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Reestablishing natural fire regimes to restore forest structure in California's red fir forests: The importance of regional context

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ABSTRACT

The reestablishment of natural fire regimes can have numerous benefits for forest ecosystems, including the restoration of stand structure through a reduction in tree densities and increased representation of large diameter trees. However, fire effects may depend on how departed the ecosystem is from its historical fire frequency. Red fir (*Abies magnifica*) forests occupy a broad geographic area across which historical fire return intervals and stand structures vary. Using historical stand inventory data from the Vegetation Type Mapping (VTM) project, we evaluated red fir forests in the Sierra Nevada in California and the Cascade-Klamath region of northwestern California and southern Oregon to determine how reintroduced fire effects vary regionally and if these differences are related to historical fire return intervals or structural conditions. We sampled a total of 29 overlapping fires and found that reestablishing fire in red fir forests consistently restored historical forest structure across a wide geographic range by reducing the density of small trees and maintaining large trees. However, the effect of fire was most evident in the Sierra Nevada where the percent difference in total tree density between unburned and burned plots was significantly greater (77% difference) than in the Cascade-Klamath (53% difference), and burned plots in the Sierra Nevada had significantly lower densities of both small (<30 cm dbh) and medium sized trees (30–60 cm dbh). These stronger fire effects may be related to greater departure from reference fire return intervals in the Sierra Nevada, as well as the region's warmer and drier conditions increasing the availability of fuel to burn and susceptibility of trees to fire-related mortality. We found that departure from reference fire return intervals followed a similar pattern to departure from historical tree density in both study regions. Unburned plots were 61% departed from reference fire return intervals in the Cascade-Klamath and 69% departed in the Sierra Nevada. In these same plots, departure from VTM total tree density estimates were 37% in the Cascade-Klamath and 44% in the Sierra Nevada. We suggest that incorporating historical references for structural conditions together with regional or local estimates of historical fire return intervals contributes to an improved understanding of how reference conditions varied at local and regional scales, and their importance in the restoration of fire-dependent forests.

1. Introduction

The recent rise in western U.S. fire activity has resulted in an increase in forest acreage that has burned after a relatively long period of fire exclusion (Westerling 2016). A fraction of this fire activity has contributed to the reestablishment of natural fire regimes (i.e., fires burning within the historical range of variation for frequency, severity, and size), either through the deliberate application of prescribed fire or the management of wildfires to support natural resource objectives (van Wagtendonk 2007, Collins et al. 2011, Meyer 2015, North et al. 2021). This can restore many attributes of stand structure, including reduced tree densities, increased structural heterogeneity, and retention of large

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diameter trees (Holden et al. 2007, North et al. 2007, Webster and Halpern 2010). These attributes are common restoration targets for fire-excluded forests that are currently characterized by higher tree densities (especially in smaller size classes) and lower structural variation and complexity than under the historical (i.e., pre-Euro-American settlement) reference conditions (Franklin and Norman Johnson (2012), Stoddard et al. 2020, Stephens et al. 2021).

The magnitude of these fire effects, however, may be less obvious in forests with moderately long (>30 years) historical fire return intervals where current fire frequency is less departed from historical conditions (Steel et al. 2015). For example, in the upper montane red fir (*Abies magnifica*) forests of California and Oregon, historical fires burned at moderately long intervals, with a mean fire frequency of approximately 40 years (range: 15–130 years; van de Water and Safford 2011). The heavy snowpack and cool growing conditions in these forest types result in slow fuel accumulation and compact fuel beds that are difficult to ignite, making fire occurrence often dependent on warmer and drier conditions that are suitable for ignition and spread (Agee 1993, Taylor and Skinner 2003). Moreover, current fire severity patterns in red fir forests have not departed significantly from historical conditions, which are predominantly (80 to 95%) characterized by low- to moderate-severity (Mallek et al. 2013, Miller and Safford 2012). As a result, many contemporary red fir forests have missed only one to three fire intervals and exhibit lower departure from their historical fire frequency and severity compared to forest types with more frequent historical fire return intervals such as mixed-conifer and yellow pine (i.e., ponderosa pine, Jeffrey pine) forests (van Wagtendonk et al. 2002, Mallek et al. 2013, Safford and van de Water 2014, Safford and Stevens 2017).

