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Historical pyrodiversity in Douglas-fir forests of the southern Cascades of Oregon, USA

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ABSTRACT

Our understanding of forest dynamics and successional pathways in coastal Douglas-fir (*Pseudotsuga menziesii var menziesii*) forests with relatively frequent mixed-severity fires is limited by a lack of annually precise dendroecological reconstructions that combine records of historical fires and tree establishment. The processes by which old-forest heterogeneity developed under historical fire regimes with recurrent low- and moderate-severity fires has not been well studied at fine temporal scales and across spatial scales. We developed crossdated multi-century records of fire and tree establishment histories in old forests (170 – 550 years) at 34 plots distributed across six sites. Study sites include warm-dry to cool-moist Douglas-fir forest types found in the southern west Cascades of Oregon, USA. Spatial variability in historical fire frequency and fire effects resulted in tremendous diversity in forest developmental histories, age structure, and forest conditions. Most historical fire intervals were very frequent (<10 years) to frequent (<25 years) in dry Douglas-fir forests. Exceptionally high fire frequency and an abrupt decrease in fire frequency after European colonization in dry Douglas-fir forests adds to growing evidence and recognition of Indigenous fire stewardship in montane Douglas-fir forests. In moist forests where Douglas-fir is seral to western hemlock, fire intervals were frequent to moderately frequent (<50 years), but intervals varied substantially over time. Relatively young moist forests burned frequently while mature moist forests had long fire intervals (50–160 years). Nearly all tree establishment cohorts were preceded by either stand-replacing (28 %) or non-stand-replacing fires (64 %). However, tree cohorts only provided evidence of 16 % of historical fire events that we reconstructed from cambial fire scars. This study demonstrates that frequent fire can be an important driver of forest development and in some contexts shapes the structure of coastal old-growth Douglas-fir forests, which are often characterized as developing from endogenous disturbances during long fire-free periods. The high level of pyrodiversity we observed was associated with variation in and interactions of micro-climate, topography, fuels, and Indigenous fire stewardship. We recommend rigorous dendroecological reconstructions across the coastal Douglas-fir region to refine our understanding of the geography of fire-mediated forest developmental dynamics in this important forest type, to inform forest management, conservation, and ecocultural restoration.

1. Introduction

Wildland fire is a driver of ecosystem dynamics in many forest regions, but its role is complex and varies with biophysical setting, climate, and human activity. Fire is a major component of the history of coastal Douglas-fir (*Pseudotsuga menziesii var menziesii*) forests – hereafter Douglas-fir forests – across the maritime climate west of the crest of the Cascade Mountains in the Pacific Northwest and northern California in the western United States (Agee, 1993). This productive region is home to some of the largest, tallest, and longest-lived species of nine conifer genera, including Douglas-fir (Franklin and Dryness, 1988), and support critical ecosystem services including carbon sequestration, biodiversity, economies, recreation, and cultural relationships (Charnley et al., 2018). The role of forest fire in this climatically and topographically complex region has been the focus of considerable research in the last few decades (Spies et al., 2018), but until recently few studies have employed rigorous dendroecological methods, i.e. annually resolved (crossdated) fire scars and tree cohorts, to

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characterize historical fires regimes, their diversity, and their influence on historical forest dynamics. This methodology is needed to better understand how the pattern and role of fire varies at multiple spatial and temporal scales within ecosystems of the large and diverse Douglas-fir region.

Improved knowledge of fire history in coastal Douglas-fir forests is needed to direct forest management and conservation. For example, United States Forest Service (USFS) land managers are directed by the 2012 Planning Rule (USFS, 2012) to restore natural successional and disturbance processes including fire to maintain biodiversity and ecosystem services in the context of natural and anthropogenic stressors (Spies et al., 2019). However, the 1994 Northwest Forest Plan (NWFP; USFS and BLM, 1994) that frames USFS federal forest management across a broad region of the Pacific Northwest describes a simplified characterization of disturbance-succession dynamics in the Douglas-fir region, dividing them into moist and dry forests. Moist forests are characterized as having long fire return intervals between mostly stand-replacing fires that allow centuries-old late successional stands of old-growth Douglas-fir and western hemlock (*Tsgua heterophylla*) to develop (Franklin and Johnson, 2012, Spies et al.2019). This heuristic model of succession is largely based on fire regimes and successional patterns from the Cascade Range in Washington and northern Oregon and wet, west sides of the Coast Ranges (Spies et al., 2019). The simplified characterization of fire regimes does not incorporate knowledge of the complexity and variability in typologies of historical fire regimes in moist forests in the coastal Douglas-fir region in the central and southern Cascades demonstrated by Morrison and Swanson (1990), Tepley et al. (2013), Spies et al. (2019), Johnston et al. (2023). These studies reveal that while the infrequent fire regime occurs in some landscapes, fire was much more frequent and variable in severity than was previously hypothesized in moist Douglas-fir forests. However, management direction and culture for moist forests codified by the 1994 NWFP does not include this variability, and accordingly stewardship of the moist coastal Douglas-fir forests on these federal lands simplifies characteristic heterogeneity that would be provided by variable fire regimes or by emulating that disturbance effect through management. Furthermore, emerging science highlights the role of cultural burning by Indigenous peoples, which is being recognized as an underappreciated driver of fire regimes and historical vegetation conditions in the Douglas-fir region that is critical to ecological and social restoration (Long et al., 2021, Johnston et al., 2023). An ongoing (2024/2025) NWFP amendment process (USFS, 2023) aims to modernize management direction for the region, including broader recognition of diverse fire regimes and their geographies, the importance of Tribal stewardship and sovereignty, and adaptation required in the context of climate change. Continued development in knowledges of fire history, Indigenous fire stewardship, and forest ecosystem processes will be critical to evolution of forest management of the region in years to come.

In the well-known model that has dominated characterizations of old-growth development in relatively moist forests, historical fires were infrequent and included extensive areas of high-severity or stand-replacing fire effects (*sensu* Hemstrom and Franklin, 1982, Agee and Krusemark, 2001). Historical fire activity in these moist settings is hypothesized to be largely limited to periods of severe drought and extreme fire weather including synoptic east winds events (Agee, 1993). The 2020 Labor Day fires and extensive and severe wildfires of the 19th century and early 20th century in the region provide clear evidence of infrequent, high-severity fires (Reilly et al., 2022). Forest succession in a Douglas-fir ecosystem with an infrequent, stand-replacing fire regime largely proceeds via endogenous ecological processes (e.g. fine-scale tree mortality from wind, disease, and pathogens) in a series of stages culminating, in the development of complex old-growth structure composed of a mixture of shade intolerant and shade tolerant species (*sensu* Oliver and Larson, 1996, Franklin et al., 2002). Canopy tree mortality creates small (<0.1 ha) canopy gaps that provide mineral and decayed-wood seedbeds and understory sunlight that facilitate the development of spatial heterogeneity and multi-layered canopies that are characteristic of late-successional Douglas-fir and western hemlock forests (Spies and Franklin, 1989, Gray and Spies, 1997). This disturbance-succession pathway certainly occurs in some locations; however, it is important to recognize it is not the monolithic model for the Douglas-fir region.

Forest developmental pathways with low- and moderate-severity or non-stand replacing (NSR) fires are additional typologies that extend beyond the infrequent, stand replacing fire successional pathway, and are increasingly recognized in the coastal Douglas-fir region. The NSR fire effects are important to the development of key old-growth forest characteristics including multi-storied canopy structure, horizontal gaps and openings, mixed-species composition, and large snags and logs (Poage et al., 2009, Tepley et al., 2013). NSR fires occurring after a high-severity fire provide opportunities for additional tree cohorts by killing a portion of the recruiting forest, removing understory competition, and by exposing mineral soil. Across a landscape, variation in the amount, timing, and effects fires occurring within a previous patch of extensive high-severity fire, drives forest structure and composition toward a fine-grained and dynamic mosaic of forests with different development histories and conditions (Morrison and Swanson, 1990). Tepley et al. (2013) developed a systematic and crossdated reconstruction of tree establishment in the central Cascades that provides strong evidence that variation in the frequency, timing, and effects of historical fires formed multiple fire-mediated developmental pathways that resulted in distinct forest structure and composition in contemporary old forests. However, our ability to reveal fine-scale temporal and spatial variation in forest dynamics that are shaped by NSR fires in this region has been limited by a lack of rigorous landscape-scale dendroecological reconstructions that combine crossdated records of historical fires with crossdated reconstruction of tree establishment.

Dendroecology uses the exact dating of tree rings to characterize spatial and temporal variation in fire frequency and severity, and its influence on tree population dynamics. Crossdating is a standard method in modern dendroecology that uses temporal variation in annual ring widths driven by the hydroclimatic sensitivity of tree growth to assign annual rings and fire scars to exact calendar years (Douglass, 1941). Crossdated records of historical fires that are directly evidenced by cambial fire scars provide critical information for understanding the interactions of fire, climate, terrain, forests, and people through time (Margolis et al., 2022). Studies that combine crossdated records of historical fires and tree establishment are common across the southwestern U.S. (e.g., Roos and Swetnam, 2012), the Appalachian region (Lafon et al., 2017), the mid-Atlantic states (e.g. Stambaugh et al., 2018), and the inland Pacific Northwest (Merschel et al., 2021) where pine (*Pinus* spp.) that reliably record historical fires are relatively abundant and well-preserved. In Douglas-fir forests, annually resolved reconstructions of historical fires developed by sectioning, surfacing, and crossdating cambial fire scars are limited. The only known examples include a study of riparian areas in a small watershed in the southern Cascades (~500 ha; Olson and Agee, 2005), two small areas (<30 ha) in the San Juan Islands (Bakker et al., 2019), and a fire history that documents exceptional variability in historical fire regimes in Douglas-fir forests associated with aridity in a 15,000-ha study area in the central Cascades (Johnston et al., 2023). Johnston et al. (2023) did not include a full reconstruction of tree establishment dates, but multiple tree establishment cohorts opportunistically identified from stumps of harvested trees and logs sampled to develop fire records provide strong evidence of complex developmental histories that were mediated by NSR fires. Increasing our knowledge of historical fire and forest developmental patterns requires detailed investment in reconstruction of both fire history and tree establishment together.

The dearth of crossdated dendroecological records of historical fires and tree establishment in the Douglas-fir region stems from the challenges of locating, removing, and processing well-preserved cambial scars from coastal Douglas-fir trees combined with the dominant characterization that forest succession, dynamics, and conditions were largely shaped by an infrequent, high-severity fire regime. Douglas-fir's rapid growth and thick insulating bark means it may not reliably records fires in comparison to pine species (Appendix 1). When cambial fire scars do form, they may be difficult to identify and sample because small scars are quickly grown over and concealed by bark (Taylor and Skinner, 1998), and large scars that remain open are susceptible to rot (Morrison and Swanson, 1990) or combustion in subsequent fires. In addition, some landscapes where old trees were killed by extensive high-severity fire may lack evidence of historical fires. Extensive high-severity fires that occurred during extremely hot, dry, and windy weather (Reilly et al., 2022) from 1840 to 1933 were landmark events in the Douglas-fir region that initiated young and relatively even-aged Douglas-fir forests across broad areas (Morris, 1934, Impara, 1997, Gray and Franklin, 1997, Zybach, 2004). The effects and legacy of these wildfires helped shape the perception that Douglas-fir forests were chiefly shaped by infrequent, high-severity fire, and likely de-emphasized consideration of the historical significance of relatively frequent NSR fires (Tepley, 2010) and cultural burning by Indigenous peoples (Zybach, 2004).

Given the challenges Douglas-fir posed to reconstructing fire and the hypothesis that NSR fires were rare, most researchers did not invest resources to develop annually resolved (i.e., crossdated) records of historical fires and tree establishment (Morrison and Swanson, 1990, Weisberg and Swanson, 2001). Instead fire history and tree establishment datasets were developed by inventorying tree ages and fire scars by conducting imprecise "field counts" on minimally prepared stumps in recent clearcut harvests of old-growth forests that were abundant on federally owned lands in the late 20th century (Morrison and Swanson, 1990). In a small comparison of field counted and crossdated samples from the western Cascades, the mean error for identifying the year fire scars formed and trees established was $\pm$ 25 years (standard deviation 19, range +13 to −78 years) and 12 % of fire scars were not detected in field counts (Weisberg and Swanson, 2001). These dating and omission errors in field count datasets confound analyses that are fundamental to characterizing how historical fire regimes and forest dynamics were influenced by climate and humans (*sensu* Taylor et al., 2016, Guiterman et al., 2019) and local biophysical setting (*sensu* Heyerdahl et al., 2019, Merschel et al., 2018). For example, dating errors from field counts led to the erroneous conclusion that postfire Douglas-fir establishment periods typically lasted for nearly a century theoretically because of competition with shrubs, harsh postfire microclimates, and long distances to seed sources (Tappeiner et al., 1997, Poage and Tappeiner, 2002). While competition and seed limitation are important factors for postfire tree establishment patterns, this theory required further testing. Tepley et al. (2014) simulated dating errors (Weisberg and Swanson, 2001) onto thousands of crossdated trees and demonstrated dating errors effectively blur tree cohorts that established within four decades into tree cohorts that established over several decades to more than a century. The predominant pattern of postfire Dougals-fir establishment culminating at 40 years found in crossdated datasets, supports an alternative hypothesis that Douglas-fir establishment is resilient to wide variation in fire effects across a broad range of biophysical settings (Tepley et al., 2014). Overall, accurate and precise crossdated fire and tree establishment dates are prerequisite for refining our understanding how historical fires influence tree establishment and forest dynamics.

