

Disjunct and decoupled? The persistence of a fire-sensitive conifer species in a historically frequent-fire landscape

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ABSTRACT

Local and regional species extirpations may become more common as changing climate and disturbance regimes accelerate species' *in situ* range contractions. Identifying locations that function as both climate and disturbance refugia is critical for biodiversity conservation. Here, we investigate the persistence of a disjunct, fire-sensitive conifer population, yellow-cedar (*Callitropsis nootkatensis*), in the historically frequent-fire landscape of the Blue Mountains in eastern Oregon, USA. We used tree rings to reconstruct multi-century fire histories, which were then used to compare historical mean fire return intervals (MFRIs) inside of the cedar grove to the surrounding dry forest matrix, as well as to examine relationships between historical fire occurrence and reconstructed climate. We also examined trends in post-fire yellow-cedar mortality and regeneration between 2006, when the grove burned in a wildfire, through 2017. Results indicated that fire was less frequent in the cedar grove (MFRI = 35.8 years) than in the surrounding dry mixed-conifer forest (MFRI = 14.4 years). Historical fire occurrence was associated with hotter and drier conditions. Following the 2006 fire, cedar mortality was high (>90 %), but by 2017 post-fire regeneration was abundant (median = 8125 seedlings ha⁻¹). The eastern Oregon cedar grove appears to occupy a fire refugium historically decoupled from the frequent-fire regime of the broader landscape. The topographic position of the grove suggests it is also a climate refugium. Managing for climate and disturbance refugia has been identified as an important option for conservation in the context of rapid global change, and this study provides evidence that locations where climate and disturbance refugia overlap may be disproportionately important for the maintenance of regional biodiversity. However, active management may be required for populations to persist in some of these locations as anthropogenic change is capable of overwhelming the underlying buffering capacity of refugia.

1. Introduction

Understanding how shifting climate and changing disturbance regimes will impact biodiversity is a critical ecological question for the 21st century. Physiological stress associated with climate warming is resulting in global-scale forest mortality (Allen et al., 2010; Lindenmayer, Laurance, & Franklin, 2012), and many species' ranges are expected to shift more rapidly than populations can respond via migration (Fettig et al., 2013; Loarie et al., 2008; 2009). Ecological state changes during periods of directional climate change have historically been catalyzed by disturbance processes that are closely linked to climate (Crausbay, Higuera, Sprugel, & Brubaker, 2017). Such disturbance-induced type-shifts are occurring now (Allen & Breshears, 1998; Savage, Mast, & Feddema, 2013), and more widespread

ecological change is anticipated as disturbance regimes continue to shift in response to climate change and human activities (Johnstone et al., 2016; Millar & Stephenson, 2015; Ogee et al., 2015). Identifying locations where species have persisted despite disadvantageous climatic conditions and disturbance regimes is essential for understanding the capacity of organisms to persist *in situ* in the context of rapid global change.

Refugia are locations that are relatively decoupled from surrounding areas, where populations survive in the context of unfavorable conditions. Interest in contemporary refugia is increasing (Ashcroft, 2010), particularly as "safe havens" in the context of anthropogenic climate change and its biological effects (Keppel et al., 2011; Morelli et al., 2016). The refugia framework has been broadened to include not only climate change, but ecological processes associated

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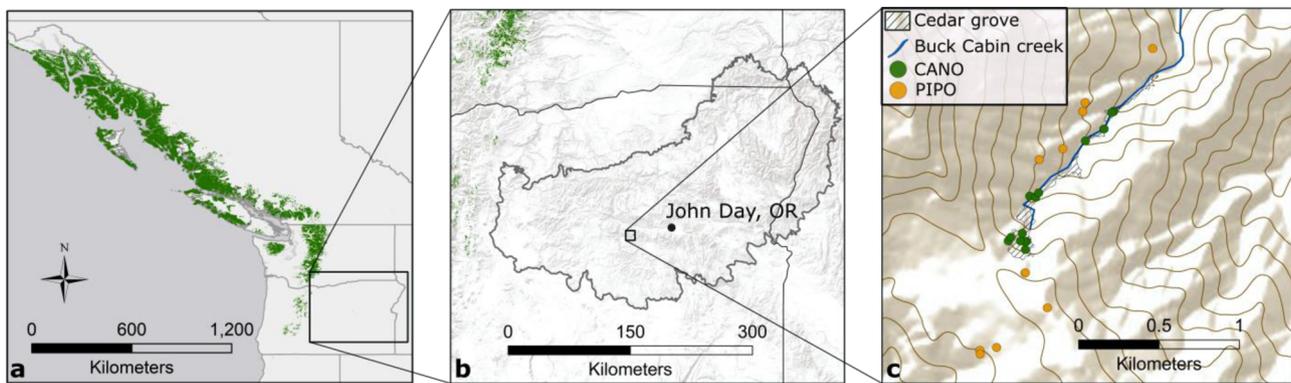


Fig. 1. (a) Yellow-cedar's range extends from northwestern California to southeastern Alaska. Two disjunct populations north and west of the main distribution in Alaska occur in Prince William Sound and Icy Bay and are not shown. (b) The Aldrich yellow-cedar grove is located in the Blue Mountains ecoregion in eastern Oregon, approximately 30 km southwest of John Day, OR. (c) The study area, fire scar sample locations for yellow-cedar (CANO; green) and ponderosa pine (PIPO; orange), and extent of the Aldrich yellow-cedar grove. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with climate, including wildfire (Mackey et al., 2012; Meddens et al., 2018). Fire refugia are locations that burn less frequently or less severely relative to the surrounding landscape (Krawchuk et al., 2016). These areas may be critical in some systems for the maintenance of later-seral forest structure (Camp, Oliver, Hessburg, & Everett, 1997) and the persistence of fire-sensitive plant and animal populations (Adie, Kotze, & Lawes, 2017; Robinson et al., 2013; Wood, Murphy, & Bowman, 2011).

Identifying current and future refugia is important for long-lived, sessile species which may be particularly vulnerable to changes in climate and disturbance regimes, especially if such species cannot migrate fast enough to keep pace with changing conditions. One such long-lived tree species that is currently undergoing widespread climate-induced mortality is yellow-cedar (*Callitropsis nootkatensis*). An ecologically, economically, and culturally important species, yellow-cedar's range extends from southeast Alaska and the coastal mountains of British Columbia, through the Cascades Mountains in Oregon and Washington, and south to the Siskiyou Mountains in Northern California (Fig. 1a) (Hennon et al., 2016). Yellow-cedar is considered to have a low tolerance to fire and is not expected to survive even low-intensity fire because its thin bark provides little protection from heat injury to the cambium (Hennon et al., 2016). Fire return intervals in cedar habitat in Oregon and Washington are estimated to be between 1150 (Fahnestock & Agee, 1983) and 1500 years (Lertzman & Krebs, 1991), and fire effects are generally stand-replacing (Hennon et al., 2016).