Historical estimates of fire frequency in red fir forests are generally longer in more northern latitudes (Meyer and North 2019), consistent with patterns observed in mixed conifer forests in the Sierra Nevada (Krasnow et al. 2017) and other coniferous forests in western North America (Heyerdahl et al. 2001). , Across the state of California, historical fire return intervals averaged 40 years but varied widely geographically (range:15–130 years; Van de Water and Safford 2011). This considerable geographic variation may be attributed to topographic features and forest composition (Taylor 2000), stand isolation and local climate conditions (North et al. 2009), and regional climate patterns (Beaty and Taylor 2008, Taylor et al. 2008). Regional differences in historical fire return interval estimates generally correspond to differences in fire return interval departure (FRID), defined as the difference between current and historical fire frequencies (Safford and Van de Water 2014). The potentially shorter historical fire return interval in Sierra Nevada red fir forests, in combination with other contributing factors (e.g., warmer, drier climate), suggest that forests in this region may currently experience a greater degree of departure from their natural fire regime than those in the southern Cascades and Klamath Mountains (Meyer and North 2019, Coppoletta et al. 2021).

The level of departure in natural fire frequency may influence the degree to which fire, when reintroduced as a natural process, elicits change in forest ecosystems (Safford and van de Water 2014). For example, Steel et al. (2015) found a strong correlation between high-severity fire effects and long periods of fire exclusion in forest types that historically experienced frequent low-severity fire (e.g., lower elevation mixed-conifer and yellow pine forests). Coppoletta et al., (2019) documented a similar trend in natural areas across California, with the highest proportion of severe fire effects found in areas that also exhibited the highest departure in fire frequency. While the link between fire return interval departure and fire effects may be less apparent in upper montane forest types like red fir (Steel et al. 2015), there is recent evidence that contemporary red fir forests are experiencing more severe fire effects than would be expected under a natural fire regime and that this may be related to increasing fire regime departure and other interacting stressors such as climate change (Meyer and North 2019, Coppoletta et al. 2021). For example, Haugo et al. (2015) compared contemporary wildfires (1984–2015) with modeled historical fire regimes in the Klamath Mountains and eastern Cascades and found that the current proportion of high severity fire in red fir forests was above the expected proportion under the historical fire regime; they attributed this to a pronounced fire deficit in these and other forest types across the region. Similarly, van Wagtendonk et al. (2012) found that fire return interval departure in combination with other fire variables (e.g., years since last fire, prior burn severity) was associated with increased fire severity in mixed conifer, yellow pine, and red fir forests of Yosemite National Park. In upper montane red fir forests, an increase in the length of time between fires can facilitate an increase in the density of smaller shade-tolerant red fir, which historically may have been killed by fire (Taylor and Halpern 1991) and is associated with higher severity fire effects (Skinner 2003).

Although fire frequency and stand structure are inherently linked in red fir and other forest types (Agee 1993, van Wagtendonk et al. 2018), we are not aware of studies that correlate fire return interval departure with departure from historical structural conditions, or that evaluate how the degree of departure might influence the effects of reintroduced fire. In a previous study, Meyer et al. (2019) established that burning (primarily prescribed fires and wildfires managed to support natural resource objectives) had restorative effects on red fir forest conditions in the Sierra Nevada, especially with respect to changes in forest structure (e.g., reductions in small tree density, retention of large trees, and flattening of the diameter distribution). Here, we expand the scope of that study to evaluate if the effects of reintroduced fire vary across regions and if these regional differences are related to differences in historical fire return intervals or structural conditions, focusing on tree density in different size classes, using historical stand inventory data. Specifically, we asked: 1) Do the effects of reintroduced fire in red fir forests vary between the Sierra Nevada and Cascade-Klamath regions?; 2) Are differences in fire effects associated with regional estimates of departure in historical fire frequency or historical stand densities? and 3) Does burning restore forest densities to within the range of conditions found in historical stand inventories, irrespective of the study region?

2. Methods

2.1. Study area

Our study included two montane regions of California: (1) the Sierra Nevada (Yosemite, Sequoia, and Kings Canyon National Parks and the Giant Sequoia National Monument); and (2) the southern Cascade Range (Lassen Volcanic National Park) and Klamath Mountains (Marble Mountain Wilderness, Klamath National Forest; Fig. 1). Although the southern Cascade Range and Klamath Mountains are often considered distinct ranges, we combined the two areas for this analysis (hereafter "Cascade-Klamath" region) because of their geographic proximity, floristic and climatic similarities, and the dominance of Shasta red fir (*A. magnifica* var. *shastensis*) in both areas (Baldwin et al. 2017). The two other varieties of red fir (*A. m. magnifica* and *A. m. critchfieldii*) are largely confined to the Sierra Nevada.