Field-dated tree establishment years and specifically tree establishment cohorts – hereafter tree cohorts – have been used as a primary line of evidence of historical fire events, and to characterize historical fire and forest dynamics at landscape (Morrison and Swanson, 1990) and regional scales (Weisberg and Swanson, 2003, Poage et al., 2009). However, the relationship of cohorts to historical fires has not been precisely characterized. Tree cohorts are temporally distinct groups of trees establishing in response to disturbance and may provide indirect evidence of fires (Kent, 2014). Historical fires should be associated with tree cohorts in Douglas-fir forests because Douglas-fir establishment requires open canopy conditions and bare mineral soils (Hermann and Lavender, 1990). By inventorying tree cohorts, Tepley et al. (2013) presented strong evidence that historical fires mediated tree establishment, stand development pathways, and the characteristics of mature and old forests in the central Cascades. Still, using tree cohorts alone as indirect evidence of fire, without the direct evidence from cambial fire scars, has important limitations for reconstructing historical fires and their influence on forest dynamics. The fire year associated with a tree cohort cannot be determined in the absence of a crossdated fire scar because tree establishment may not begin for multiple years after a fire (Naficy 2016). Detecting fires from tree cohorts is biased towards fires that induce tree establishment; low- and moderate-severity fires that do not provide conditions required for tree establishment would not be detected using this approach. (Agee and Krusemark, 2001). Alternatively, tree cohorts may provide false evidence of fires when tree establishment occurs in openings created by insects and pathogens (Gray and Spies, 1996) or by severe storms (Halpern and Lutz, 2006; Sinton et al., 2000). Identifying the relationship between historical fire records derived from crossdated cambial fire scars and tree establishment cohorts is required to clarify the role NSR fires have in shaping the structure and composition of old trees and forests and diversity of these characteristics in moist Douglas-fir forests.

Our study is the first to apply analysis of precisely dated fire scars and tree cohorts to reconstruct historical fire regimes and their influence on forest development and species succession over time, hereafter forest development, in forests where coastal Douglas-fir is the predominant species. Our overall goal for this research is to characterize spatial and temporal variability in fire and its influence on mature and old forest development over a broad climatic gradient in Douglas-fir forests of the southern western Cascades of Oregon. Research objectives for this investigation are to: 1) Create annually precise multi-century records of historical fires using multiple lines of tree ring evidence, including fire scars and cohort analysis; 2) Characterize spatial and temporal patterns in fire extent, frequency, and effects; 3) Quantify the relationship between fire and tree establishment and describe how historical fires influenced forest development in mature and old-growth forests.

2. Methods

2.1. Study area

We collected data on the Umpqua National Forest located on the west slopes of the southern extent of the Oregon Cascades (Fig. 1a). We selected this portion of the Douglas-fir region because it allowed us to evaluate the importance and practicality of characterizing historical fire regimes across a range of Douglas-fir dominated forest types covering a gradient from drier to moister settings. This western portion of the Cascade Range is a heavily eroded volcanic mountain range composed of sinuous ridges generally reaching 1500 m (m) in elevation that are dissected by narrow stream and river valleys (Franklin and Dryness, 1988). Winter and summer are distinctly wet and dry respectively, with ~90 % of precipitation accumulating from October- April (PRISM, 2021). Douglas-fir is the dominant tree species across the study area, the abundance of other tree species varies with biophysical environment and stand development history (Appendix 1). In warm-dry environments ponderosa pine, (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana*) are shade-intolerant trees, and shade-tolerant trees include grand fir (*Abies grandis*) and incense-cedar (*Calocedrus decurrens*). In warm-moist to cool-moist environments, western hemlock is the predominant shade-tolerant species. Noble fir (*Abies procera*) is a common shade-intolerant species, and Pacific silver fir (*Abies amabilis*) is a common shade-tolerant species in cool-moist to cold, wet environments.

The southern western Cascades are the ancestral home of the Kalapuya, Umpqua, Molalla, and Takelma cultures (Suttles and Sturtevant, 1990). Cultural burning was essential to support plants used in textile production, to increase production and facilitate harvest of staple foods, to provide forage for game species, and to facilitate hunting of game

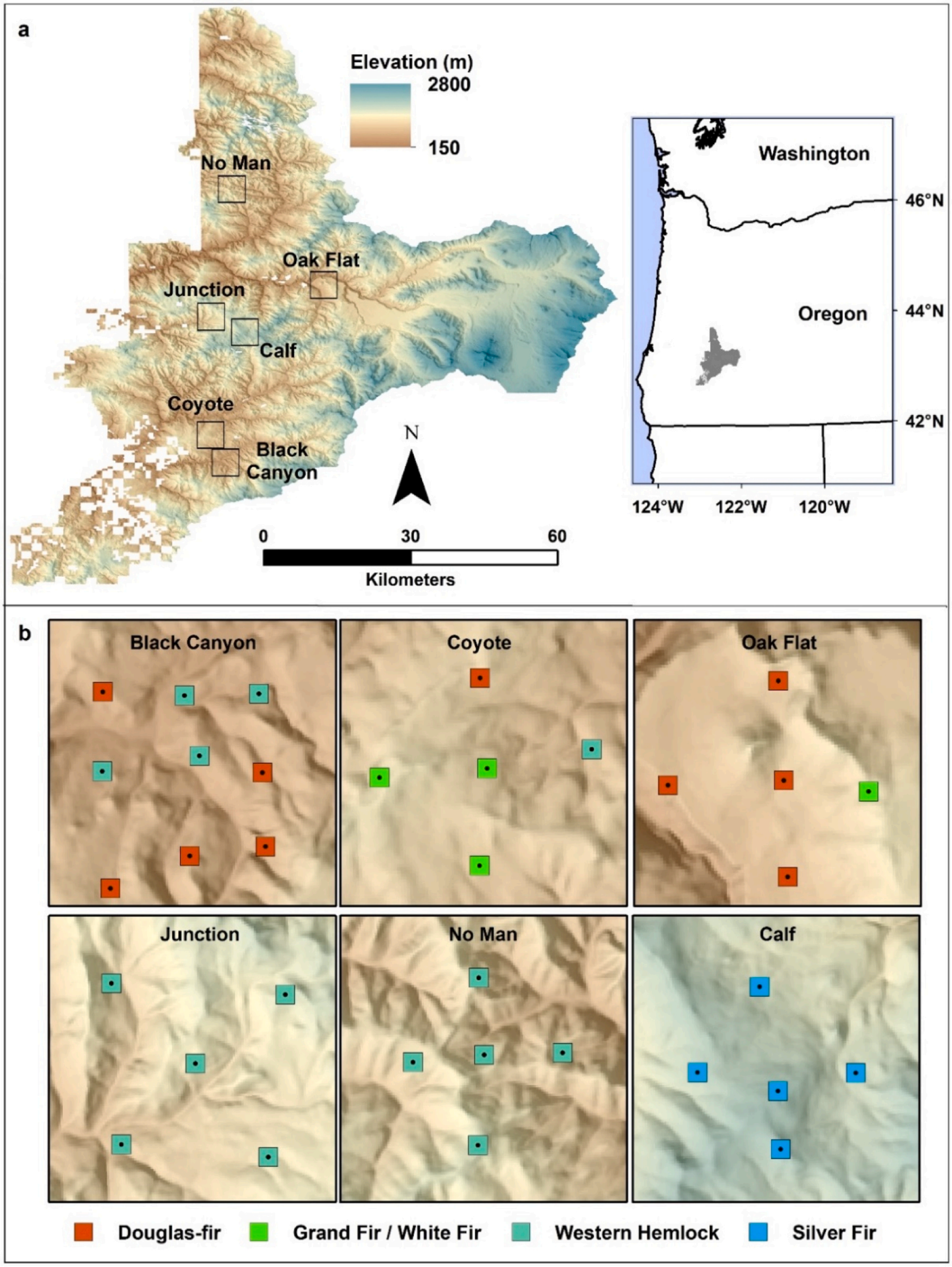

Fig. 1. **:** Study Area. Panel (a) displays the location of six sites on the Umpqua National Forest where we reconstructed fire and forest development history. The right inset panel shows the location of the UNF in grey in Oregon, U.S.A. Panel (b) displays 5–9 sample plots at each study that are color coded based on potential vegetation type. Plots in panel (b) are ~ 1 km apart. In panels (a) and (b) background color indicates elevation (m) and shading describes topography.

species in the Pacific Northwest (Pullen, 1996, Turner et al., 2011, Steen-Adams et al., 2019, Boyd, 2022). The arrival of Europeans and settler-colonialism in the late 18th century resulted in devasting impacts to Indigenous economies and lifeways and resulted in enormous socio-ecological changes (Boyd, 2022). Impacts on Native American populations, the regional economy, and ecosystems and fire stewardship occurred over several decades with distinct impacts during the pre-settlement and settlement periods (Cole and Darling 1990). During the pre-settlement period Native Americans were impacted by diseases, but their stewardship practices and economies persisted until ~1830. A devastating malaria epidemic that resulted in up 85 % mortality beginning in 1830 marks the transition to the European settlement period where unoccupied land and the collapse of the fur trade catalyzed a shift in the economy and land management practices in the region (Cole and Darling, 1990). Forcible removal of Indigenous peoples and erasure of their stewardship practices in the southern western Cascades culminated in the Rogue Indian Wars in the 1850s, after which most remaining Native Americans were forcibly removed to the Grand Ronde reservation in 1856.

2.2. Sample site and plot selection

We reconstructed annually resolved records of fire occurrence, hereafter fire events, with a stratified random sample of older forest stands at six sites that spanned the broad climatic gradient found within the study area (Fig. 1). Within each site we located nine individual plot centers approximately 1 km apart that allowed us to investigate how fire and tree establishment varied with fine-scale variability in topography, microclimate, and vegetation within approximately the same climatic conditions. Sites were named based on nearby major waterbodies (Black Canyon Creek, Coyote Creek, Calf Creek, Junction Creek, and No Man Creek) or existing landmarks (Oak Flat).

We focused site selection on extant older forest stands, since extensive logging precludes reconstruction of stand development history across many sites on the Umpqua National Forest. We used gradient nearest neighbor mapping products (Ohmann and Gregory, 2002 (GNN); available at https://lemma.forestry.oregonstate.edu) of old-growth structure index greater than 80 years (OGSI-80) to identify potential sample sites. The OGSI-80 is an index that represents mature or late-successional forest structure based on the density of live and dead trees and the diversity of live tree size classes in inventoried mature forests (Heather et al., 2015) under current conditions. To identify and exclude areas with past harvest, we examined a 200 m radius buffer from plot center and eliminated all potential plots where <50 % of the buffer met OGSI-80 requirements. The remaining plots were aggregated into contiguous 3×3 grids of 9 plots (potential sampling sites), with each plot in, or near, forest that met OGSI-80 requirements. In this way, potential sample sites were primarily located in older forests where age structure and forest development had not been influenced by tree harvest but may have been influenced by fire exclusion.

To stratify sample sites across a climate gradient, we classified the Umpqua National Forest into three precipitation zones with equal land area, based on mean of annual precipitation totals from 1981 to 2010 (PRISM, 2021): lower: 94–134 cm, intermediate: >134–156 cm, and higher: >156 cm. We randomly selected two potential sample sites in each precipitation zone. One of these sites (Junction Creek) was located in the Little River watershed, which was sampled in earlier characterizations of the historical fire regime by Van Norman (1998) and Carloni (2005); note these studies used field dated fire scars not crossdated samples. One site (Coyote Creek) was intentionally centered on the South Umpqua Experimental Forest and one site in the upper precipitation zone was dropped to accommodate Coyote Creek. The Coyote Creek site provided the opportunity to inform silvicultural treatments and reconstruct historical streamflow from tree rings on the South Umpqua Experimental Forest. Due to time constraints, only 5 of 9 plots were sampled at all sites except at Black Canyon where all 9 plots in the site grid were sampled. The outcome provided a set of 6 sites and 34 plots sampling a broad gradient in elevation and climate and represented the diversity of potential vegetation types (Halofsky et al., 2014; Table 1) where coastal Douglas-fir is predominant in the western Cascades (Fig. 1).

2.3. Data Collection

2.3.1. Field sampling

Field sampling took place in 2018 and 2019. Each plot included a 0.25 ha (50 by 50 m) sampling area where we measured contemporary forest structure and composition and reconstructed tree demography (Fig. 2). We focused sampling on trees > 25 cm DBH to reconstruct tree establishment prior to fire suppression efforts that began in the early 20th century. For trees > 25 cm DBH, species, diameter, and distance

Table 1
The distribution of potential vegetation types (PVTs) across the study area where Douglas-fir is a keystone species. PVTs summarize variability in biophysical environment (e.g. microclimate, topography, soil characteristics) that develop forest communities of similar composition and structure in the absence of major disturbances including fire and are commonly used to characterize forest types in the region. The distribution of tree species among PVTs sampled in this study is reported in Appendix 1. PVTs are often intermingled at fine scales in the west Cascades because rugged topography drives variation in microclimate.