Extensive (200,000 ha) mortality is occurring across 1000 km of yellow-cedar's range in southeast Alaska and British Columbia where mortality rates average approximately 70 % in affected areas (Hennon, D'Amore, Schaberg, Wittwer, & Shanley, 2012). Mortality appears to be the result of root injury during hard freezes in early spring in the absence of an insulating layer of snow—conditions that have become increasingly common as the climate warms and more precipitation falls as rain (Buma et al., 2017; Hennon et al., 2012). Over the next century, approximately half of the current climatically suitable range of yellow-cedar is expected to warm beyond the snow-rain threshold at which yellow-cedar begins to decline (Buma et al., 2017). Despite this ongoing climatological press, yellow-cedar's migration along its leading edge appears to be very slow despite available habitat (Krapek & Buma, 2018).

There is a small, disjunct population of yellow-cedar embedded within a dry, fire-prone landscape in eastern Oregon's Blue Mountains. Located approximately 200 km east of yellow-cedar's main distribution in the Cascade Mountains (Fig. 1b), the eastern Oregon yellow-cedar grove is presumed to be a relic of a larger regional population that existed during the cooler and moister late-Pleistocene (Devine, Aubry,

Bower, Miller, & Maggiulli Ahr, 2012; Frenkel, 1974). The cedar grove is confined to the banks of a perennial stream in a steep, northeast facing drainage and is managed by the Malheur National Forest as a botanical special interest area. Despite the species' presumed high sensitivity to fire, the grove occurs within a dry mixed-conifer landscape that historically burned every 10–20 years on average prior to European settlement (Johnston, Bailey, & Dunn, 2016). Concerns emerged in the 1990s that fuel buildup associated with fire exclusion could result in uncharacteristically severe fire effects in and around the grove, causing the extirpation of yellow-cedar from the region (Agee, 1996; USDA Forest Service, 1990). These concerns were partly realized in 2006 when the grove and the surrounding landscape burned during a wildfire. However, the 2006 fire burned primarily as a low-intensity surface fire in the grove and resulted in very low mortality in other conifer species. In contrast, initial assessments indicated that fire-induced yellow-cedar mortality was very high. Substantial fire-induced mortality from low-intensity surface fire raised an intriguing question: how had the eastern Oregon yellow-cedar grove persisted in a landscape in which such fire effects occurred almost every decade prior to European settlement?

Our aim was to address this question of yellow-cedar persistence, which could be framed more broadly as: what are the mechanisms that allow a population to persist in a climate and disturbance regime context for which it is maladapted? This question is particularly important for disjunct populations that contribute disproportionately to regional biodiversity, and for populations that may become disjunct as climate change results in significant range reductions for many species (Loarie et al., 2008). To provide context for analyses, we began by orienting the eastern Oregon cedar grove in the climate space of the species' broader distribution. Next, we used 12 years of post-fire cedar mortality and regeneration data, along with tree-ring fire history reconstructions to address three primary objectives: (1) Quantify yellow-cedar mortality and regeneration following fire in 2006, (2) Compare the historical fire frequency inside the cedar grove to the historical fire frequency of the surrounding dry mixed-conifer forest, and (3) Examine relationships between historical fire occurrence and reconstructed climate. We hypothesized that one mechanism responsible for the persistence of yellow-cedar in eastern Oregon was that the grove's fire regime was historically decoupled from the surrounding frequent-fire landscape, and we predicted that fire was less frequent historically in the grove than in the dry mixed-conifer uplands. Additionally, we hypothesized that climate was historically an important control on fire occurrence in the grove and predicted that fire years coincided with unusually hot and dry conditions.

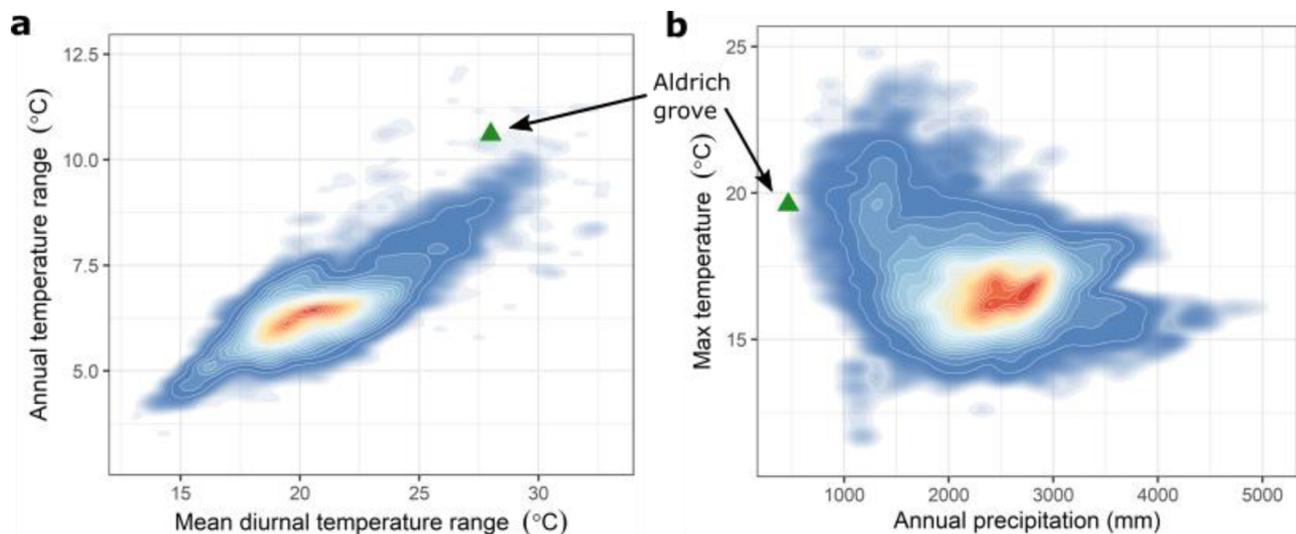


Fig. 2. (a) Temperature in the area occupied by the Aldrich yellow-cedar grove (green triangle) is much more variable at diurnal (x-axis) and annual (y-axis) time scales than the majority of yellow-cedar's range. (b) Annual precipitation (x-axis) in the area occupied by the Aldrich grove is substantially lower, and the maximum temperature (y-axis) is higher than the bulk of yellow-cedar's range. WorldClim climate data (Hijmans et al., 2005) were extracted from ~ 1 km resolution grids for the eastern Oregon study site and 10,000 points randomly distributed across yellow-cedar's range (Buma et al., 2017). Heat maps represent the density in climate space of the randomly distributed points, including very high densities (warm colors, tight contour lines) and very low densities (transparent blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Study design

2.1. Study area

The eastern Oregon yellow-cedar grove is located approximately 30 km southwest of John Day, OR, in the Aldrich Mountains, a subrange of the southern Blue Mountains. The majority of precipitation in the Blue Mountains falls between November and May as snow; thunderstorms which ignite wildfires are common during hot, dry summers (Burns, 1983). Fine-scale climate data for the grove itself was not available, but according to 1-km resolution interpolated climate data, the average maximum summer temperature in the area occupied by the grove is 19.6°C, and the average annual precipitation is 452 mm (WorldClim, Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The forest surrounding the yellow-cedar grove is composed of a mosaic of dry mixed-conifer forest consisting of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*), with lithosolic openings composed of western juniper (*Juniperus occidentalis*), mountain mahogany (*Cercocarpus ledifolius*), and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). Understory plant communities in the uplands surrounding the grove are composed primarily of pinegrass (*Calamagrostis rubescens*), elk sedge (*Carex geyeri*), numerous bunchgrass species, and a variety of low-growing understory shrubs (Fig. 3a).