Within our study area, red fir is generally a dominant or co-dominant (i.e., $\geq$10% total tree cover and $\geq$ 35% of tree density or basal area) conifer species in the upper montane zone, often mixed with white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), or sugar pine (*P. lambertiana*) at lower elevations, and lodgepole pine (*P. contorta*), western white pine (*P. monticola*), or mountain hemlock (*Tsuga mertensiana*) at higher elevations. We selected several landscapes in the upper montane zone with active fire regimes, which we defined as: (1) not impacted by prior logging activity; and (2) having experienced at least two overlapping fires, with the most recent fire (since 1980 or one fire return interval) classified as low to moderate severity (based on one-year post vegetation burn severity derived from relative differenced Normalized Burn Ratio (RdNBR) satellite-based imagery; Miller and Thode 2007). Our use of two recent fires to define red fir forests with an active fire regime is based on mean fire return interval estimates for

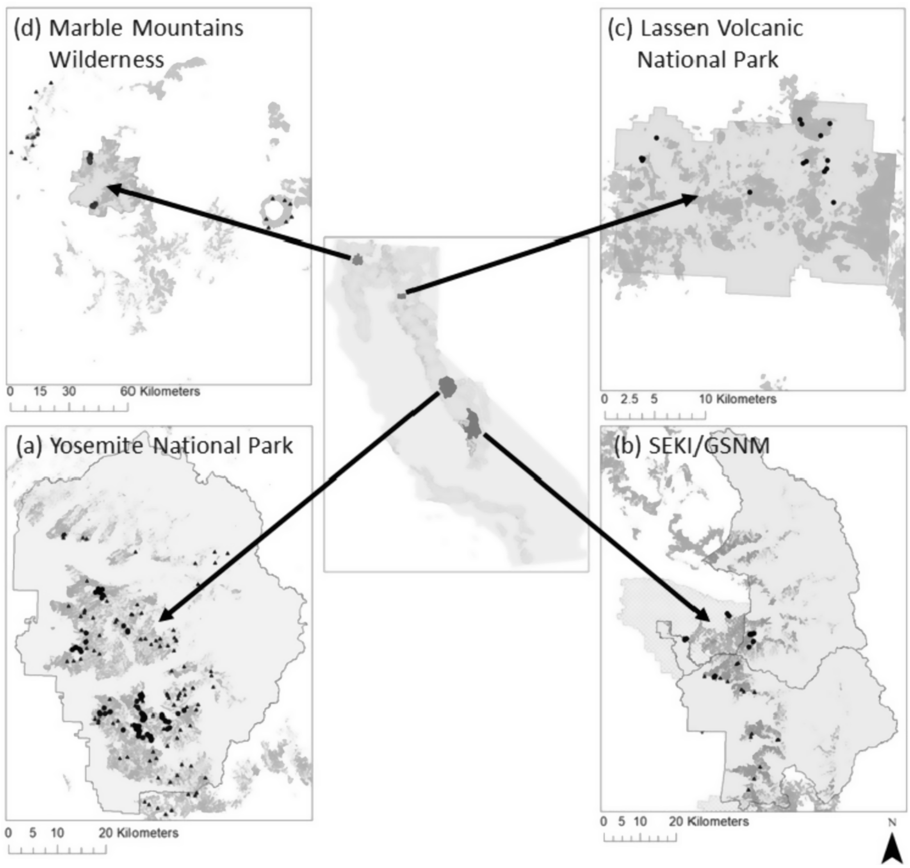

Fig. 1. Study site locations in the Sierra Nevada (Yosemite National Park (a), and Sequoia and Kings Canyon National Parks and Giant Sequoia National Monument (SEKI/GSNM) (b); 22 sites including 80 plots) and the Cascade-Klamath (Lassen Volcanic National Park (c), and Marble Mountains Wilderness (d); 7 sites including 32 plots) regions of California, USA. Field plots (established 2014–2017) are shown as circular points, and historical plots (established 1929–1936) extracted from the Vegetation Type Mapping (VTM) project (n = 145) are shown as triangular symbols. Only general location information of VTM plots were available for Lassen Volcanic National Park. The distribution of red fir forests is shown in dark gray shading in panels (a) through (d).

California's red fir forests (Meyer and North 2019, Coppoletta et al. 2021). We avoided high severity burned areas (>75% tree mortality) because these sites lacked the necessary ≥ 10% total tree cover required for a related study (i.e., Meyer et al. 2019), high severity burn sites were an infrequent component of historical fire regimes in red fir forests (Mallek et al. 2013), and high severity burned sites were generally ≤ 5% of our potential sampling area based on other site selection criteria. Using these criteria, we identified and sampled a total of 29 overlapping fires (Sierra Nevada = 22; Cascade-Klamath = 7), across a wide range of elevational gradients and fire management objectives, including fires managed for multiple objectives as well as those subjected to full suppression tactics (Table 1).