Potential Vegetation Type	Elevation (m)	Precipitation (cm)	Description of Distribution
Dry Douglas-fir and Grand Fir	<1000	<125	Dry Douglas-fir and Grand Fir types are intermingled in warm-dry microclimates with the Grand Fir type in relatively mesic and productive aspects
Western Hemlock	1000–1500	125–165	The Western Hemlock type occurs in warm-moist to cool-moist productive microclimates and is intermingled with Douglas-fir and Grand Fir types in riparian areas and on mesic north aspects
Pacific Silver Fir	> 1300	>160	The Pacific Silver Fir type is restricted to cool-wet sites that have a deep winter snowpack

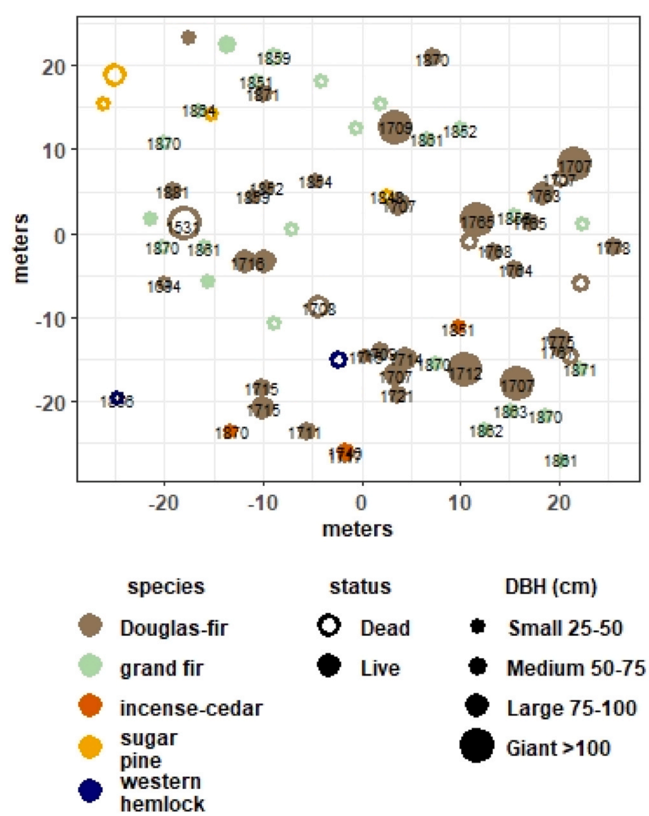

Fig. 2. : An example of data collected at each plot using plot BC4 at the Black Canyon study site. At each square ¼ ha plot we stem mapped all live and dead trees >25 cm DBH, recorded their status, species, and DBH (cm), and collected cores or cross sections from all sound trees to determine tree establishment dates. Establishment dates are shown for each sound tree (not rotten) in calendar years.

and bearing from plot center were recorded for all live and dead trees. A hand powered increment borer was used to remove increment cores from sound trees and snags. Trees were usually cored at ~40 cm in height, but collection height was recorded if a sample was collected higher on the tree. Trees were bored multiple times to intercept the pith or extract a ring field-estimated to be within 10 rings of the pith. For all sound logs and stumps at each plot, we removed partial cross sections with a chainsaw, usually including the pith, and recorded estimated sample height. When a sound increment core or cross section could not be obtained from a live or dead tree within the plot a "proxy" tree of the same species and similar DBH and crown and bark morphology was sampled as near the plot as possible.

Our goal was to obtain a complete census of establishment of trees > 25 cm DBH over time, and in most plots we collected samples from all of these trees. However, in 7 plots it was clear that nearly all trees established within the same short period based on field counts of tree cores, tree sizes, and tree bark and crown characteristics. At these plots, we did not sample every tree present, but ensured that we sampled across the range of establishment dates and species present by removing wood samples from at least 20 individual trees for each species present in each of four DBH classes (25–50 cm, 50–75, 75–100, >100 cm). For example, at plot NM5 (No Man site), field dating of tree cores and morphological characteristics of trees within the plot clearly demonstrated that all trees were established during 1896–1915. We removed cores from 20 Douglas-fir that were 25–50 cm DBH, and 20 Douglas-fir that were 50–75 cm DBH, but did not core the remaining Douglas-fir in those size classes that were established in the same short period. However, we still recorded the species, diameter, and location of trees that were not cored to attribute these trees to the most likely age class and to represent contemporary forest structure and composition within plots.

To collect direct evidence of fire, we searched each plot and the immediate surrounding area with no abrupt changes in slope or aspect for dead trees (snags, logs, and stumps) that contained cambial scars consistent with fire damage. Partial or full cross sections were removed with a chainsaw from 1 to 10 trees (average = 5.6) at 32 plots. The average distance from plot centers where we collected fire scars was 104 m and 30 % of fire scarred trees were sampled from trees within the 0.25 ha plot. We believe it is reasonable to assume that fires burned over all or most of the area within and in the immediate vicinity of plots given the plot and surrounding area had consistent terrain, forest composition, and no topographic or edaphic barriers to fire spread.

2.3.2. Sample processing and crossdating

All increment cores and cross sections were transported to the Tree Ring Lab at Oregon State University and sanded until cell structure could be seen with a binocular microscope following standard dendrochronological methods (Speer, 2010). Samples were precisely crossdated using tree ring chronologies developed for each species. Chronologies were developed by visually crossdating the oldest and highest quality samples using the list-year method (Yamaguchi, 1991). Annual ring widths of dated samples were measured to a precision of 0.001 mm using an Acu-Gage linear measuring system (Acu-Gage Systems, Hudson NH). Crossdating accuracy was then evaluated statistically using COFECHA software (Holmes, 1983). Samples with potential dating errors were checked, re-dated, and re-measured as necessary. We used our Douglas-fir master chronology to crossdate samples from rare species (e.g. western redcedar) with low sample depth in early centuries. Our Douglas-fir master chronology was developed by measuring 222,899 ring widths from 1089 trees sampled across all the plots in this study. Hardwoods including Pacific madrone (*Arbutus menziesii*), Oregon white oak (*Quercus garryana*), and bigleaf maple (*Acer macrophyllum*) were excluded from further analysis because they could not be reliably crossdated and were rare across all plots (1.3 % of all trees sampled).

Tree establishment dates were corrected for off center samples and the estimated time required to reach sample height. For 1122 of 1748 samples that did not intersect the pith, the number of rings to pith was estimated geometrically in the lab (average correction 2.9 years, range 1–20 years; Duncan, 1989). Samples from trees that were > 20 years off-center from the pith (102 samples from 26 plots) were excluded from analysis of tree cohorts and reconstruction of historical fires. Establishment dates were estimated by subtracting 4 years from each pith date based on the average years for a Douglas-fir to reach the 40 cm coring height (Tepley, 2010). Years required to reach coring height for trees sampled above 40 cm was estimated using trees of the same species, similar DBH, and age in the plot. Despite good precision there were some examples where these procedures likely overestimated either the number of rings to pith for off center samples or the years required to reach coring height. In cases where an estimated tree establishment date occurred in a fire year or the three years prior to a fire year, we examined establishment dates of other similarly aged trees in the plot. If there were no other tree establishment dates in the fire year or in the three years prior to the fire, we adjusted the tree establishment date to the year following the fire.

2.4. Detection of tree cohorts

Previous studies using tree establishment to infer fire events in moist Douglas-fir forests did not have direct annually precise evidence of historical fires to aid in identification of tree cohorts that developed after fire, and to distinguish tree cohorts from gradual tree establishment and tree establishment related to other disturbances. Given this limitation, earlier studies used fixed *a priori* criteria to identify tree cohorts and these criteria may fail to detect some tree cohorts related to fire. For example, Tepley et al. (2014) identified cohorts when five or more trees established after an 80-year period without tree establishment. This means that multiple tree cohorts that established after different NSR fires in an 80-year period would be identified as a single cohort and could only provide evidence of one fire. In our study, we used tree establishment data and an unbiased simulation procedure to characterize whether trees sampled within a plot belonged to a distinctive tree cohort. We then evaluated whether and how those cohorts were related to fire using fire scar records at each plot (see example in Fig. 3). Using this flexible method to identify cohorts and then comparing them to fire records developed from direct evidence of past fires allows us to evaluate the usefulness of different lines of "cohort" evidence that have previously been used to reconstruct historical fires in Douglas-fir forests. It also allows us to characterize the influence of fire on tree establishment and forest development more precisely in Douglas-fir forests.

To detect tree cohorts, we used a simulation procedure to resample random tree establishment dates with replacement from a uniform distribution that was bounded by the first and last establishment date in each plot (Fig. 3; Johnston et al., 2023). This simulation procedure provides the null distribution against which actual tree establishment at a plot was tested to identify cohorts. The same number of trees as present in each plot was simulated 10,000 times for each plot. Then a kernel density estimate was calculated for both the actual tree establishment data and simulated establishment data, to develop probability density functions for each population. When the density of actual tree establishment dates present across a kernel bandwidth (Sheather and Jones, 1991) was greater than 95 % of the density estimates for simulated tree establishment data, we considered tree establishment dates within that bandwidth to belong to a distinctive tree cohort. See Johnston et. al. (2023) for rationale for cohort detection method, and for the simulation procedure and code for running the simulation procedure using R software version 3.1.6 (R Core Team, 2023).

2.5. Identification of fire scars

We relied on crossdated cambial fire scars to reconstruct historical fire events. All injuries found on each partial cross section were carefully examined to determine whether they were consistent with necrosis of the tree's vascular cambium from heat exposure during a fire (Smith

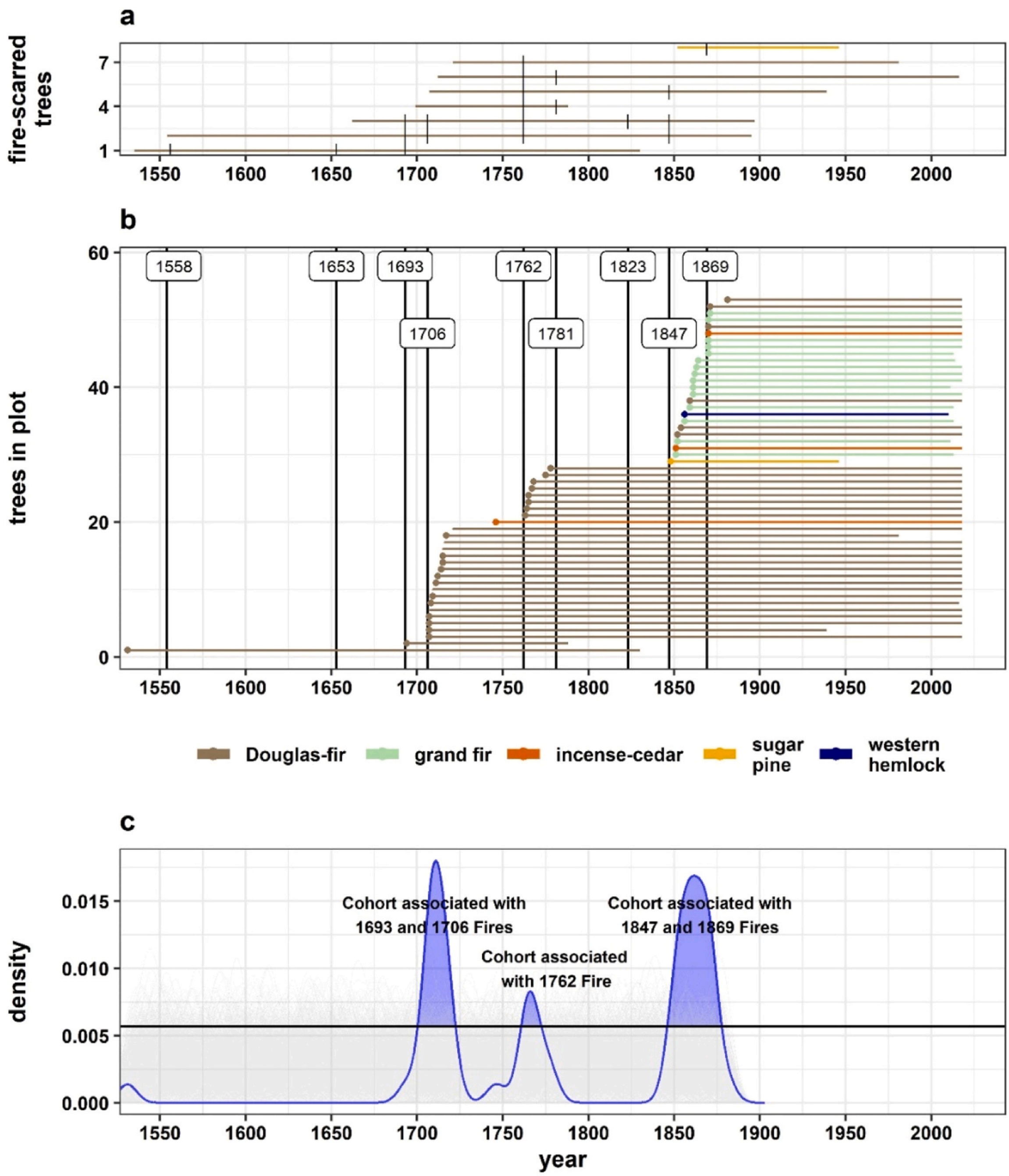

Fig. 3. : An example (from plot BC4) of how the fire record was developed from fire scars, tree establishment data, and our cohort detection procedure at each plot in this study. In panel (a) line segments represent inner and outer years of eight fire-scarred trees that were sectioned with a chainsaw to reconstruct fire years. Vertical tick marks indicate the year of 20 precisely dated fire scars in those samples. Panel (b) displays the composite record of nine unique fire years as vertical lines and tree establishment in the ¼ ha plot. Horizontal line segments indicate the inner and outer year of each tree, color describes tree species composition, and circles indicate precise estimates of tree establishment dates. Panel (c) identifies three tree cohorts that established during periods where actual tree establishment density from plot BC4 was greater than 95 % of the density estimates for (horizontal line) simulated tree establishment data. The first and third tree cohorts were associated with multiple fires, so we were unable to identify a single fire event that resulted in the cohort. Stand-replacing fire was inferred in 1693 because only one tree in the plot predated the fire.

et al., 2016) versus mechanical damage (Fig. 4). Cambial fire scars have four distinctive characteristics: 1) cambial necrosis that occurs neatly along a single boundary of cells, 2) compartmentalization of the wound with a fire induced resin response to resist pathogens and infections, 3) wound closure, which is the reactive formation of wound wood that closes the wound surface, and 4) missing annual rings where wound wood meets the portion of the tree bole with cambial necrosis. If a cambial injury included these characteristics, we inferred a fire event occurred. If a cambial injury crossed ring boundaries or moved perpendicularly (across) cells within an individual ring, we did not include that injury as evidence with a fire because these injuries are consistent with mechanical damage. Cambial fire scars in the dormant position were assigned to the preceding calendar year because spring fires prior to the growing season are unlikely in the western Oregon Cascades given a cool, wet springtime climate.