Fire burned dry mixed-conifer forests in the southern Blue Mountains every 11–21 years on average prior to European settlement (Johnston et al., 2016). Fire activity sharply declined in the late 1880s as unregulated grazing substantially reduced the abundance of fine fuels that historically propagated surface fire (E. K. Heyerdahl, Brubaker, & Agee, 2001), and subsequent fire suppression efforts effectively eliminated frequent fire from the Blue Mountains in the 20th century (Heyerdahl et al., 2001; Johnston et al., 2017).

The eastern Oregon yellow-cedar grove is confined to 5.68 ha along the banks of Buck Cabin Creek on the northeastern flank of Aldrich Mountain (Fig. 1a). The southernmost extent of the grove begins at approximately 1750 m elevation where a series of springs merge to form the perennial creek. The grove extends 1.4 km below the springs, contracting into a steep, narrow, northeast-facing drainage and terminating at 1450 m elevation. Yellow-cedar intermixes with grand fir and

western larch at higher elevations, and ponderosa pine and Douglas-fir at lower elevations (Fig. 3a-b). Several important factors differentiate the area occupied by the grove from the surrounding uplands. First, unlike the surrounding dry mixed-conifer forest, understory communities in the grove are composed primarily of woody species and an assortment of uncommon or rare herbaceous and non-vascular species. Second, the drainage occupied by the grove is more topographically sheltered from solar insolation than the surrounding uplands. Third, Buck Cabin Creek and the associated spring complex support a relatively cool, moist microclimate. These factors, together with the presence of a highly fire-sensitive tree species (yellow-cedar), support our prediction that fire frequencies in the grove were longer than in the surrounding uplands.

On August 22, 2006, lightning ignited 10 fires near Aldrich Mountain. These fires grew together to form the Shake Table Fire, which eventually burned approximately 6000 ha before it was contained on September 29th. As the fire burned towards the cedar grove in late August, firefighters back-burned the area in an attempt to spare the grove from potential high-severity fire effects from the main fire.

2.2. Data collection and analysis

2.2.1. Range-wide yellow-cedar climate

We used yellow-cedar distribution and climate data to orient the eastern Oregon grove in the climate space occupied by yellow-cedar's broader North American distribution. This does not represent a stand-alone analysis, rather it is intended to provide context for the field data and interpretation, similar to the geographical context provided by a map. We extracted climate data from WorldClim (Hijmans et al., 2005) for the cedar grove and 10,000 points randomly distributed across a high-resolution range map developed by Buma et al. (2017). Because the grain of available climate data (~ 1 km) did not allow us to directly compare conditions in the grove to the uplands immediately surrounding it, our goal was to represent the grove's climatic context rather than the microclimatic conditions within the grove itself.

We explored yellow-cedar climate along numerous gradients, and we ultimately chose to represent yellow-cedar climate space in a pair of two-dimensional plots (Fig. 2). The first plot quantifies yellow-cedar's range along gradients of maximum temperature in the warmest month

