Suggestions for Change." *Conservation Biology* 20(2): 277–287.
Thompson, J., S. Duncan, and K. Johnson. 2009. "Is There Potential for the Historical Range of Variability to Guide Conservation Given the Social Range of Variability?" *Ecology and Society* 14: 18.
Waring, R. H., and J. F. Franklin. 1979. "Evergreen Coniferous Forests of the Pacific Northwest: Massive Long-Lived Conifers Dominating these Forests Are Adapted to a Winter-Wet, Summer-Dry Environment." *Science* 204(4400): 1380–86.
Weisberg, P. J. 2004. "Importance of Non-Stand-Replacing Fire for Development of Forest Structure in the Pacific Northwest, USA." *Forest Science* 50(2): 245–258.
Weisberg, P. J., and F. J. Swanson. 2003. "Regional Synchroneity in Fire Regimes of Western Oregon and Washington, USA." *Forest Ecology and Management* 172: 17–28.
Westerling, A. L. 2008. "Climatology for Wildfire Management." In *The Economics of Forest Disturbances* 107–122. Dordrecht: Springer.
Winter, L. E., L. B. Brubaker, J. F. Franklin, E. A. Miller, and D. Q. DeWitt. 2002. "Initiation of an Old-Growth Douglas-Fir Stand in the Pacific Northwest: A Reconstruction from Tree Ring Records." *Canadian Journal of Forest Research* 32(6): 1039–56.
Zald, H. S., and C. J. Dunn. 2018. "Severe Fire Weather and Intensive Forest Management Increase Fire Severity in a Multi-Ownership Landscape." *Ecological Applications* 28(4): 1068–80.
Zenk, H. B., and B. Rigsby. 1998. "Molalla." In *Handbook of North American Indians*, Vol. 12, 439–445. Washington, D.C: Smithsonian Institute.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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