2.2. Data collection

In July through September of 2014 to 2017, we randomly established a total of 112 circular plots (12.61 m radius; 0.05 ha), including 80 plots (58 twice burned, 22 unburned) in the Sierra Nevada and 32 plots (22 twice burned, 10 unburned) in the Cascade-Klamath. We identified suitable sites based on our selection criteria and maintained a minimum distance of 100 m between plots and 100 m from the fire boundary, existing roads, and trails. At each site, we established between one and four (average: 3) plots in burned red fir stands and one plot in a nearby (generally within 3.5 km) unburned red fir stand (i.e., no record of fire occurrence for the site in fire history databases dating back to 1908–1930; FRAP 2017, NPS, 2017). We established only single plots in unburned areas because previous studies and preliminary sampling indicated unburned red fir stands exhibit substantially less stand structural variation than burned sites that experienced a range of fire effects (Taylor 2004, Kane et al. 2013, Kane et al. 2014, Meyer et al. 2019). Within each 0.05 ha plot, we recorded site attributes, such as slope (%) and aspect (degrees). We calculated northness as a cosine of aspect (1 = north-facing, 0 = east or west-facing, −1 = south-facing). The percent cover of rock, bare ground, woody debris, and litter was visually estimated within the 0.05 ha plot. Based on the sampling methodology of Meyer et al. (2019), we recorded the attributes of all trees ≥ 5 cm diameter at breast height (dbh), including species, status (live or dead), and dbh. For each plot, we extracted 30-year averages (1981–2010) for climatic water deficit (mm), actual evapotranspiration (AET; mm), and 1 April snow water equivalent (snowpack; mm) from 270-m resolution raster data available from the California Climate Commons (http://climate.calcommons.org/). We used a 30-m digital elevation model from the U.S. Geological Survey national elevation dataset to estimate elevation for each plot (https://www.usgs.gov/core-science-systems/national-geospatial-program/national-map).

2.3. Analysis

We calculated the mean FRID for unburned and burned plots based on the methods of Safford and van de Water (2014). This metric quantifies the extent (in percent) to which contemporary fires (since 1908) are burning at frequencies similar to the mean historical fire return interval. To obtain estimates of mean historical fire return interval (FRI), we conducted a comprehensive review of published and unpublished fire history studies that provided estimates of FRI in red fir forests prior to extensive Euro-American settlement (Table 2). We then averaged mean FRI values from these studies to obtain a single mean estimate for each region. We used these regional estimates of historical FRI to calculate FRID for each plot using Eq. (1) when the current FRI was longer than the historical estimate and Eq. (2) when the current FRI was shorter than the historical estimate (Safford and van de Water 2014).

$$FRID_{(L)} = \left[1 - \left(\frac{historicalFRI}{currentFRI}\right)\right] \times 100 \quad (1)$$

Table 1
Red fir study sites in the Cascade-Klamath and Sierra Nevada regions of California, listed by fire events, location, elevation range, and number of burned inventory plots established in the overlapping fire perimeters (number does not include one or more unburned plots per site). Unless otherwise noted, all fires were categorized as natural ignitions that were primarily managed for resource objectives with the exception of those fire names in italics, which were lightning or human-ignited wildfires managed with full suppression objectives.

Most recent fire name and year	Second fire name and year	Location [1]	Elevation range (m)	No. of burned plots
Titus 2006	*King Titus 1987*	KNF	1739–1924	6
Hancock 2006	*Yellow 1987*	KNF	1758–1827	1
Jake 2008	*Yellow 1987*	KNF	1790–1898	4
Reading 2012	Prospect Peak 2005[2]	LVNP	2161–2256	3
Reading 2012	Fairfield 2009	LVNP	1952–2134	2
Crescent 2009 [2]	Unnamed 1918	LVNP	1993–2044	3
Fairfield 2009/ Bluff 2004 [3]	*Unnamed 1987*	LVNP	1894–2010	3
Harden Lake 2009	*Ackerson 1996*	YNP	2221–2345	3
Slope 2010	Harden 2005	YNP	2220–2261	1
Dark Hole 2014	Dark 1999	YNP	2317–2375	3
Rim 2013	PW-3 Gin Flat 2002[2]	YNP	2034–2179	3
Tamarack 2011	*Walker 1988*	YNP	2122–2260	4
Unnamed 1984	Gordo 1980	YNP	2398–2437	3
Hoover 2001	Fat Head 1980	YNP	2358–2421	2
Hoover 2001	Alaska 1988	YNP	2215–2274	2
Meadow 2004	Buena Vista 1981	YNP	2106–2242	3
Meadow 2004	*Unnamed 1980*	YNP	2112–2142	3
Grouse 2009	*Steamboat 1990*	YNP	2054–2274	4
Horizon 1994	Buena Vista 1981	YNP	2133–2186	3
Lost Bear 1987	*Unnamed 1980*	YNP	2120–2252	3
Lost Bear Bruno 1999	Lost Bear 1985	YNP	2151–2229	3
Lost Bear Bruno 1999	Horizon 1988	YNP	2177–2263	3
Lost Bear Bruno 1999	Ostrander 1992	YNP	2287–2528	3
Lost Bear Bruno 1999	Twin Snake 1978	YNP	2548–2594	3
Rough 2015	Sheep 2010	GSNM	2478–2541	1
Williams 2003	Williams 1999	SEKI	2463–2504	3
Williams 2003	Sugarloaf 1985	SEKI	2371–2564	2
Buena Vista 2004[2]	Redwood 1974[2]	SEKI	2198–2267	2
Dorst 1996	Halstead 3 1987	SEKI	2405–2432	1