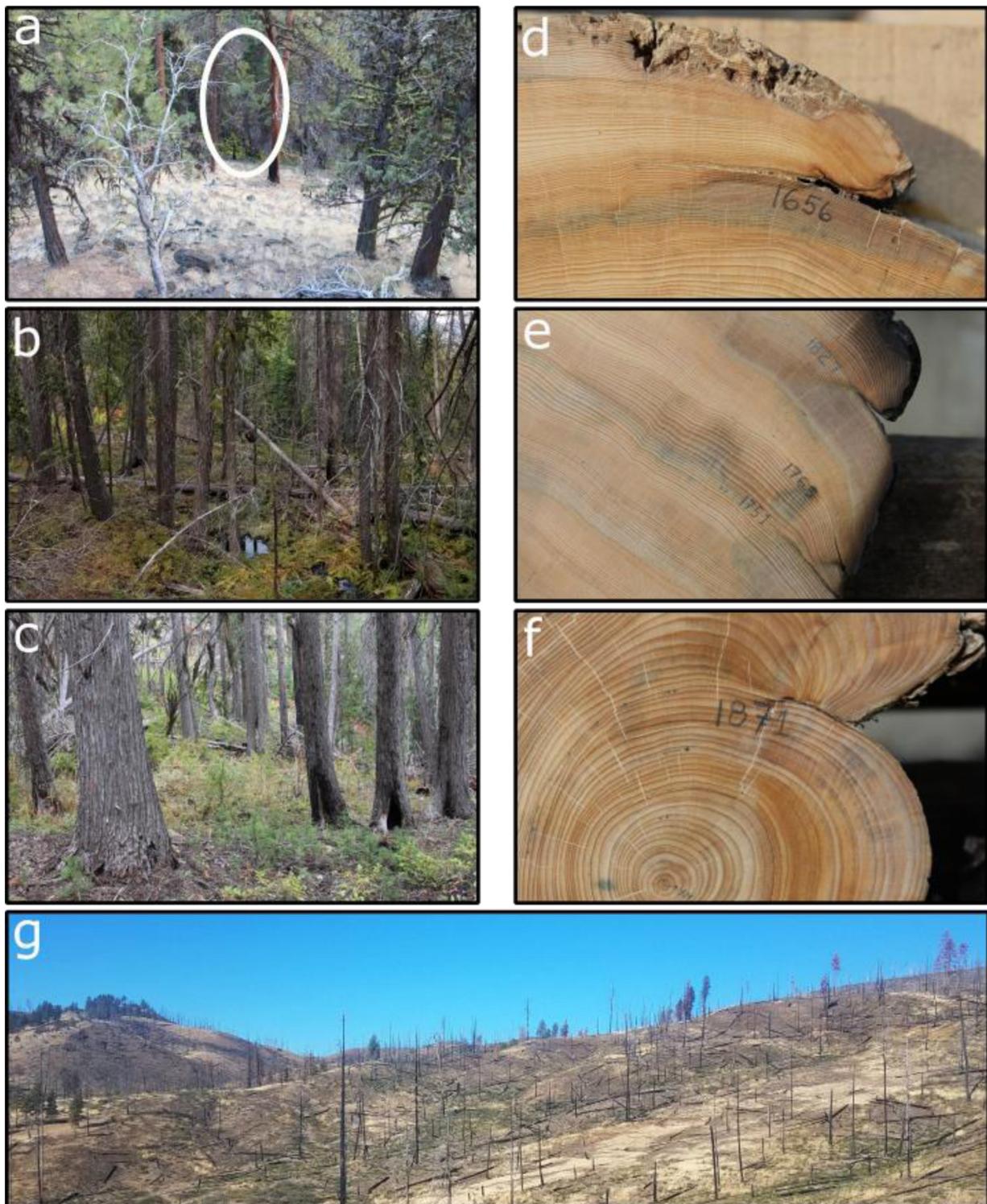


Fig. 3. (a) Dry mixed-conifer upland forest with herbaceous understory surrounding yellow-cedar (white circle) confined to the riparian area around Buck Cabin Creek. (b) Pocket of surviving yellow-cedar clustered around a spring where water may have stopped fire spread and high fuel moistures may have mitigated fire intensity. (c) Standing dead yellow-cedar, some with minimal evidence of bole scorch – these trees may have been killed by soil heating from higher-than historical surface fuel loadings. (d-f) Fire scarred yellow-cedar. (g) Stand-replacement fire effects from the Shake Table Fire in 2006, approximately 2 km from the cedar grove on the same northeast-facing aspect. In the absence of landscape-scale restoration of dry forests surrounding the grove, the eventual high-severity fire-induced extirpation of the grove is likely.

and annual precipitation, two key controls on fire regimes (Whitman et al., 2015). The second plot represents yellow-cedar's range along gradients of diurnal and annual temperature ranges, selected to represent climatic variability at two temporal scales. These plots demonstrate that the climate of the landscape including the Aldrich grove

is hotter and substantially drier than the climate space occupied by the majority of yellow-cedar's distribution.

2.2.2. Cedar mortality and seedling regeneration

We recorded yellow-cedar mortality in 12 permanent transects and

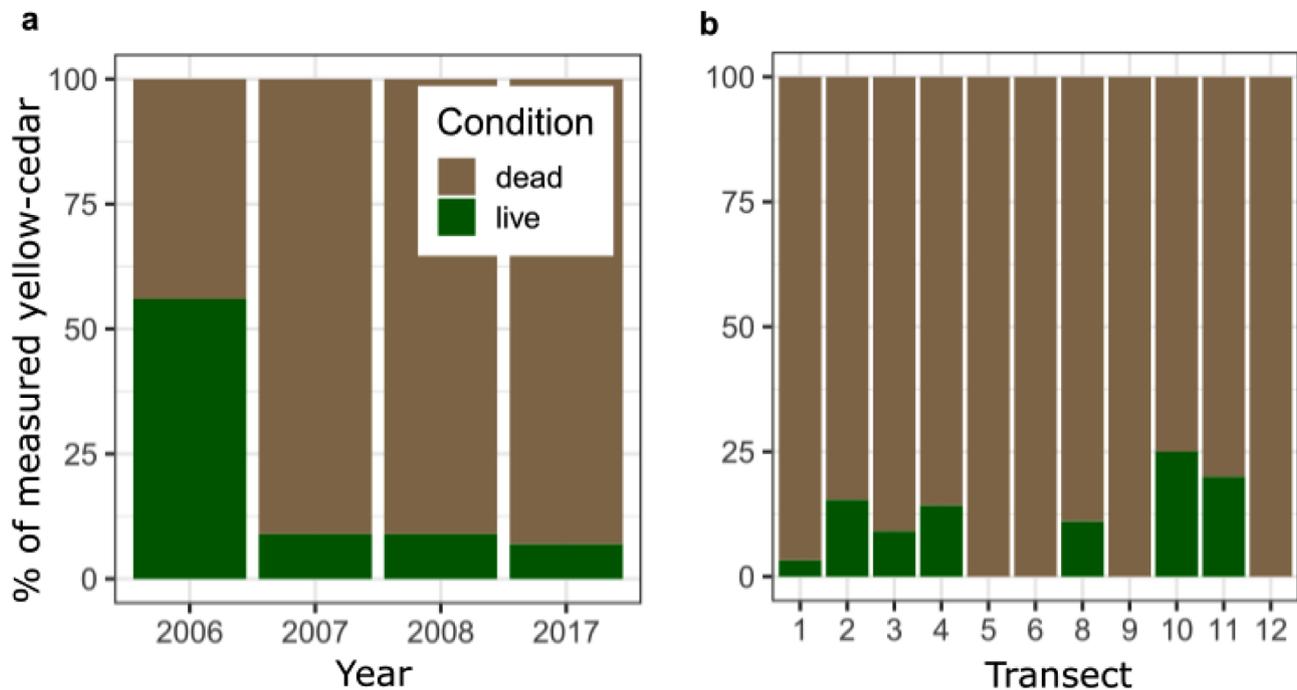


Fig. 4. (a) The 2006 Shake Table Fire initially resulted in moderate yellow-cedar mortality. However, within one year post-fire, approximately 90 % of measured yellow-cedar (x-axis) were recorded as dead. (b) Only 7% of mature yellow-cedar remained alive in 2017, but surviving individuals were distributed across the length of the grove.

conifer regeneration in 32 sub-plots in the fall of 2006, 2007, 2008, and 2017. Transects (constituting ~7% of the grove) were installed every 100 m along the length of the grove, with the starting point for the series of transects chosen based on a random distance from the southern edge of the grove. Transects were oriented perpendicular to the flow of Buck Cabin Creek, and transect length was determined by the extent of yellow-cedar on either side of the creek. We recorded the status (live/dead) and diameter at breast height (dbh) of every mature (dbh > 11.43 cm) cedar within each 9.14-m (30-ft) wide transect. Circular 3.59-m (0.004-ha) subplots (~0.12 % of the grove) were installed every 30.5 m starting from 15.3 m on either side of the transect centerline, within which we recorded all regenerating seedlings. Yellow-cedar is capable of vegetative reproduction via layering (Hennon et al., 2016), and we attempted to differentiate between ramets (individual clones) and germinated seedlings by determining whether or not seedlings originated from an independent stem. In addition to yellow-cedar, we recorded regeneration for all other conifer tree species present in subplots in 2008 and 2017. Here, we present within- and across-transect data to investigate temporal and spatial trends in post-fire yellow-cedar survival. Similarly, we present seedling data at the subplot-scale and across all subplots for each sample year to explore post-fire regeneration.