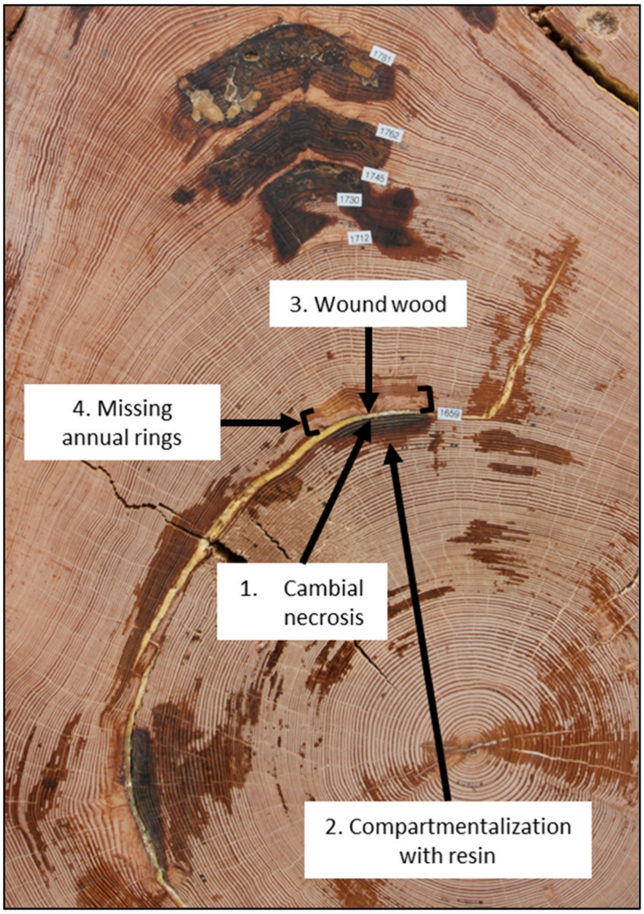

Fig. 4. : The anatomy of cambial fire scars used to reconstruct the year of fire events. Cambial fire scars were identified by 1) cambial necrosis along a single boundary of cells, 2) compartmentalization of the wound with resin, 3) wound closure with "wound wood", and 4) missing annual rings in the years following cambial necrosis. The photo highlights characteristics of a cambial fire scar formed in 1659, and displays additional cambial fire scars in 1712, 1730, 1745, and 1762 recorded on a Douglas-fir log sampled at the Coyote site. Note that resin compartmentalization occurs on annual rings formed in the years prior to each section of cambial necrosis on the tree bole. Resin compartmentalization for the 1712 fire event was evident on another sample collected from the same log.

2.6. Plot records of historical fires

We reconstructed plot-scale fire histories by compositing evidence of fire events from fire scars and tree cohorts at each plot. Fire scars collected at a plot provided direct evidence of historical fire events at that plot. A tree cohort at a plot was conservatively used as indirect evidence of a fire event at a plot. In each case, a tree cohort was used as evidence of a fire event at a plot if the fire event was corroborated by a crossdated fire scar in an adjacent plot in the 10 years preceding the tree establishment cohort.

We classified each fire event at each plot based on the lines of evidence available for that fire event. There were four classifications: 1) fire events reconstructed from crossdated fire scars with no evidence of a tree cohort that established at the plot following the fire event, 2) fire events documented by both a fire scar and a tree cohort that established in the same plot in the decade following a fire event, 3) fire events documented by a tree cohort at the plot that established in the decade following a fire event corroborated by a fire scar in an adjacent plot, and 4) tree cohorts that were not associated with a fire event documented by a fire scar at any plot at the site. This last classification includes no direct evidence of fire from a fire scar and may be the result of undetected fire events or other disturbances (e.g. wind storms, insects, or disease). The year of the disturbance that may have preceded the cohort cannot be determined for this classification. We compare the portion of fire events reconstructed from each of the four lines of evidence at each site to evaluate the strengths and limitations of each line of evidence of historical fires.

We summarized all fire intervals at plots using the first three lines of evidence of fire during the period each plot had a reliable record of fire events. We considered a plot's fire record to be reliable beginning in the year of the first fire event recorded at the plot that was also recorded at another plot at the same site, and after the year 1600. This criterion eliminated long intervals in earlier centuries for which there were relatively few extant fire-scarred trees that resulted in a sparse record of fire events. We used the more reliable records of historical fire events to characterize fire intervals including their variability over time, their variability among plots at a site, and their variability among sites.

2.7. Relationships between tree cohorts and historical fire events

We classified tree cohorts into three cohort typologies to describe how historical fires influenced tree establishment and the development of structure and composition in Douglas-fir forests. The three types are: (1) fire-resistant, shade intolerant, one fire event; (2) fire-resistant, shade intolerant, multiple fire events; (3) fire-sensitive, shade tolerant. This characterization of tree cohorts also helps interpret earlier studies that relied on tree establishment data without fire scar data to accomplish the same objectives as our study. For example, quantifying the number of fire events that occurred during the years over which a cohort established describes how often repeated fires occurring at relatively short intervals (i.e. re-burns) would not be documented by tree establishment data alone.

To classify tree cohorts, we first quantified the duration of tree establishment for each tree cohort that was associated with a fire event documented by a fire scar at the same site. The duration of tree cohort establishment is the interval in years between the first and last tree established in a cohort. Next, we classified tree cohorts based on whether they were associated with one fire event or multiple fire events. The number of fire events for each tree cohort includes any fires that occurred in the decade preceding the first tree established in the tree cohort, and any additional fire events that occurred within the duration of cohort establishment. Last, we classified the fire-resistance and shade tolerance (Appendix 1, Table 1) of each tree cohort based on the species composition of the trees in the cohort. A tree cohort was classified as fire-resistant, shade intolerant if >66 % of trees in the cohort were Douglas-fir, ponderosa pine, sugar pine, or incense-cedar. A tree cohort was classified as fire-sensitive, shade tolerant when shade tolerant species were well-represented (i.e., > 1/3 of the trees were shade tolerant). Fig. 3 illustrates different types of tree cohorts we identified. The oldest cohort at plot BC4 had an establishment duration of 27 years (1694–1721), was associated with two fires in 1693 and 1706, and was classified as fire-resistant and shade intolerant. The second oldest cohort had an establishment duration of 15 years, was associated with a single fire in 1762, and was classified as fire-resistant and shade intolerant. The most recent cohort had a duration of cohort establishment of 33 years (1848–1881), was associated with two fires in 1847 and 1869, and was classified as fire-sensitive and shade tolerant.

We distinguished between non-stand-replacing and stand-replacing fire effects during periods when tree cohorts and tree survival could be used to infer fire effects. A fire event was classified as stand-replacing at a plot when few trees (≤5, mean 1.0) in the plot pre-dated and survived the fire event, and a tree cohort established in the two decades after the fire event. The oldest tree cohort in Fig. 3 provides an example of a stand-replacing fire event. Accordingly, all other fire events were classified as non-stand-replacing fire, when >5 trees survived fire within the small ¼ ha plots where we inventoried tree ages. We could not distinguish between non-stand-replacing and stand-replacing fire effects for fire events that preceded a stand-replacing fire event because evidence of earlier tree survival and tree cohorts was not available. We combined records of fire events, fire effects, tree cohorts, and tree establishment data to synthetically reconstruct how historical fires influenced tree establishment and forest development dynamics across our study area.

3. Results

3.1. Tree cohorts

The tree cohort identification procedure resulted in 75 tree cohorts and at least one of these tree cohorts occurred at each of the 34 plots (Fig. 5). There were six tree cohorts not associated with direct evidence of a fire event from fires scars at the same site (Table 2), and we excluded them from further analysis. Five of these tree cohorts established prior to reliable records of fire events in the plot where they occurred. The

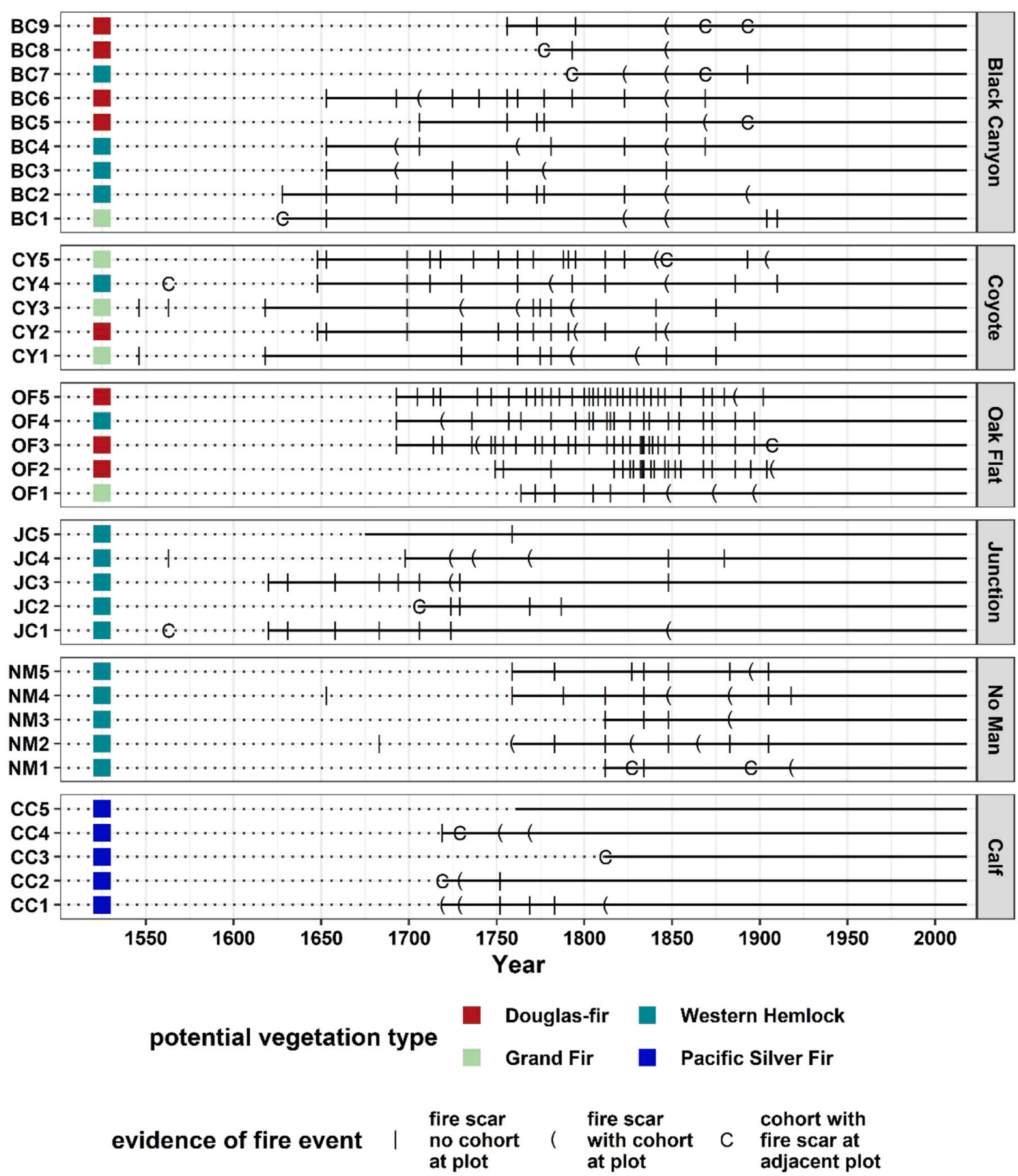

Fig. 5. : Lines of evidence used to develop histories of fire events at sample plots. Plots are grouped in panels corresponding to their sample site. Potential vegetation type is indicated by colored squares at the beginning of the composite history for each plot. A solid horizontal line corresponds to the period when a plot met criteria for a reliable record of fire events. Vertical tick marks indicate fire events reconstructed from a fire scar without an extant cohort at the plot. Fire events evidenced by both a fire scar and a tree cohort at the plot are indicated by a "(" symbol. Seventeen fire events that were reconstructed from a tree cohort at the plot and a fire scar at an adjacent plot are indicated by a "C" symbol. Six cohorts that were not preceded by a fire scar at the same site are not displayed. Fire scars provided evidence of 92 % of fire events.