[1] Locations include Lassen Volcanic National Park (LVNP), Klamath National Forest (KNF), Yosemite National Park (YNP), Sequoia and Kings Canyon National Parks (SEKI), and the Giant Sequoia National Monument (GSNM).
[2] Prescribed fire.
[3] Sampled locations that burned in the 1987 Unnamed Fire and 2004 Bluff Fire were also burned in the 2009 Fairfield Fire.

$$FRID_{(S)} = -\left[1 - \left(\frac{currentFRI}{historicalFRI}\right)\right] \times 100 \quad (2)$$

Greater positive FRID values (especially those exceeding 67%) are associated with fewer fires in the current period relative to the historical reference period, whereas negative values (especially below −67%) indicate a higher frequency of current fires relative to the mean historical fire return interval (Safford and van de Water 2014). Time since last fire was calculated by subtracting the year of the last fire from the year of plot data collection. In this analysis, plots with no record of a fire since 1908 were assigned a default value of between 107 and 110 years (depending on the date of sampling); since the actual time since last fire could have been much longer, the calculated difference between unburned and burned plots is considered conservative in our analysis (Safford and van de Water 2014). We also calculated the fire severity index for each fire as the sum of the proportional areas of each fire severity class multiplied by their fire severity value (i.e., unchanged = 1, low = 2, moderate = 3, and high = 4), excluding fires that burned prior to 1984 where satellite-derived fire severity information was unavailable. Fire severity index is a composite metric that is useful for summarizing fire effects of individual fires for comparison within and among studies (e.g., Meyer 2015).

Table 2
Historical fire return interval (FRI) estimates for red fir forests in the study area listed by region and data source. Mean, minimum, and maximum values represent grand means (i.e., the mean of the mean, minimum, and maximum values presented in the studies assessed). - = no estimate available.

Region	Mean FRI (yrs)	Min FRI (yrs)	Max FRI (yrs)	Data Source
Cascade-Klamath (CK)	40	–	–	Atzet and Martin (1992)
	28	5	61	Bekker and Taylor (2001)
	59	–	–	Bekker and Taylor (2010)
	39	15	71	Chappell and Agee (1996)
	71	33	175	Foster (1998)
	32	4	78	Sensenig (2002)
	43	6	126	Skinner 2003
	41	5	65	Taylor and Halpern (1991)
	54	–	–	Taylor and Solem (2001)
	22	–	–	Taylor (1993)
	45	26	109	Taylor (2000)
Mean (CK)	***43***	***13***	***98***	
Sierra Nevada (SN)	21	12	34	Beaty and Taylor (2009)
	30	–	50	Caprio and Lineback (2002)
	17	3	115	North et al. (2005)
	65	–	–	Pitcher (1987)
Mean (SN)	***33***	***8***	***66***	

We used historical data obtained from the Vegetation Type Mapping (VTM) project as a reference with which to make broad comparisons between burned and unburned plots sampled in our study. The VTM project collected data from over 18,000 plots across California between 1929 and 1936 (Kelly et al. 2016). Within each rectangular field plot (0.08 ha), forest surveyors tallied all trees > 10 cm dbh in four diameter classes: 10–30 cm, 31–60 cm, 61– 91 cm, and > 92 cm. VTM data provide useful insights into historical stand structure in California's forests (e.g., Dolanc et al. 2013, McIntyre et al. 2015). The VTM data used in our study from national parks and wilderness areas were unlikely to be impacted by historical logging (Meyer and North 2019, Coppoletta et al. 2021), although they contain several important limitations such as the absence of small (<10 cm dbh) stem densities, influence of earlier (~1850–1930) fire exclusion activities on stand structure (i.e., 60–80 years of fire exclusion prior to sampling), and potential plot selection bias (Lutz et al. 2009, Safford and Stevens 2017). For this analysis, we evaluated data from a total of 145 VTM plots, established in stands dominated by red fir (i.e. > 35% of the total trees per hectare), in the Sierra Nevada (n = 119 plots) and Cascade-Klamath region (n = 26 plots; Fig. 1). The percent departure from historical forest structure was calculated using a modified version of Eqs. (1) and (2), with current and historical estimates of mean tree density substituted for FRI.