2.2.3. Fire histories

We sampled fire-scarred trees to reconstruct fire histories for both the cedar grove and the surrounding dry mixed-conifer forest. We used a chainsaw to remove partial cross sections from dead, basal-scarred yellow-cedar to determine historical fire frequency inside the grove, and we sampled fire-scarred ponderosa pine adjacent to the grove to determine historical fire frequency in the uplands. We systematically searched for evidence of fire and preferentially sampled yellow-cedar and ponderosa pine with more than one basal-scar to maximize the number of fires recorded and to minimize the impact of our sampling on the study area. Sampled trees were well distributed both inside and outside of the grove (Appendix S1). In addition to sampling basal-scarred cross sections, we cored live and standing-dead cedar trees to develop a yellow-cedar tree ring chronology.

We sanded all samples until we could see the cell structure with a binocular microscope and assigned calendar years to tree rings by visually cross-dating ring widths. We used an existing ponderosa pine chronology to cross-date pine samples (Johnston et al., 2016), and we cross-dated cedar samples based on the chronology developed using cedar tree cores. Cross-dating accuracy was confirmed using COFECHA software (Grissino-Mayer, 2001). Because mechanisms other than fire are known to form basal-scars in yellow-cedar (Hennon et al., 2016), we identified yellow-cedar basal-scars as fire years if a scar definitively matched a fire year in the ponderosa pine record.

To compare historical fire frequency inside the grove to the surrounding uplands, we determined historical mean fire return intervals (MFRIs) from both the yellow-cedar fire record and the ponderosa pine fire record. MFRIs were calculated as the arithmetic mean of the intervals between fires that occurred between 1560 and 1890. This time frame was adopted because the earliest fire in our reconstructions occurred in 1561 and the most recent historical fire occurred in 1888.

We used superposed epoch analysis (SEA) to examine relationships between the occurrence of historical fire and reconstructed climate records. SEA uses bootstrap resampling to test for departures of mean annual values for fire years and the years preceding and following fire years. We used 1000 bootstrapped trials to test for statistically significant relationships between reconstructed Palmer Drought Severity Index (PDSI, Cook, Woodhouse, Eakin, Meko, & Stahle, 2004) in the year of fire, for six years preceding fire, and for three years following fire. PDSI values used in our analysis represent the average values from four reconstructed PDSI grid points surrounding the study area.

3. Results

3.1. Post-fire mortality and regeneration response

Yellow-cedar mortality was initially moderate after the fire in 2006, but by the following year, 90 % of measured cedar were dead. The population stabilized after 2007, although there was some isolated, delayed mortality recorded in 2017, which may or may not have been fire-induced. Estimated yellow-cedar mortality in 2017 was 93 %.

Table 1

Post-fire tree regeneration densities (seedlings ha⁻¹) for five conifer species regenerating in the yellow-cedar grove. Regeneration densities for grand fir, Douglas-fir, western larch, and ponderosa pine were not recorded in 2006 and 2007. Values represent the minimum and maximum observed seedling densities and the median density across all sub-plots, for each measurement year. The rightmost column represents the percentage change between 2008 and 2017. Percentage change for western larch is not reported because it was not present in any plots in 2008.

Species	Seedlings ha ⁻¹				
	2006	2007	2008	2017	% change (2008–2017)
yellow-cedar	125 (0–35250)	2750 (0–41000)	7375 (0–10100)	8125 (0–69250)	+ 10 %
grand fir	–	–	2750 (0–20250)	17,750 (0–205500)	+ 545 %
Douglas-fir	–	–	1250 (0–16000)	1625 (0–13250)	+ 30 %
western larch	–	–	0	250 (0–3500)	NA
ponderosa pine	–	–	0 (0–1750)	0 (0–2000)	0 %

Mortality was high across all transects, and surviving individuals were distributed across the length of the grove (Fig. 4).

Yellow-cedar regeneration was present in 50 % of subplots after the fire was controlled in the fall of 2006 (median = 125 seedlings ha⁻¹, Table 1). Regeneration densities increased substantially in the following two years, and yellow-cedar seedlings were present in all but one subplot by 2008. Yellow-cedar regeneration densities stabilized between 2008 and 2017 at relatively high levels (median = 8125 seedlings ha⁻¹). When we began collecting seedling data for other conifer species in 2008, grand fir, Douglas-fir, and ponderosa pine were regenerating at comparatively low densities, and western larch was not recorded (Table 1). However, between 2008 and 2017 the median grand fir seedling density increased by more than 500 %, eclipsing the median density of yellow-cedar regeneration by more than a factor of two (Fig. 5).

3.2. Historical fire dynamics

Fire was frequent in the dry mixed-conifer forest surrounding the grove prior to 1890. We identified 23 fires that occurred between 1560 and 1890 in 11 ponderosa pine cross sections (Fig. 6). The MFRI for the upland forest outside of the grove was 14.4 years. Basal-scarred yellow-cedar were common and widespread across the grove. We cross-dated 16 cedar samples with basal-scar years that corresponded to fire years in the ponderosa pine record. We found evidence of seven fires that

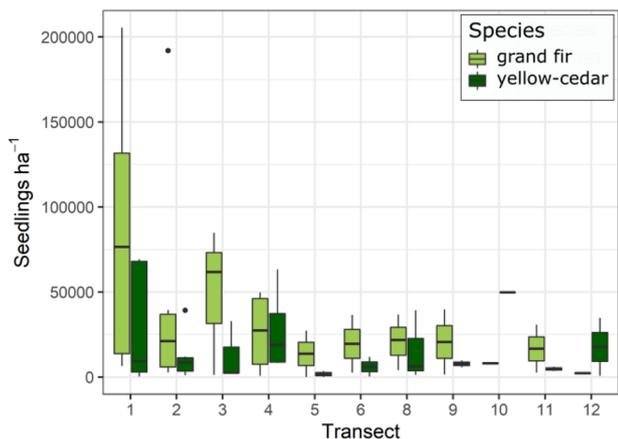


Fig. 5. Yellow-cedar (dark green) and grand fir (light green) regeneration densities in 2017 by transect. Yellow-cedar is regenerating across the grove, but grand fir is substantially more abundant in many transects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