Table 2
A comparison of different lines of evidence of historical fires. Six tree cohorts with no contemporaneous fire scar at the site were not used for fire event reconstruction at the plot where they were sampled.

Site	Total Fire Events	Fire Scar with no tree cohort	Fire Scar with a tree cohort	Tree cohort at the plot, and a fire scar in an adjacent plot	Cohort with no fire scar at the site
All Sites	327	258	51	18	6
Black Canyon	64	40	16	7	1
Coyote	66	53	11	2	0
Oak Flat	118	110	6	1	1
No Man	35	25	8	2	0
Junction	29	23	8	2	2
Calf	15	6	6	3	2

remaining cohort at plot JC2 established over 39 years during a long period without a fire event, and was composed of fire-sensitive, shade-tolerant species. The remaining 69 tree cohorts all began establishment in the decade after a fire event that was documented by fire scars at the same site.

3.2. Fire scars

We collected partial cross sections from 181 trees and identified 613 fire scars. Most fire scars were sampled from Douglas-fir (Appendix 2). Douglas-fir trees with cambial fire scars usually recorded 1–3 fires (mean =2.3), and rarely had traditional “cat faces” found on ponderosa pine and sugar pine “recorder trees”. However, in some cases Douglas-fir trees recorded several fires over multiple centuries along a bole buttress just above the litter and duff soil layers (Fig. 4). Fire scars on ponderosa pine, sugar pine, and incense-cedar reliably recorded fire events, but these species were relatively rare and restricted to warm-dry sites in the study area. Western hemlock and western redcedar were sampled in a few cases where they had cambial damage consistent with a fire scar that was apparent during field sampling. Cambial injuries that we attributed to fire events on western hemlock did not have resin compartmentalization. However, we included them as evidence of five fire events that were corroborated by cambial fire scars on other tree species sampled at the same plot or at an adjacent plot. Healed fire scars that were included in tree cores removed from live trees were used to reconstruct a total of five fire events in five plots. Each of the fire events in tree cores were corroborated by fire scars in the same year identified in cross sections collected from trees at adjacent plots.

Fire scars were mostly recorded in the dormant position (70 % of scars), which indicates historical fires predominantly burned in the late summer and fall. Only 5 % of fire scars were clearly found in the earlywood or latewood of tree rings, which respectively indicates fires that burned in the growing season (i.e., late May to late July). We could not precisely determine the ring position for the remaining fire scars and classified these fire scars as undefined. We did not find any fire scars in cross sections or tree cores at plots CC3 or CC5 at the cool-moist Calf Creek site. A cohort at plot CC3 combined with cambial fire scars at plot CC1 formed in 1812 provided evidence of a single fire at plot CC3 in 1812. No fires were reconstructed at plot CC5. We considered plots CC3 and CC5 to each have a reliable fire record after a tree cohort established following the 1812 fire at plot CC3 and after several trees established in the second half of the 18th century at plot CC5.

3.3. Lines of evidence of historical fires

Multi-century fire records were reconstructed for all plots at each sample site (Fig. 5). The majority (94 %) of 326 historical fire events were reconstructed from direct evidence of a historical fire (i.e., a fire scar collected at the plot identified the year of the fire event; Table 2). We conservatively used 17 tree cohorts as indirect evidence of 17 additional fire events at 14 plots. In each of these cases, a fire scar at an adjacent plot provided evidence the tree cohort was related to the fire event and identified the precise year of the fire event. Tree cohorts did not provide evidence for most reconstructed fire events. Of the 308 fire events that were documented by a fire scar, only 50 (16 %) were also documented by a tree cohort that established in the same plot in the decade following the year of the fire event. The absence of tree cohorts associated with most historical fire events means that fire scars did not always provide for the establishment of tree cohorts, or that tree cohorts that established after fire events were killed by subsequent fire events.

3.4. Spatial and temporal variability in historical fire frequency and extent

There was clear spatial variability in historical fire return intervals prior to 1920, calculated from the period deemed the reliable fire record (Fig. 6). Most fire return intervals were less than 25 years even in the cool-moist environments at the Junction, No Man, and Calf sites. However, fire return intervals of 25–60 years occasionally occurred in warm-dry environments at the Black Canyon and Coyote sites. Fire return intervals at the warm-dry Oak Flat site were remarkably frequent. Most intervals were $\leq$ 5 years, and there were several fire events that occurred in consecutive years at the same plot. Nearly all of the longest fire return intervals (e.g. > 65 years) occurred at the cool-moist Junction and Calf sites. Similarly long fire return intervals were not observed at the cool-moist No Man site. There was also considerable fine scale variability in fire frequency among plots at the same site. For example, there were nine fire return intervals <15 years at plot CY5 where fire frequency was highest at the Coyote site. In contrast, only two of these short intervals were documented by fire scars at plot CY4 (Fig. 6). Similarly, from 1600 CE to present 6 – 9 fire events were reconstructed at plots JC1, JC2, JC3, and JC4, but only 1 fire event was reconstructed at plot JC5.

Small and large fire events all occurred at each of the six sample sites. For example, the number of plots that recorded a reconstructed fire event ranged from one to nine plots at the Black Canyon site in years with reconstructed fires (Fig. 5). During the period when all plots at the Black Canyon site had a reliable fire record, a fire event was recorded at 3 plots in 1793, 1 plot in 1795, 5 plots in 1823, and at all 9 plots at the site in 1847. Most historical fire events were large enough to be recorded at $\geq$ 3 plots at a site (plots were $\sim$ 1–2 km apart). Some fire events in earlier centuries were likely larger than we reconstructed because evidence of early fire events was truncated by stand-replacing fires at some plots (Fig. 8), and some fires may not have been recorded on the trees we sampled.

The number of plots recording each fire event and the frequency of fire events varied considerably over the last several centuries. The relatively warm-dry Black Canyon and Coyote sites showed a similar pattern of decreasing fire frequency and fire extent in the middle of the 19th century following a relatively large fire event in 1847 (Fig. 5). Most fire events after the 1847 fire at the Coyote site were relatively small and documented by fire scars at just 1–2 plots. At Oak Flat where fire events were most frequent, relatively small fire events recorded at 1 or 2 plots were common prior to 1860. From 1860–1910, fire return intervals were longer, and fire events were more extensive, usually occurring at 3–4 plots. No 20th century fires were recorded after 1918 at the Black

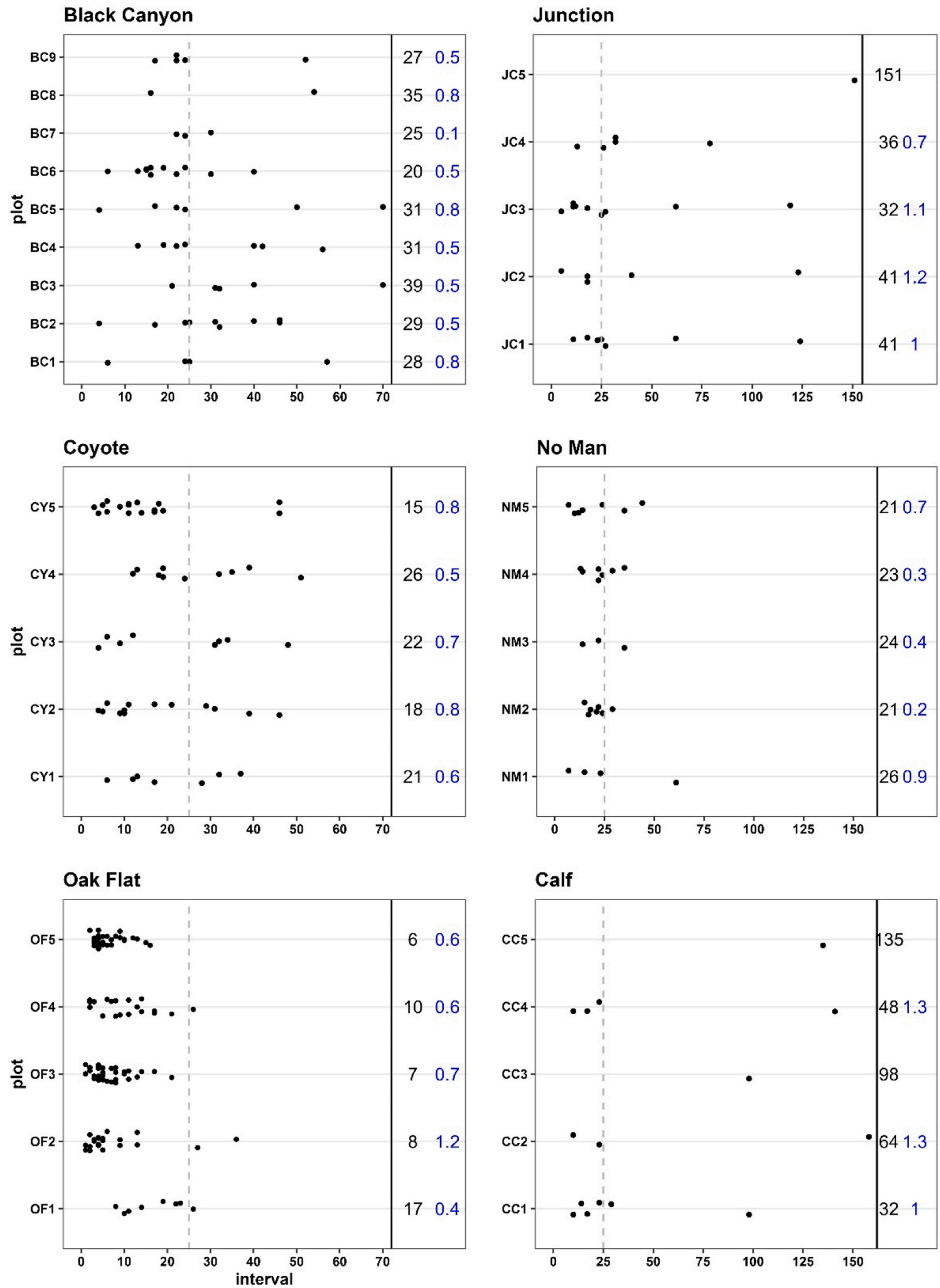

Fig. 6. : Variation in fire return intervals. Fire return intervals are represented by black dot at each plot grouped by site. Fire return intervals are reported during the period with a reliable record at each plot (See Fig. 5). The mean and coefficient of variation for fire intervals is reported in black and blue text respectively at each plot. Note that the range of the x-axis is twice as long for sites in cool-moist environments. Fire return intervals varied within plots, within sites, and among sites. Most reconstructed fire return interval were <25 years (dashed vertical line).

Canyon, Coyote, and Oak Flat sites. The cool-moist Junction and relatively cold-wet Calf sites each had non-stationary or variable fire frequency over time that included a majority of relatively short <25-year intervals, but also some intervals that lasted for 50–160 years (Fig. 6). A transition from relatively frequent to infrequent fire events occurred more than a century before 20th century fire suppression efforts. At the Junction site, fire events were recorded at multiple plots at <25-year intervals prior to 1750. After 1750 fire intervals were much longer and only one fire event was recorded at multiple plots in 1848. At the Calf site, 6 fire events occurred from 1700 to 1812, but no fire events were reconstructed after 1812. The No Man site had a unique temporal pattern of fire extent and frequency in comparison to all other sites because frequent and relatively extensive fire events continued into the early 20th century. No fires were detected after 1918 at the Junction site.

3.5. Relationships between historical fires, fire effects, tree establishment, and forest development

Tree cohorts, and tree establishment in general, occurred following fire events directly documented by cambial fire scars. Only 6 of 75 tree cohorts were not associated with a fire event documented by a fire scar. Of the 69 tree cohorts clearly associated with a fire event (Fig. 7), most (n=44) were composed of fire-resistant, shade-intolerant trees, and associated with one fire event. The remaining fire resistant, shade-intolerant cohorts (n=13) were associated with 2–4 fire events. Most (n=8) of the 12 fire-sensitive, shade-tolerant cohorts were associated with one fire event. The duration of establishment was significantly shorter and usually <20 years for most fire-resistant, shade-intolerant tree cohorts (e.g., Douglas-fir, sugar pine, noble fir) associated with a single fire event (n=44) compared to tree cohorts associated with multiple fires of any composition (n=17), and in comparison to tree cohorts with fire sensitive, shade tolerant (e.g., western hemlock, grand fir) composition (n=12; Fig. 7).