We used two-way analysis of variance (ANOVA) to examine whether tree densities were different between burned and unburned red fir plots and between plots in the Cascade-Klamath and Sierra Nevada regions. We focused on tree density in our analysis because of its responsiveness to the effects of reestablished natural fire regimes in a related study (Meyer et al. 2019). We used Mann-Whitney U tests to evaluate differences in plot, topographic, and climate variables (e.g., slope, aspect, climatic water deficit); fire severity index; and tree density by size class in our study plots between regions. For statistical analysis of elevation in our study plots, we used regionally (i.e., latitude) adjusted values based on published elevational ranges of red fir forests in Meyer and North (2019) and Coppoletta et al. (2021). We used Mann-Whitney U tests to evaluate differences in tree density by size class between burned and unburned plots in both regions and a Kruskal-Wallis test to evaluate whether the percent difference in tree density with burning (unburned – burned) was different between regions. We evaluated all variables for normality, homoscedasticity, and independence of residuals and log-transformed tree density to meet the parametric assumptions of ANOVA. We conducted all statistics with Statistica 6.1 (StatSoft Inc., Tulsa, OK, USA).

3. Results

Across both regions, burned plots had significantly lower total tree densities than unburned plots (Fig. 2.; $F_{1,108} = 47.302$, $P < 0.001$). The average total tree density in our burned red fir plots was three times lower (257 ± 17 trees ha-1) than in unburned plots (804 ± 93 trees ha-1). There were no differences between the Sierra Nevada and Cascade-Klamath regions in total tree density irrespective of burn status ($F_{1,108} = 0.726$, $P = 0.396$), and there was a marginally insignificant interaction between burn status and region ($F_{1,108} = 3.384$, $P = 0.069$). However, the percent difference in total tree density between unburned and burned plots was significantly greater in the Sierra Nevada (median: 77% difference) than in the Cascade-Klamath (median: 53% difference) (Kruskal-Wallis test $H = 6.089$, $P = 0.014$).

Tree density in the second smallest size class (10–30 cm dbh) was significantly lower in burned than unburned plots in both regions (Fig. 2). Tree density in the smallest (5–10 cm dbh) and medium (30–60 cm dbh) size classes were significantly lower in burned plots in the Sierra Nevada region, but not in the Cascade-Klamath. In both regions, the size class distribution of trees in burned plots followed a relatively flat or hump-shaped distribution, while unburned plots were characterized by an inverse J-shaped distribution, with the highest density of trees occurring in the smallest size classes (Fig. 2).

We found slight differences in plot-level fire history characteristics between the two regions (Table 3). All unburned plots in our study area had experienced a long period (>100 years) of fire exclusion. In contrast, our selection criteria ensured that all burned plots had experienced at least one fire in the past 31 years, resulting in an average fire frequency of 36 years (range: 27–37 years). Our review of historical fire return interval estimates from the primary literature suggest slight differences among regions, with mean historical fire return interval ranging from 33 years (range: 8–66 years) in the Sierra Nevada to approximately 43 years (range: 13–98) in the Cascades and Klamath Mountains. These slight differences in mean reference FRI resulted in small regional differences in percent departure in unburned plots (Table 3). In the Cascade-Klamath, fire return intervals in unburned plots were 61% departed from reference fire return intervals, equivalent to moderate departure as categorized by the interagency Fire Regime Condition Class program (Hann and Strohm 2003). In the Sierra Nevada region, fire return intervals in unburned plots were 69% departed from reference fire return intervals, corresponding to a highly departed condition class. These values indicate that unburned plots in our study area are currently characterized by a lack of fire, with fire return intervals ranging from two to three times longer than historical estimates. In contrast, burned plots in both regions exhibited much lower percent departure in fire return interval, ranging from −17% in the Cascade-Klamath to 7% in the Sierra Nevada region. In burned plots, the average time since last fire was slightly shorter and fire severity was slightly higher in the Sierra Nevada region, however these differences were not significant (Table 3).

Table 3
Fire-related variables in burned and unburned plots in the Sierra Nevada and Cascade-Klamath. For fire severity index, the same superscript letter denotes no significant difference between regions. Values in parenthesis represent the range of values.