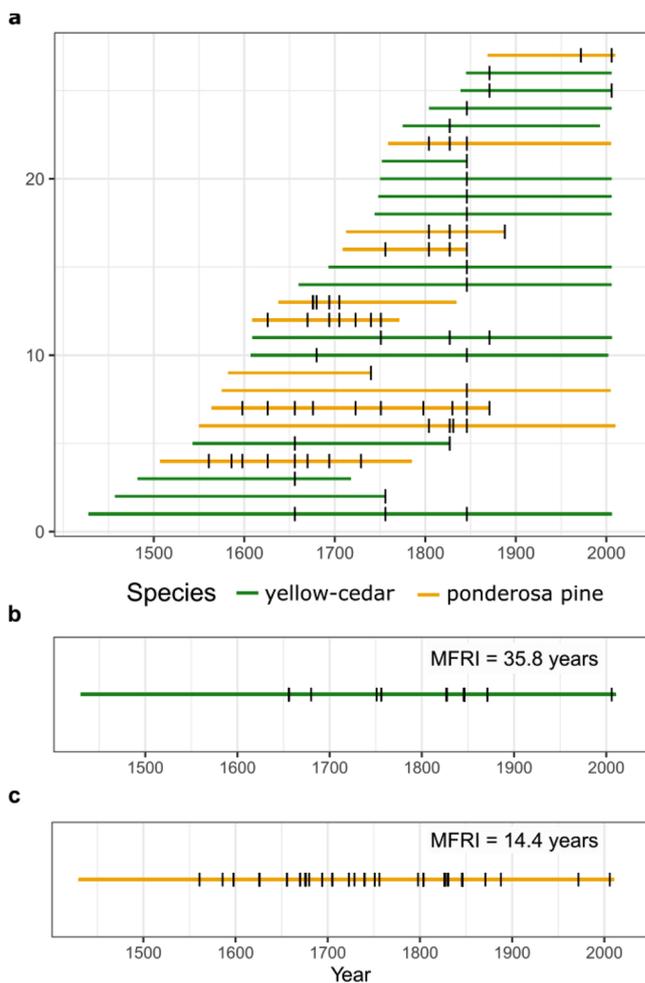


Fig. 6. (a) Reconstructed fire chronologies for yellow-cedar (green) and ponderosa pine (orange). Reconstructed fire was substantially (2.5x) less frequent in (b) the cedar grove than in (c) the surrounding dry mixed-conifer uplands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impacted the grove between 1650 and 1871. The MFRI for the cedar grove was 35.8 years, 2.5 times longer than the MFRI for the dry mixed-conifer forest surrounding the grove (Fig. 6).



Fig. 7. Examples of yellow-cedar scars (dated to 1844 and 1821) that were not included in mean fire return intervals because these fire years were not also identified in ponderosa pine samples. We speculate that these scars may have eroded (for instance, an 1846 fire scar may have eroded to the current dating of 1844) or been caused by mechanical damage (fallen trees or frost heaving) or animal damage (bear are known to forage on yellow-cedar cambium). Alternately, by not including these records we may have underestimated fire frequency (i.e., there was more frequent fire in the cedar grove than we report).

3.3. Fire-climate relationships

SEA demonstrated that fire years in both the cedar grove and the surrounding uplands were associated with hotter and drier conditions than non-fire years, as measured by PDSI (Fig. 8). Mean PDSI departures during fire years exceeded 95 % bootstrapped confidence intervals in both the ponderosa pine record (mean departure = -0.976 , 95 % CI = 0.934 , -0.948) and in the ponderosa pine + yellow-cedar fire record (mean departure = -1.005 , 95 % CI = 1.008 , -0.918). Mean PDSI departure for cedar-only fire years (-1.529) provided evidence of a similar relationship but did not exceed the 95 % confidence interval (1.679 , -1.726) (Fig. 7).

4. Discussion

The Aldrich yellow-cedar grove, the only such disjunct population in the contiguous US, appears to occupy both a climate refugium buffered from unfavorable conditions that have developed since the late-Pleistocene, and a fire refugium historically decoupled from the frequent-fire regime of the broader landscape. Our cross-dated yellow-cedar fire history reconstruction, the first of its kind to our knowledge, demonstrates that yellow-cedar can survive and record surface fire. Importantly, we provide evidence that yellow-cedar can survive more frequent fire than previously thought. Although yellow-cedar's persistence in the Blue Mountains of eastern Oregon was compatible with periodic burning prior to European settlement, our data indicate that fire was less frequent historically in the grove than in the upland dry mixed-conifer matrix. Recent fire resulted in substantial yellow-cedar mortality. However, yellow-cedar regeneration was robust and widespread in as little as two years post-fire, and it appears likely that the species will persist on the site for the foreseeable future in the absence of future high-mortality disturbance. Conserving biodiversity at regional scales requires the preservation of disjunct populations—like the Aldrich grove—that occur at the margins of their climatic and disturbance regime tolerances. Our study highlights the importance of integrating disturbance into efforts to identify locations where populations are more likely to persist despite directional climate change and resultant contractions of species' *in situ* ranges.

The effects of the 2006 fire demonstrate the sensitivity of the Aldrich yellow-cedar population to fuel dynamics and fire severity. Yellow-cedar mortality was initially moderate in the fall of 2006, and we observed very low mortality in other conifer species and low or

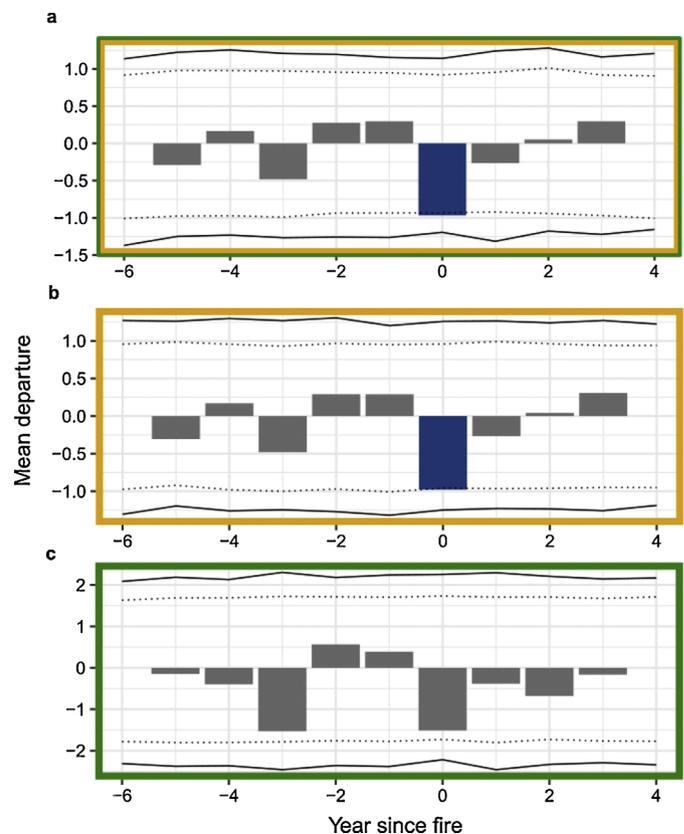


Fig. 8. Superposed epoch analyses for fire occurrence and PDSI demonstrates that fire years in the combined yellow-cedar-ponderosa pine (a), ponderosa pine-only (b), and yellow-cedar-only (c) records were associated with hotter, drier conditions. The y-axis represents scaled mean PDSI values for year of fire (year 0 on the x-axis), six years prior to fire (negative values on the x-axis), and three years post-fire (positive values on the x-axis). Blue colored bars indicate a PDSI value that is departed from mean values at the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

absent bole scorch on many mature trees inside the grove (Fig. 3c), indicating that the fire burned at low-intensity. Some areas appear to have remained unburned, and the presence of live yellow-cedar seedlings in the fall of 2006 suggests that patchy fire effects allowed for the survival of some pre-fire cedar regeneration. With the exception of a small patch of stand-replacement fire effects in the northernmost (lowest elevation) portion of the grove, surviving yellow-cedar are distributed across the species' pre-fire distribution.