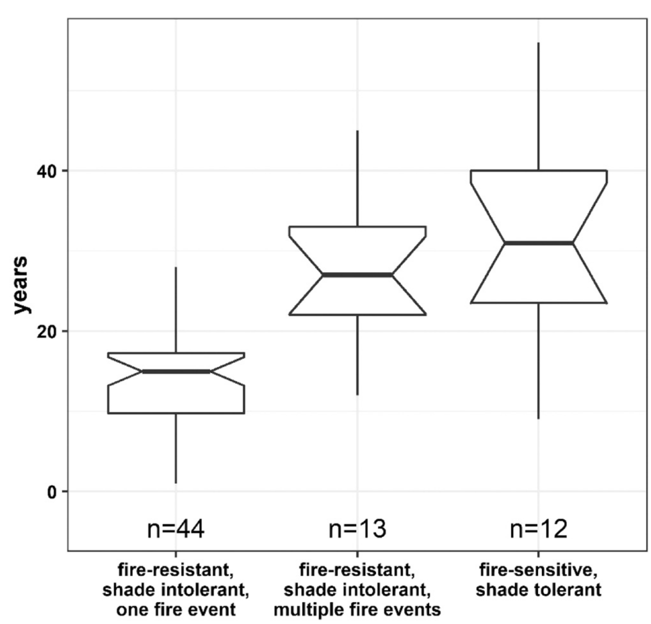

Fig. 7. : Cohort establishment periods. The duration in years of tree establishment is summarized with Tukey's boxplots for 69 tree cohorts that were associated with at least one fire event. Duration is summarized separately for cohorts composed of fire-resistant, shade intolerant trees that were associated with one versus multiple (2−4) fire events, and for cohorts where fire sensitive, shade tolerant trees comprised ≥ 33 % of trees in the cohort. Boxplot notches indicate the 95 % confidence interval for the median duration of tree establishment. There's statistically significant evidence that the median duration of cohort establishment is shorter for fire-resistant, shade intolerant trees associated with one fire event versus cohorts associated with multiple fires, and cohorts composed of fire sensitive, shade tolerant species. Three of the twelve fire sensitive, shade tolerant cohorts were associated with multiple fires. The six cohorts that were not associated with a fire event evidenced by a fire scar are not included.

Stand-replacing fire effects were reconstructed in 22 fire events at 22 plots (Figs. 8 and 9). We could not infer fire effects for 42 fire events (13 %) that were detected but occurred prior to stand-replacing fire effects. Most stand-replacing fire effects were asynchronous across plots except at the cool-moist Calf Creek site where a stand-replacing fire was reconstructed at 3 plots in 1719.

Fire and forest developmental histories were diverse among plots at the warm-dry Black Canyon and Coyote sites (Fig. 8). The age of the oldest shade-intolerant trees at each plot varied among plots based on the year of the last stand-replacing fire. Similarly, the age of cohorts of trees established after NSR fires varied across these sites. However, a widely distributed cohort of trees (primarily Douglas-fir) established after an extensive fire in 1847 at both sites. The net effect of variability in the timing of stand-replacing fires and tree cohorts established after NSR fires is that age structure and tree composition was unique to each sample plot at the Black Canyon and Coyote sites. Most shade-tolerant trees established in cohorts following NSR fires in the mid late to 19th century, and many of the relatively fire-sensitive grand fir and western hemlock we sampled survived multiple NSR fires. The warm-dry Oak Flat site had distinct developmental history that reflects very frequent fire until the mid-19th century and then gradually cessation of frequent fires by the 20th century. During the period of frequent fires tree density was very low, with open woodland tree structure composed of ponderosa pine, Douglas-fir, and sugar pine. Oregon white oak with crowns developed in open canopy low-density woodlands can be found outside of our relatively small ¼ ha sample plots at the Oak Flat site. The contemporary closed-canopy Douglas-fir forest structure at Oak flat developed from tree cohorts that established during the late 18th and early 19th centuries as fire frequency decreased.

Fire and forest developmental histories were distinct among plots sampled within each cool-moist site and were also distinct among sample sites (Fig. 9). Most trees at the No Man site were relatively young and established after stand-replacing patches of fire that occurred in different fire events and years among plots throughout the 19th century. In contrast, plot NM2 at the No Man site had no evidence of stand-replacing fire and several trees that were established during the 16th century. Three plots with relatively old trees were composed of 2–3 cohorts, while two plots that experienced stand-replacing fire in the late 19th century were composed of a single cohort. At the Junction site, Douglas-fir were older and multi-aged with establishment occurring throughout the 16th, 17th, and 18th centuries during the period with recurrent fires. Shade-tolerant, fire-sensitive trees (e.g., western hemlock) established steadily during a period of low fire activity from 1760 to 1900. Stand-replacing fires were asynchronous among plots and the timing and amount of NSR fires and tree cohorts varied among plots. This variability fire history resulted in plots with distinct development histories at the Junction site. For example, old trees developed at plot JC5 with only one NSR fire and there were no tree cohorts identified. In contrast, old trees occurred in three cohorts at plot JC4, the stand was initiated by stand-replacing fire, and tree and stand development was shaped by at least 5 NSR fires. At the Calf site, most trees were established after a stand-replacing fire in 1719 that occurred at three plots and may have occurred at all plots at the site. Douglas-fir and noble fir established in several cohorts that followed several NSR fires in the 18th century. Most shade-tolerant, fire-sensitive trees (e.g., silver fir, grand fir, hemlock) established in a cohort following the last reconstructed fire in 1812. Fire frequency was high in the first century or centuries of forest development at each of the cool-moist sites. The decrease in fire frequency at the Junction and Calf sites coincides with the development of mature Douglas-fir trees and the onset of steady recruitment of shade-tolerant tree species.

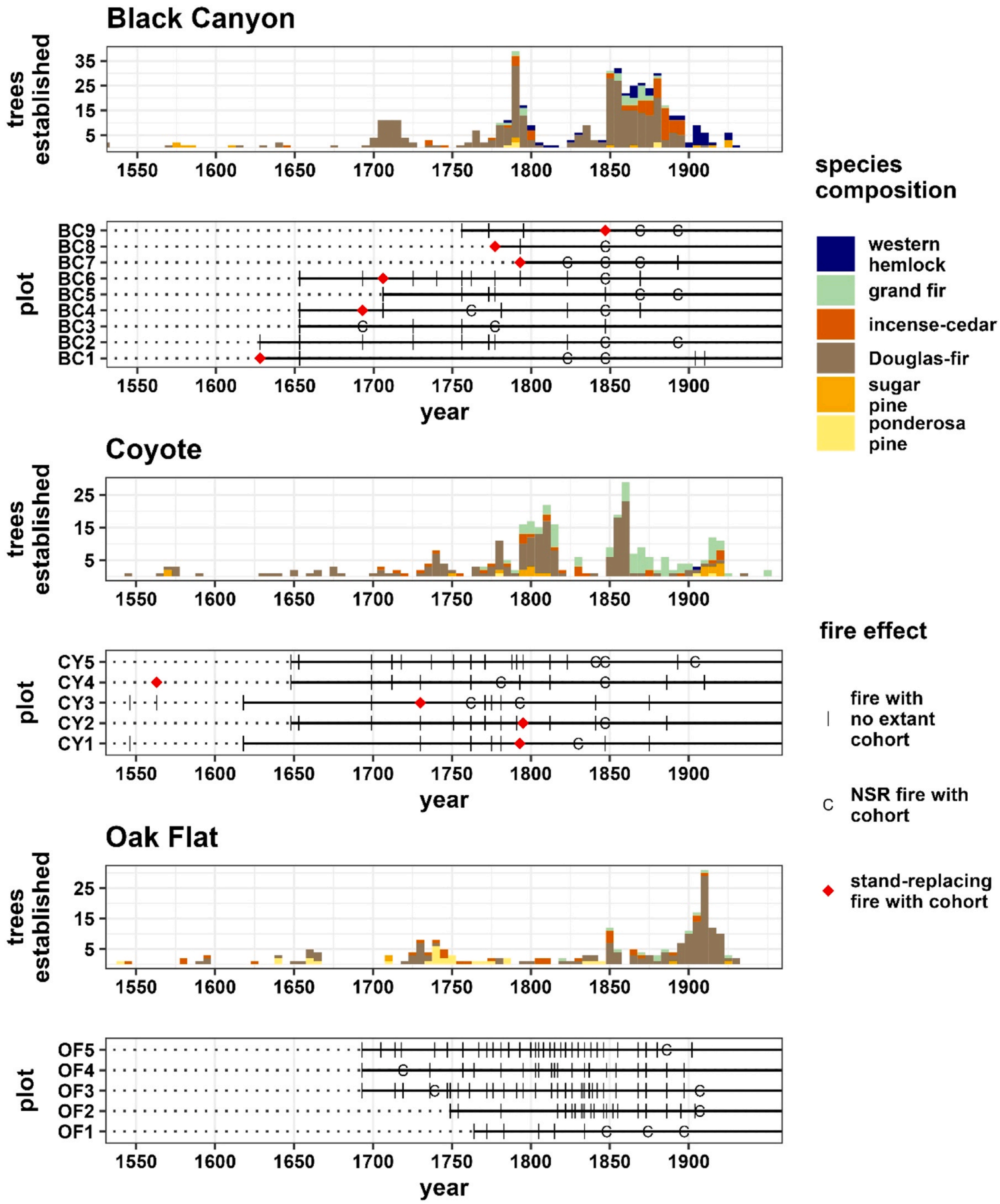

Fig. 8. **:** Fire and forest development history at warm-dry sites. Each sample site has a top panel that displays the species composition and number of trees established in each decade from 1550 to 2000 CE. The bottom panel displays fire events and their fire effects (no extant cohort, cohort, stand-replacing fire) at each plot at the sample site.

4. Discussion

We use crossdated fire scar and tree establishment data to characterize spatial and temporal variation in fire frequency and fire effects, and how fire mediates tree establishment and stand development history in coastal Douglas-fir forests. Our analysis of fire years and tree establishment records provides direct and temporally precise evidence of abundant historical NSR fires in Douglas-fir forests, in addition to stand-replacing fire. We also illustrate how these NSR fires facilitated tree-cohort establishment and the development of multilayered structure and mixed-species composition across warm-dry to cool-moist Douglas-fir environments in Oregon's southern western Cascades. Historically NSR fires were common, and they preceded most of the tree cohorts we identified. This provides clear evidence of NSR fire as a key process that shapes forest developmental patterns, the establishment of early and shade-tolerant late-successional species, and the variety of old-forest stand conditions currently observed in the region. A critical clarification to understanding of historical fire dynamics provided by our findings is that fire frequency was non-stationary. Although most intervals were relatively frequent (i.e. <25-years) intervals, we also documented intervals that lasted for several decades in warm-dry forests and in some cases over a century in cool-moist western hemlock and Pacific silver fir forests.

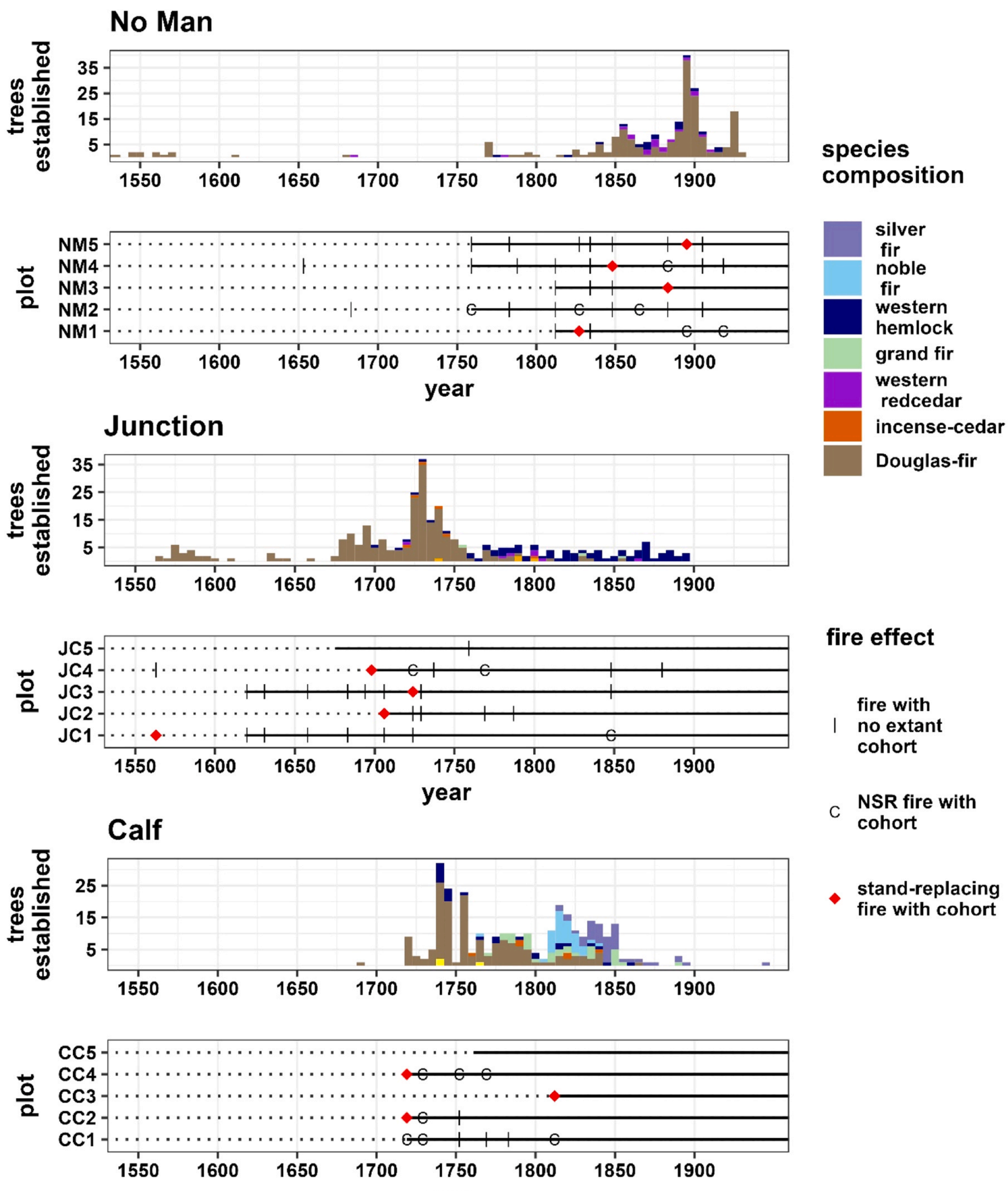

Fig. 9. : Fire and forest development history at cool-moist sites. Each site has a top panel that displays the species composition and number of trees established in each decade from 1550 to 2000 CE. The bottom panel displays fire events and their fire effects at each plot at the sample site. Six trees established in the late 13th century are not displayed at plot CC1.