Variable	Sierra Nevada		Cascade-Klamath	
	Unburned	Burned	Unburned	Burned
Current FRI (years)	108 (107–110)	36 (27–37)	109 (109–110)	36 (28–37)
Average time since last fire (years)	108 (107–110)	13 (3–31)	109 (109–110)	9 (5–14)
Fire return interval departure (%)	69 (69–70)	7 (-18–10)	61 (−−−)[1]	−17 (-36 - −15)
Fire severity index	–	1.8 [a]	–	1.7 [a]

[1] Estimate based on a single value.

Our analysis of historical data collected by the VTM project suggests that total tree density and the distribution of trees by size class were relatively similar in red fir forests of the Sierra Nevada and Cascade-Klamath regions between 1929 and 1936 (Fig. 3). One exception was that the Sierra Nevada historically had a significantly higher density of large trees (>90 cm dbh) than the Cascade-Klamath region (Fig. 3).

Comparisons of tree density estimates from our study plots with historical VTM plot data indicate that the percent departure in forest structure from historical conditions is relatively similar in the Sierra Nevada and Cascade-Klamath regions (Fig. 4). In unburned plots, the

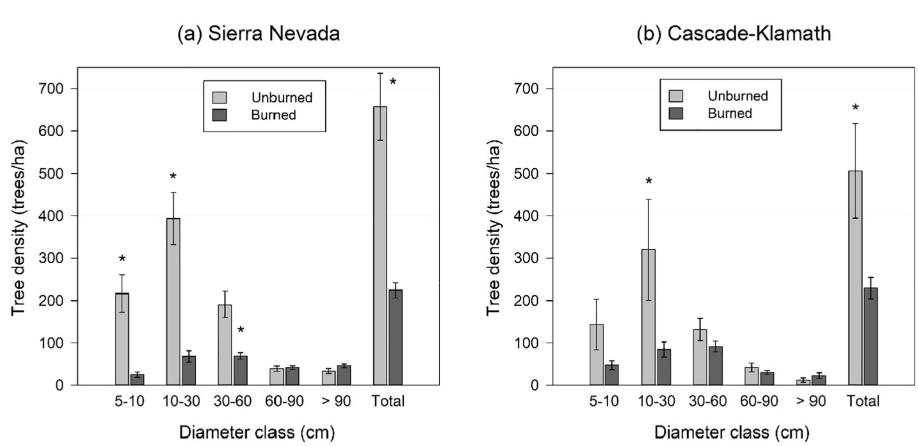

Fig. 2. Mean tree density by diameter at breast height size classes (cm) in the Sierra Nevada (a) and Cascade Klamath (b) regions. Error bars are ± 1 SE. Asterisks indicate a significant difference ($P < 0.05$) between burned and unburned plots in that size class based on Mann-Whitney U tests. Total tree density includes all trees ≥ 5 cm dbh.

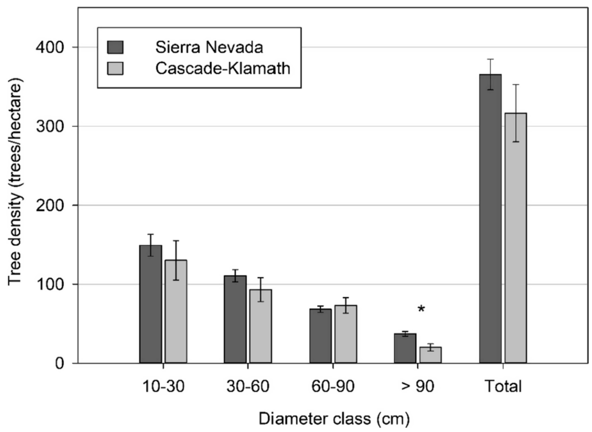

Fig. 3. Historical estimates of mean tree density by diameter at breast height size classes (cm) derived from VTM data in the Sierra Nevada and Cascade Klamath regions. Error bars are ± 1 SE. An asterisk indicates a significant difference (P < 0.05) between regions in a size class based on a Mann-Whitney *U* test. Total tree density includes all trees > 10 cm dbh.

percent departure averaged 44% in the Cascade-Klamath and 37% in the Sierra Nevada, indicating moderate departure (i.e., within 33–67% of historical estimates) in both regions. Both regions had positive departure values, indicating a surplus of trees, in the smallest size classes (<30 cm dbh). The Cascade-Klamath region had a greater deficit of large trees (-40% departure) in unburned plots than the Sierra Nevada region (-9% departure), and both regions had a similar deficit (-43% departure) of moderately-large (60–90 cm dbh) trees.