Yellow-cedar is regenerating vigorously despite a substantial fire-induced loss of seed source. Because yellow-cedar disperses its seeds between fall and spring (Bonner, 2008), high densities of yellow-cedar seedlings are likely due in part to seeds contributed by individuals that were alive in the fall of 2006 but subsequently died. Although yellow-cedar is capable of vegetative reproduction, post-fire reestablishment in the grove was almost certainly facilitated by wind-dispersed seeds that are substantially lighter (240,000 seeds/kg) than ponderosa pine, Douglas-fir, and grand fir (Burns & Honkala, 1990) and which appear to have reached and germinated in the majority of locations occupied by cedar prior to fire.

Although cedar is regenerating, it is not clear if the stand structure and composition of the grove will be representative of pre-fire conditions when the post-fire cohort recruits into the overstory. As a result of a fire exclusion, the abundance of late-seral species like grand fir has increased substantially in dry mixed-conifer forests in both the southern Blue Mountains specifically (Johnston, 2017), and across the Pacific

Northwest more broadly (Hagmann, Franklin, & Johnson, 2013; Merschel, Spies, & Heyerdahl, 2014). Higher-than-historical grand fir abundance prior to the 2006 fire may have provided the species with a post-fire regeneration advantage, and continued monitoring will be needed to evaluate how interspecific competition between regenerating conifers influences the composition of the grove in the future.

Reconstructions of pre-settlement fire frequencies provide evidence to suggest that the cedar grove has persisted, at least in part, because it burned less frequently than the surrounding landscape matrix. The MFRI derived from the ponderosa pine record outside of the grove (14.4 years) is consistent with other fire history reconstructions in the Blue Mountains (Emily K. Heyerdahl, Loehman, & Falk, 2019; Johnston et al., 2016). In contrast, our data suggest that fire was 2.5 times less frequent, on average, in the cedar grove, and we identified two 70-year periods between 1656 and 1871 for which we found no evidence of fire. The oldest yellow-cedar we sampled established prior to 1428 and was at least 578 years old when it died in the 2006 fire. During that time, the dry mixed-conifer forest around the cedar grove burned a minimum of 23 times. Our results indicate that fewer than 1/3 of those fires spread into the cedar grove itself. Despite evidence that the grove burned less frequently than the surrounding uplands, it is notable that fire was much *more* frequent in the Aldrich grove than in any other known yellow-cedar population, and our results suggest the Aldrich grove was a fire refugium relative to the surrounding landscape, rather than the species' broader distribution.

It is unlikely that the grove could have avoided extirpation if pre-settlement fires regularly resulted in yellow-cedar mortality rates comparable to those we recorded following fire in 2006. We found evidence that the grove burned three times between 1828 and 1871, and had each of these fires produced effects similar to the 2006 fire, we would expect less than 0.05 % of mature cedar to have survived into the late 1800s. We suggest that it is more likely that most pre-settlement fires produced lower-severity fire effects in the grove than the 2006 fire, some of these fires only impacted portions of the grove, or a combination of both.

The 135-year period between the most recent historical fire (1871) and the 2006 fire is the longest fire-free period in the grove for which we have evidence since at least the mid-1500s. Fuel accumulations in 2006 were likely higher than during the pre-settlement period because of this extended period of fire exclusion. Yellow-cedar's shallow-rooting habit may make it particularly vulnerable to soil heating from surface fire (Hennon et al., 2016), and widespread fire-induced yellow-cedar mortality following the 2006 fire may have resulted from higher-than-historical surface fuel accumulations and resultant increases in fire residence time and soil heating. We observed many dead cedar in the grove with minimal bole scorch (Fig. 3c), and it appears likely that root, rather than cambial, injury was the mechanism responsible for cedar mortality in some cases.

There are several potential explanations for why fire spread into the grove was limited historically relative to the uplands. First, Buck Cabin Creek and the associated spring complex may have acted as physical barriers to fire spread (Fig. 3b, Skinner, 2003). Second, fuel moistures may have been higher in the grove than the surrounding uplands due to cold groundwater inputs, shading from a relatively closed canopy, and low solar insolation in the steep, northeast-facing drainage (Agee, Wright, Williamson, & Huff, 2002; Dwire & Kauffman, 2003; Pettit & Naiman, 2007). Third, fire spread and behavior may have been influenced by differences in fuel composition and arrangement between the uplands and the grove. Long-leaf ponderosa pine litter and herbaceous species like pinegrass—the primary understory fuels in the uplands—provide a well-aerated, relatively continuous fuel bed that is readily available to burn in summer (Agee et al., 2002; de Magalhães &

Schwilk, 2012). In contrast, fuel moistures of woody understory species, like those common in the grove, remain elevated relative to herbaceous species during fire season (Agee et al., 2002), and short-leaf conifer litter in the grove may have constituted a more compact fuel bed less conducive to surface fire spread (Agee, Wakimoto, & Biswell, 1978). Variations in stream width, seasonal water availability, topography, and forest composition make it difficult to generalize about the drivers of fire frequency in riparian areas, and riparian areas in dry forest ecosystems are not always associated with longer fire return intervals (Taylor & Skinner, 1998; Van de Water & North, 2010). However, some of the mechanisms at play in the Aldrich grove may also have contributed to less-frequent fire in riparian areas reported elsewhere (Dwire & Kauffman, 2003; Olson & Agee, 2005; Pettit & Naiman, 2007).

Results from our SEA analysis demonstrate that fire years in both the ponderosa pine and yellow-cedar record were associated with hotter and drier conditions. Relatively hotter and drier conditions may have been necessary for fuels to become available to burn on the relatively shaded northeast-facing aspect drained by Buck Cabin Creek. There was evidence of a relationship between hotter and drier conditions and fire years in the cedar grove, but the small number of fires that occurred there (seven) during our study period limited our ability to detect a robust fire-climate relationship. However, the climate signal in the cedar fire data was stronger (mean departure = -1.529) than the signal in the ponderosa pine fire data (mean departure = -0.976), suggesting that climate may have been an important control on fire occurrence in the grove.