The mature and old-growth forests we sampled developed their diverse age structure, physical structure, and composition in concert with multiple NSR fires even in cool-moist biophysical settings. Fine-scale spatial variability (i.e. within study sites) in historical fire frequency and fire effects, and temporal variability in fire frequency resulted in diversity in stand development histories, age structure, tree structure, and species composition in these mature and old-growth forests. This "pyrodiversity" occurs across forest types where Douglas-fir is the predominant conifer in Oregon's southern western Cascades. Our findings add important information for understanding the geography of fire and forest dynamics beyond the simple "moist forest" and "dry forest" dichotomy of the NWFP (Thomas et al., 2006) and Franklin and Johnson's (2012) framework for strategic restoration of old-growth forest in the Pacific Northwest. Under these frameworks, most sites in our study would be classified as moist forest and would be assigned to an infrequent high-severity fire regime with intervals between fires of one to several centuries. Under these classifications forest restoration emphasizes development of late-successional old-growth forests with understories of shade-tolerant western hemlock that develop under long fire-free intervals. Spies et al. (2018) proposed a regional fire-regime classification and map for the NWFP area that recognizes moist Douglas-fir forests contain significant areas of moderately frequent

(50–200 years) and frequent (15–50 years) fire-return intervals, especially in the southern Oregon Cascades. Our study and Johnston et al. (2023) provide important empirical support for the Spies et al. (2018) regional fire regime model by demonstrating that forests in the Moist Grand Fir/White Fir, Western Hemlock, and Pacific silver potential vegetation types (PVTs) historically had a frequent or moderately frequent mixed-severity fire regime in the central to southern western Cascades. However, most of our observed historical fire intervals were <50 years in the western hemlock PVT suggesting that Spies et al. (2018) underestimates the area of the frequent, mixed severity regime type in the Umpqua National Forest and the southern Willamette National Forest. Our study and Johnston et al. (2023) support the idea that the central and southern Cascades were historically a mosaic of the moderately frequent, mixed-severity and frequent, mixed-severity regime types, and both studies provide evidence of very frequent fire at sites very likely to have a legacy of Indigenous fire stewardship. Our study also demonstrates that historical fire frequency and severity vary within forest types or potential vegetation types. This means that potential vegetation types may not be a good surrogate for fire regimes, especially at landscape and smaller scales (and see Merschel et al., 2018). Fire and forest development histories in our study suggest that topography, lightning ignitions, Indigenous fire stewardship, and the composition, arrangement, and flammability of fuels are important drivers of spatial and temporal variability in fire regimes in both dry and moist forest Douglas-fir forest types in Oregon's western Cascades.

The fire and forest development histories in moist Douglas-fir/western hemlock forest types that we studied demonstrate alternative pathways for recruitment of shade-tolerant, late-successional species and the development of old-growth conditions compared to the classic, linear successional pathway of old-growth forest development (Franklin et al., 2002) and extend the fire-mediated development pathways framework developed by Tepley et al. (2013). Our findings clearly demonstrate NSR fire should be added to the list of processes (insects, disease, wind, and woody debris decay) that create small canopy gaps and seedbeds that are essential for development of old-growth characteristics including mixed species composition, multilayered canopies, and snags and logs (Spies and Franklin, 1989, Gray and Spies, 1997). Crossdated fire and tree establishment dates demonstrate that NSR fires functioned as a gap and seedbed creation process because they facilitated establishment of both shade-tolerant and shade-intolerant tree cohorts within our 0.25 ha plots. Tree establishment in burned patches would have been facilitated by increased resources, by the creation of mineral seedbeds, and by the removal of competition from understory shrubs and herbs (Gray and Spies, 1997). Our study supports a model in which variation in the timing, frequency, and severity of past fires was an essential driver of variability in forest development, composition, and structure across some Douglas-fir landscapes (*sensu* Morrison and Swanson, 1990, Tepley et al., 2013). Notably, 92 % of the tree cohorts we detected were established after fire, and this includes cohorts composed of shade-tolerant and fire-sensitive species. The development of old forests with multiple cohorts, mixed-species composition, and multilayered forest structure was mediated or shaped by NSR fires that facilitated tree regeneration.

Other studies of tree establishment and structural development following mixed-severity 21st century wildfires in the western Cascades (Reilly and Spies, 2015, Dunn and Bailey, 2016, Dunn et al., 2020) support the hypothesis that NSR is critical to diversity of stand development trajectories and forest conditions in Douglas-fir forests. A major implication of our study and these other studies for forest conservation and restoration is that fire suppression in the central and southern Oregon Cascades has disrupted the ecological processes that produced contemporary old trees and forests. Additionally, our findings suggest that definitions of old growth and restoration targets for management consider pathways and forest conditions that depend on non-stationary NSR fire (Spies et al., 2018), however we need a precautionary approach and additional studies to understand the geography of these pathways in the broader Douglas-fir region. Continued fire suppression will result in very different old forest conditions (Tepley et al., 2013) and tree architecture (Van Pelt and Sillett, 2008, Johnston et al., 2019) than those that were produced by historical fire regimes. Management legacies of clearcutting, establishment of structurally uniform Douglas-fir plantations, and fire suppression have reduced structural and compositional diversity at fine and coarse scales in Douglas-fir forests of the southern western Cascades.

4.1. Indigenous fire stewardship shaped fire regimes and forest conditions

At the Oak Flat site, the frequency of historical fires, absence of historical fire-climate relationships, and the abrupt decrease in fire frequency that coincides with forcible relocation of Indigenous peoples in the mid-19th century collectively provide compelling evidence of Indigenous fire stewardship deep in the western Cascades. Oak Flat was a regularly used and culturally significant site (Winthrop 1993), and our data show that prior to 1856 fires occurred at least every three years with fires occurring in consecutive years on several occasions. Additional sampling of fire-scarred trees would likely decrease this remarkably short fire interval even further, especially prior to 1750 where our sample depth for trees recording historical fires decreases. In contrast to drier forests east of the Cascades where historical fires almost always occurred in moderate to severe drought (Johnston et al., 2017, Heyerdahl et al., 2008), fires at Oak Flat had no significant relationships with climate and occurred in both cool, wet conditions and hot, dry years (Merschel, 2021). In 1856, Indigenous peoples of the Upper Umpqua, Kalapuya, Takelma, and Molalla cultures were forcibly removed to reservations (Beckham and Minor, 1992). After this removal, fire frequency at Oak Flat abruptly decreased and fires no longer occurred in cool, wet years.

Erasure of Indigenous lifeways and fire stewardship during settler colonialism has likely resulted in abrupt and dramatic changes in vegetation structure and composition, and reduced diversity in some montane Douglas-fir landscapes in the western Cascades. Plot data from the Oak Flat site demonstrates that meadows and woodlands with open grown Oregon white oak, sugar pine, ponderosa pine, incense-cedar, and Douglas-fir surrounding our sample locations shifted to closed canopy Douglas-fir forests more broadly at the Oak Flat site during the 20th century. The dense closed canopy stands of mature Dougals-fir at sample plots at Oak Flat established in 6 cohorts after 1850 and account for 80 % of all trees we sampled at Oak Flat. Much older and larger sugar pine, incense-cedar and old Oregon white oak that are dead and declining across the Oak Flat site are emblematic of the loss of culturally important resources and biodiversity that were maintained through Indigenous fire stewardship and frequent fire more broadly in the Pacific Northwest (Slack et al., 2021, Long et al., 2021).

A growing body of evidence highlights that Indigenous fire stewardship was a key driver of historical fire regimes in some Douglas-fir forests and encourages inclusion of Indigenous fire stewardship in newly refined characterizations and models of historical fire regimes that guide forest and fire management. Northwest of our study area in the Willamette National Forest, crossdated fire records provide another compelling example of Indigenous fire stewardship in Douglas-fir forests (Johnston et al., 2023). Carloni (2005) demonstrated that historical meadows and woodlands align with modeled Indigenous travel networks and archaeological sites across a 53,360 ha study area on the Umpqua National Forest that overlaps much of our study area. More broadly in the Pacific Northwest, Knight et al. (2022), Steen-Adams et al. (2019) and Storm and Shebitz (2006) illustrate that Indigenous fire stewardship is critical to Indigenous lifeways in moist and relatively productive forests where many culturally important species have been cultivated for millennia. In contrast to this growing evidence, early characterizations of historical fire regimes that informed forest management, such as the 1994 NWFP assumed that fire regimes were primarily driven by broad scale climatic variation and lightning, and that outside of the Puget Lowlands and Interior Willamette and Umpqua Valleys Indigenous fire stewardship had little influence on historical fire frequency (Agee 1991, Johnson and Swanson, 2009). Managers and policy makers must be aware that existing models and maps of historical fire regimes do not include Indigenous fire stewardship as a driver of historical fire regimes. Current descriptions of historical fire regimes in Douglas-fir forests use broad scale variation in climate and lightning ignitions (Spies et al., 2018) or biophysical setting (e.g. LANDFIRE; Rollins, 2009, Agee, 1993) to describe the geography of historical fire regime across the Douglas-fir region. This means existing maps likely underestimate historical fire frequency and variability in historical fire regimes within forest types and biophysical zones with a legacy of Indigenous fire stewardship.

It is critical to note both our study and Johnston et al. (2023) did not intentionally select reconstruction sites based on a history of Indigenous use. Crossdated fire histories that demonstrate Indigenous fire stewardship was an important driver of historical fire regimes have arisen from sampling two relatively small study areas within the extensive Douglas-fir region. Broader sampling designed to understand the spatial pattern and influence of Indigenous fire stewardship is needed to characterize historical fire regimes and forest dynamics across the extensive Douglas-fir forest region. We suggest that dendrochronological reconstructions of historical fire regimes that are carefully and respectfully designed in reciprocal partnership with Indigenous partners would more clearly inform the geography and influence of cultural burning on historical fire regimes, forest dynamics, and vegetation conditions (sensu Knight et al., 2022). These studies may inform and provide support for restoration of Indigenous fire stewardship and culturally important resources that are both critical to tribal well-being (Long et al., 2018).

4.2. Sources of pyrodiversity in the southern western Cascades

The historical fire regimes in this study were characterized by 1) fine (i.e. within site) scale spatial diversity in fire frequency, fire effects, and forest development histories, and 2) non-stationarity in historical fire frequency, and 3) asynchronicity in periods of relatively high fire frequency among cool-moist environments sampled at different sites. These properties or characteristics of the historical fire regime highlight the importance of terrain, vegetation, microclimate, and anthropogenic drivers on the properties of the historical fire regime. Understanding the drivers of a fire regime and how they emerge from the interactions of multiple drivers is critical to predicting outcomes of contemporary fire regimes in the context of climate change and the effects of fire exclusion and widespread forest management. Here, we highlight key properties of the historical fire regime and discuss working hypotheses about different drivers.

The diversity in fire records and forest development histories among plots within our sample sites demonstrates that topography and microclimate, the composition and flammability of fuels, Indigenous cultural burning, and interactions between these drivers drove important spatial variation in fire effects and frequency. Plots within sites that had a shared or similar records of historical fire events had distinct age structure and were composed of a unique set of cohorts in terms of their abundance, composition, and timing of establishment. Topography, specifically slope steepness and position and how they moderate fire effects (Tepley, 2010, Estes et al., 2017), likely accounts for some of the observed variability in fire effects and forest development histories. Plots with the oldest trees or those with no evidence of past stand-replacing fire in the past 400 years (e.g. CY4 and CY5) almost exclusively occurred on lower slopes or flat areas with slope <25 % (Merschel, 2021). In comparison, younger forests that established after a stand-replacing fire and were composed of 1–2 distinct tree cohorts were located on relatively steep mid and upper slopes (e.g. CY1 and CY2).