Our SEA results do not provide evidence that climate is an important control on the differential fire frequency between the dry mixed-conifer uplands and the grove; historical fire in both areas were associated with similar broad-scale, reconstructed climate conditions. However, it is possible that sustained, unusually hot and dry conditions may have rendered live fuels and larger woody debris in the grove available to burn, overwhelming the mechanisms that otherwise limited fire spread into the grove. In 1846, the year for which we have the most widespread evidence of fire in the grove (Appendix S1), five of the six preceding years were hotter and drier than average, and 1846 was the third hottest and driest year in which any identified pre-settlement fire occurred. Fire spread during more moderate conditions may have needed to coincide with particularly favorable (hot, dry, windy) day-of-burn conditions, or the peak of the burn period (late-afternoon, evening) when fuels were driest. Fire may have stopped at, or circumvented, the grove when these conditions were not present.

Yellow cedar range-wide climate data demonstrate that grove occupies a landscape that is substantially hotter and drier than the majority of the species' range (Fig. 2). Our exploration of range-wide climate data is necessarily (and unfortunately) coarse-grained, and we were unable to capture features like warm season soil water availability and snowpack which may directly contribute to the survival and regeneration of yellow cedar on the site. Future research to develop fine-grained climate data could provide important insights into the fuel and weather mechanisms that may have limited fire spread into the grove historically and the microclimatological features that have contributed to yellow cedar's persistence on the site.

There is uncertainty associated with our estimates of historical fire frequency in the cedar grove. The distribution of fire-scarred cedar samples suggests that some pre-settlement fires may have impacted only portions of the grove (see Appendix S1), and if this were the case, fire return intervals for any one location in the grove were likely longer than our composite estimate. It is also possible that our methods overestimated mean fire return intervals in the cedar grove, i.e., fire return intervals were actually historically shorter than we report here. Uncertainty inherent in our comparison of surface fire histories derived

from two species that may have different fire scar recording probabilities is compounded by the novelty of our yellow cedar fire history reconstruction. Ponderosa pine is an exceptional recorder of fire, producing traumatic resin ducts in response to fire that preserve scars. We detected no resin ducts in yellow-cedar associated with fire scars, and we believe that fire scars in yellow-cedar are more likely to erode and be unavailable fire reconstructions. Although most of the partial cedar cross sections were from inverted V-shaped basal cavities typical of repeated surface-fire scarring, many individual scars were not associated with charcoal and were formed in years when fire was not recorded in ponderosa pine. We believe it is possible, if not likely, that some of these scars resulted from animal or mechanical damage (Fig. 7). Other scarred trees were difficult to cross-date because of complacent growth or growth that was badly distorted by scars. We chose to take a conservative approach to calculating fire return intervals in the grove and only used cross-dated fire years from cedar samples that matched fire years in the ponderosa pine record.

Our study adds to a growing body of evidence that fire refugia contribute to local and regional heterogeneity and biodiversity by promoting the persistence of fire-sensitive species. Other conifer species in western US dry forest ecosystems, such as pacific yew (*Taxus brevifolia*, Taylor & Skinner, 1998) and gray pine (*Pinus sabiniana*, Schwilk & Keeley, 2006), occur in riparian fire refugia where fire is less frequent or severe, and globally, many other fire-sensitive plant species are associated with fire refugia in fire-prone environments (Adie et al., 2017; Meddens et al., 2018; Wood et al., 2011). However, our results also contribute to a recognition that tree species have a broader amplitude than expected to adjust to local fire regimes, and forest composition at fine spatial scales appears to be driven more strongly by soil and microclimate rather than by fire regime (Johnston et al., 2016; Merschel, Heyerdahl, Spies, & Loehman, 2018).

The persistence of yellow-cedar in the Aldrich Mountains indicates that locations buffered from both unfavorable climate and disturbance can overlap, and that the mechanisms responsible may be similar. The grove's topographically sheltered setting and cold groundwater inputs appear to have supported both suitable cedar habitat as well as maintained conditions that were historically somewhat less prone to fire. However, disturbance refugia and climate refugia do not necessarily overlap, and their respective mechanisms may be quite different. Fire refugia in rocky, exposed locations where fuel is less abundant may be more vulnerable to the disadvantageous impacts of directional climate change because these locations are not decoupled from regional climate (Dobrowski, 2010; Landesmann, Gowda, Garibaldi, & Kitzberger, 2015). Similarly, riparian areas that may be relatively buffered from climate warming in the future were not necessarily protected from fire historically (Van de Water & North, 2010), and some of these locations may be more vulnerable to high-severity fire in the future because they are more productive.

Recent fire effects demonstrate that the cedar grove is highly sensitive to fuel dynamics and contemporary fire intensity. Subsequent fire events, should they occur, may result in significant contraction or extirpation of yellow-cedar from the Blue Mountains. The infrequent (~every 35 years) and careful application of prescribed fire may be appropriate in the grove to mitigate future fire risk and restore the historical disturbance regime. We recommend frequent (~every 14 years) prescribed fire treatments in the areas immediately adjacent to the grove, consistent with a restoration objective for the landscape based on knowledge of historical fire regimes (Johnston et al., 2016). In other fire prone areas of yellow-cedar's range, managers may also consider fuels reduction treatments in and around cooler microsites to promote the retention of cedar in the event of a fire. In the Aldrich grove, it is likely that the abundance and distribution of grand fir in the grove has reached an ecological threshold where this species has

adequate, well-distributed seed sources to outcompete cedar regeneration. If recruitment of regenerating yellow-cedar is a management objective, mechanical removal of grand fir is recommended.

It is less clear how directional climate change will affect the persistence of the cedar grove. A major contributor to cedar's persistence appears to be cold groundwater inputs and low solar insolation resulting from its topographically sheltered position (Fig. 1c), and there is currently little reason to think these factors will change substantially in the short and medium term. In contrast, yellow-cedar's risk of fire-induced extirpation may increase as the conditions that support large fires in the Blue Mountains become increasing common with climate warming (Davis, Yang, Yost, Belongie, & Cohen, 2017).

5. Conclusion

Managing for climate refugia has been identified as an important option for conservation in the context of rapid global change (Morelli et al., 2016), but there is a growing realization that disturbance also needs to be integrated in plans to maintain landscape resilience and regional biodiversity (Mackey et al., 2012). The risk of disturbance-induced extirpation of disjunct populations may increase as the synergistic effects of changing climate and disturbance regimes accelerate the pace of species' *in situ* range contractions (Loarie et al., 2008). As ranges contract, the persistence of populations or species may depend in part upon landscape positions that are buffered from the changes to disturbance regimes and regional climate. While we provide evidence that yellow-cedar is more tolerant of periodic surface fire than the existing literature suggests, the effect of recent fire demonstrates that the refugial capacity of the cedar grove can be overwhelmed by anthropogenic changes to pre-settlement fire regimes, and it is not clear if the grove's topographic position alone will support long-term, viable habitat. Our study indicates that locations buffered from disadvantageous climatic conditions or disturbance regimes may require active management in order to continue to function as species refugia in the context of accelerating global change.

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Declaration of interests

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.

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