A few plots had much longer fire intervals (e.g. OF1 and JC5) or shorter fire intervals (e.g. CY5) than the adjacent 4 plots within 1–2 km at a site (Fig. 6). Plot OF1 was relatively far from historical oak woodlands and was topographically distinct among Oak Flat plots because it was located at the bottom of a steep draw in a moist microsite and had a higher density of relatively old Douglas-fir, incense-cedar, and grand fir. The absence of grass understory and pine and oak litter that provide fuels required for very frequent surface fire may account for longer fire intervals at plot OF1. Similarly, the much higher frequency we observed at plot CY5, may be explained by its relatively dry microsite and proximity to a historical oak-pine woodland south of the Coyote site. We observed no obvious explanations for the much lower fire frequency observed at plot JC5. Old trees were available to record several fire events that occurred at multiple plots at the Junction site in the 18th century, but we found no evidence of these fires despite twice revisiting plot JC5 and conducting thorough searches for fire scars. Our findings suggest a need to focus on the topographic template, landscape context, and inclusion of Indigenous perspectives for future research and applications to planning and management.

Fire frequency was non-stationary, or variable, over time at each of our study sites Interestingly, the timing of abrupt decreases in frequency varied among study sites, and this suggests different social and ecological drivers of fire among warm-dry and cool-moist Douglas-fir forest environments. Temporal variability in fire frequency in warm-dry sites suggests that humans were key drivers of fire frequency. The initial decrease in fire frequency at Oak Flat in the 1850s corresponds with settler-colonialism and disruption of Indigenous lifeways. The steep second decline in fire frequency at Oak Flat coincides with abrupt cessation of fire at the warm-dry Black Canyon, and Coyote sites in the early 20th century. The synchronous decline of fire frequency across the three warm-dry study sites is consistent with implementation of fire exclusion and suppression policies that abruptly altered fire regimes and forest conditions in seasonally dry conifer forests across the western U.S. in the late 19th and early 20th centuries (Marlon et al., 2012, Hagmann et al., 2021).

Fire frequency at the No Man, Junction, and Calf sites varied over time with frequent fires in young forests developing after stand-replacing fires and then infrequent fire in forests with mature Douglas-fir cohorts and canopies. Climatic variation does not provide a plausible explanation for these observed fluctuations in historical fire frequency because periods of high versus low frequency fire frequency were asynchronous among cool-moist study sites. Fire frequency and extent decreased in the mid-18th century at the Junction site, in the early 19th century at the Calf site, and remained frequent at the No Man site until the last recorded fire in 1918. In each site fire frequency declined when Douglas-fir canopies were mature (i.e., 100–150 years old). We cannot eliminate Indigenous fire stewardship and Euromerican settlement as drivers of the transitions from high to low fire frequency at the Junction and Calf sites. However, the decreases in fire activity precede the major effects of Euro-American colonization on Indigenous lifeways in western Oregon by almost a century at the Junction site and by several decades at the Calf site (Cole and Darling, 1990).

We hypothesize that the variability in historical fire frequency in cool-moist forests was driven by temporal variation in the flammability of fuels and microclimates as vegetation structure develops in Douglas-fir forests. Surface fuels that are critical to fire spread including herbs, shrubs, grasses, young trees, and fine litter from dead and dying trees reach their maximum abundance in young, early seral Douglas-fir forests and support significantly higher flame lengths and rates of fire spread (Agee and Huff, 1987). The open-canopied structure and abundant sunlight, wind, and evapotranspiration in young, pre-canopy closure Douglas-fir forests makes surface fuel flammable over a longer fire season, a very different microclimate and fire environment in comparison to mature and old-growth forests. Summer afternoon temperatures were up to 8°C higher, and relative humidity was up to 31 % lower in a comparison of young (~15 year old) and old-growth Douglas-fir forests (Chen et al., 1995). As Douglas-fir forests mature their fuel structure becomes progressively less flammable because the continuity and abundance of fine surface fuels decreases as biomass shifts to fire resistant tree boles and crowns, and mature closed-canopies create a mesic microclimate (Agee and Huff, 1987). The pattern of frequent burning (e.g. reburns) during the early development of cool-moist Douglas-fir forests in our study is supported by earlier dendroecological studies (Yamaguchi, 1993, Tepley et al., 2014), the well-documented reburns of the extensive Yacolt (Gray and Franklin, 1997) and Tillamook Fires (Pyne, 1982), and by recent reburns of contemporary wildfires (Halofsky et al., 2020).

In cool-moist Douglas-fir forests managing for a mean frequency or central tendency of fire and excluding fire in young forests may be counterproductive to the development and recruitment of old forests that fall within their historical range of variation. The paired record of historical fires and tree establishment data in this study illustrates how temporally variable fire frequency contributed to the development of mature and old forest structure and composition. Several cohorts of Douglas-fir established during periods of high fire frequency in young forests over several decades to a century across our cool-moist study sites. After multi-aged canopies matured, fire frequency declined, and shade tolerant and fire sensitive species steadily established creating multilayered mixed species stands. Therefore, structurally complex multi-layered old forests composed of several age classes may result from reburns early in stand development, rather than the absence of fire over the course of stand development. At the scale of our study sites, variation in the frequency, effects, and year of reburns resulted in distinct development histories among plots. In other words, the effect of spatial variability in reburns was to create structurally and compositionally unique patches of forest in what originally was likely a more extensive and homogenous patch following relatively rare high-severity wildfires. Although our methods reconstructed a relatively extensive stand-replacing fire at the Calf site in 1719, the diversification of cool-moist forests by mixed-severity reburns may have obscured the occurrence of extensive stand-replacing fires at the Junction and No Man sites. Our findings help frame expectations from widespread high-severity fires occurring in the region over the last decade. Extensive wildfires with larger patches of stand-replacing fires including the recent 2020 Labor day fires are not unprecedented in Douglas-fir forests (Reilly et al., 2022). Reburns following contemporary fires should be expected given the higher flammability of fuels in early seral Douglas-fir forests and are not necessarily inconsistent with historical fire regimes and forest dynamics. Future reburns may play a critical role in recovering diversity in vegetation structure and composition in landscapes that experience extreme wildfire effects during severe fire weather.

4.3. The need for rigorous dendroecological methods in Douglas-fir forests

Our study demonstrates that annually resolved fire scars and tree cohorts are required to characterize fire and development histories in Douglas-fir forests. The onerous methodology of crossdating and using multiple lines of tree ring evidence, beyond just tree cohorts and field counts, is required because fire events and tree cohorts occurred at high frequencies over time, and because the frequency, fire effects, and spatial patterns of fire events varied considerably at fine temporal and spatial scales. Using tree establishment data without fire scars would have failed to provide evidence of most historical fire events across the warm-dry to cool-moist environments of the study area. Our study confirms that tree cohorts in these Douglas-fir forests are almost always associated with fire events, both stand-replacing and non-stand-replacing. Despite the dependence of tree establishment on fire, tree cohorts provided evidence of only 68 of 325 of all reconstructed fire events documented by fire scars. This likely occurred because recurrent fires killed regenerating trees, and removed evidence of earlier cohorts in some cases, and because many fires burned at low-intensity and did not release enough resources for pulses of tree establishment. Thus, while tree cohorts are a good indicator of fire, they do not provide a complete picture of fire history, since many fires do not result in a tree cohort. The role of fires that do not result in a cohort of trees remains to be studied but likely includes effects on herbs, shrubs, forest floor biodiversity, and nutrient cycling.

Another important limitation to reconstructing historical dynamics using tree establishment data alone is the occurrence of reburns after high severity fire. In our data set 18 tree cohorts were associated with another 42 fire events because two to four additional fires occurred as these tree cohorts established in the context of multiple fires. This means another 24 fire NSR events would not be identified by the tree cohort evidence. This limitation would be exacerbated in studies that used more rigid cohort identification rulesets that require decades without tree establishment to identify a tree cohort (e.g. a conservative period of 80 years without tree establishment in Tepley et al. (2014). Overall, a robust census of historical fires cannot be inferred from tree establishment data in forests with a mixed-severity fire regime. Historical fire events can be robustly reconstructed from cambial fire scars in Douglas-fir trees in moist Dougals-fir forests. Future investment in crossdated reconstructions of fire history and stand dynamics in coastal Douglas-fir forests is needed to refine our understanding of these forests.

5. Conclusion

Historically frequent low- to moderate-severity fires and reburns of stand-replacing fires were a common component of forest dynamics in the southern western Cascades of Oregon. Recurrent fires gave rise to diversity in tree ages, structure, and composition, and facilitated tree cohort establishment during the development of contemporary old-growth forests in today's landscape. Notably the establishment of shade-tolerant, "late-successional" species that are thought to require long fire free periods established after NSR fires. Reconstructing historical fire regimes in Douglas-fir forests requires the labor-intensive removal and crossdating of fire scars and precise detection of cohorts to identify connections between fires, tree establishment, and forest development critical for deciphering complex forest development histories. Our study provides strong support for the inference made by several earlier studies (Morrison and Swanson, 1990, Weisberg, 2009, Poage et al., 2009, and Tepley et al., 2013) that fire regimes and forest dynamics in Douglas-fir forests in relatively dry Douglas-fir forests follow different pathways than general model proposed for the wetter parts of the Douglas-fir region. Improving and applying the methods developed in this study more broadly can help clarify the geography of Douglas-fir forests with an infrequent, high-severity fire regime versus more frequent historical fire regimes that included a significant role for low and moderate-severity fire. Understanding the geography of these Douglas-fir forest typologies is critical to sound stewardship and management of mature and old forests into the future.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Fire records and tree establishment data are archived with the NOAA Tree Ring Databank: www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/fire-history

Appendix 1. - Fire ecology of major tree species in the study area. Species traits are described from field observations and using species reviews from the Fire Effects Information System (Available: www.fs.usda.gov/database/feis/plants [2022, Accessed September 10, 2022])

Species	Species Distribution among PVTs	Successional role	Adaptations to fire	Longevity and rot resistance	Fire Recording Potential
Douglas-fir (*Pseudotsuga menziesii*)	Common in all PVTs	Mainly a shade intolerant, early successional species, but mid- to late-successional in the Dry Douglas-fir PVT	High resistance after mature thick bark develops, high regeneration potential after severe fire	500+ years, fair rot resistance	Good
Ponderosa pine (*Pinus ponderosa*)	Restricted to the Dry Douglas-fir PVT	Shade intolerant, early-successional	High resistance even among young trees, persistent and dominant species with frequent low-severity fire	500+ years, excellent rot resistance	Excellent
Oregon white oak (*Quercus garryana*)	Xeric sites in the dry Douglas-fir PVT	Shade intolerant, poorly adapted to closed-canopies and competition with conifers	High resistance to top-kill and surface fire for saplings over 3 m tall and mature trees. Top-killed trees sprout vigorously	300+ years, fair rot resistance	Good
Sugar pine (*Pinus lambertiana*)	Dry Douglas-fir and Grand Fir PVTs	Shade intolerant, early successional	High resistance, regenerates in open conditions, not tolerant of competition in late successional stands	500+ years, fair rot resistance	Excellent
Incense-cedar (*Calocedrus decurrens*)	Dry Douglas-fir and Grand Fir PVTs	Intermediate shade tolerance, early to mid-successional	High resistance when mature, regenerates in open and moderately closed canopies	500+ years, rot resistant	Fair
Grand fir (*Abies grandis*)	Grand fir and Western Hemlock PVTs	Shade tolerant mid- to late-successional	Low resistance when young, moderate when mature	250 years, susceptible to rot	Poor
Western hemlock (*Tsuga heterophylla*)	Common in the Western Hemlock PVT	Very shade tolerant late-successional; 300 years occasionally much older	Low resistance in all life stages	300+ years, very susceptible to rot	Poor
Western redcedar (*Thuja plicata*)	Western Hemlock and Silver Fir PVTs	Intermediate to high shade tolerance, mid- to late-successional	Low resistance when young, moderate when mature	500+ years, fair rot resistance	Fair
Noble fir (*Abies procera*)	Silver Fir PVT	Shade intolerant early successional species;	Low resistance when young moderate when mature, regenerates in open conditions	300 years, rarely >400 years, low rot resistance	Poor
Pacific silver fir (*Abies amabilis*)	Silver Fir PVT	Very shade tolerant late successional species; 250–350 years	Low resistance in all life stages	250–350 years, low rot resistance	Poor

Appendix 2. - Fire scars recorded by tree species. The table reports the number of trees sampled because they displayed evidence of cambial fire scars (TS) and the number of crossdated fire scars (FS) that we used as evidence of a fire event. Values are reported for each tree species at each sample site

Site	Douglas-fir		ponderosa pine		incense-cedar		sugar pine		western hemlock		western redcedar		All species	
	TS	FS	TS	FS	TS	FS	TS	FS	TS	FS	TS	FS	TS	FS
Black Canyon	26	59	2	10	5	19	5	17	2	2	0	0	40	107
Coyote	17	57	3	7	7	32	5	27	0	0	0	0	31	120
Oak Flat	2	6	23	174	4	20	5	46	0	0	0	0	34	246
No Man	12	27	0	0	3	0	1	3	0	0	5	17	21	47
Junction	36	70	0	0	3	3	0	0	0	0	0	0	39	73
Calf	9	18	0	0	0	0	2	0	3	3	2	0	16	20
All Sites	102	237	28	191	22	74	18	93	5	5	7	17	181	613

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