Total tree density in burned plots was lower than historical density estimates in both regions, corresponding to a departure of −39% in the Sierra Nevada and −28% in the Cascade-Klamath (Fig. 4). Most of this reduction in tree density was in the smaller size classes in the Sierra Nevada, while the Cascade-Klamath experienced greater relative losses of medium sized trees (60–90 cm dbh). Large trees (>90 cm dbh) were retained and had positive departure values (indicating greater densities of large trees relative to historical estimates) in burned plots in both regions (Fig. 4).

Differences in environmental and climatic variables between plots in the two regions are shown in Table 4. Although regionally adjusted elevation and litter cover did not differ, other plot-level variables, such as soil type, differed between the Sierra Nevada and Cascade-Klamath regions. Plots in the Cascade-Klamath region were generally situated on steeper slopes with a higher amount of rock and bare ground cover, and lower amounts of woody debris cover, than plots in the Sierra Nevada. Snowpack and actual evapotranspiration were also higher in the Cascade-Klamath region, suggesting greater biological availability of water and energy to red fir stands in the Cascade-Klamath. Climatic water deficit was higher in the Sierra Nevada, suggesting greater moisture stress for red fir stands in that region.

4. Discussion

We found that reintroduction of fire brought red fir forest conditions closer to historical estimates of stand density and fire return interval. Unburned plots in our study area are currently characterized by a fire deficit, with fire return intervals ranging from two to three times longer than historical estimates. Repeated burns restored fire return intervals to near reference values in our burned study plots in both the Sierra Nevada and Cascade-Klamath regions (Table 3). Across our study area, burned plots had significantly lower tree densities, including fewer small

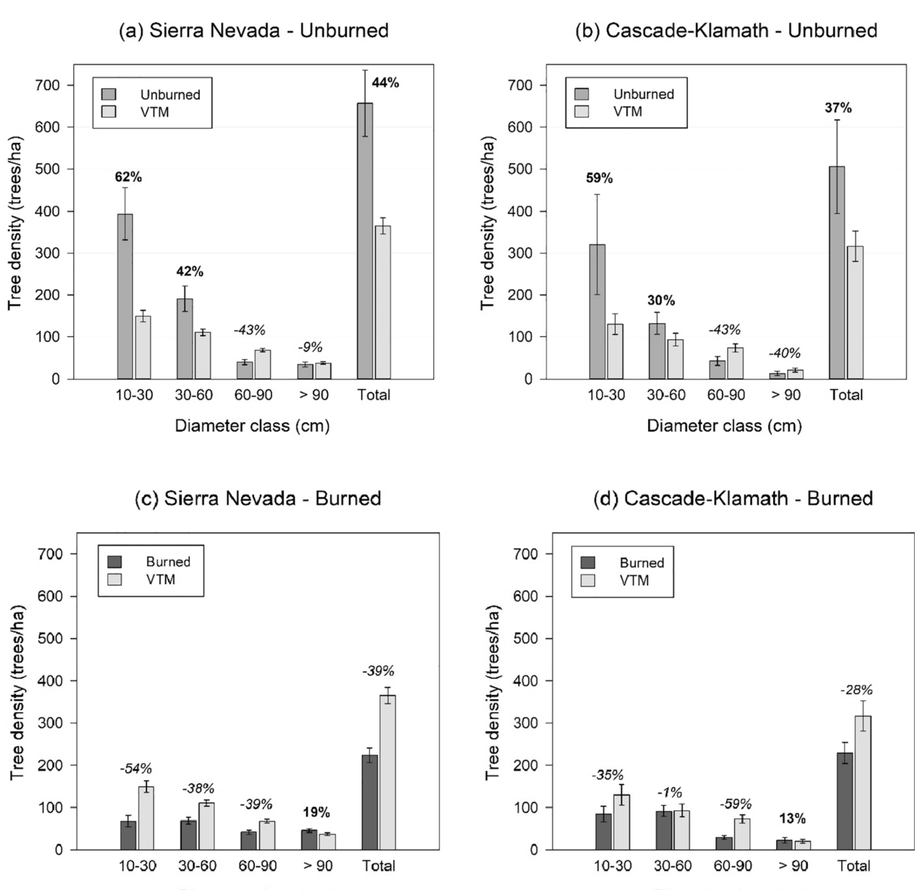

Fig. 4. Estimates of tree density by size class from unburned (top) and burned (bottom) plots and from historical VTM plots in the Sierra Nevada and Cascade-Klamath. Estimates of current percent departure from historical tree density VTM estimates are provided for each size class. Negative values (italics) indicate a deficit of trees in that size class, while positive values (bold) indicate a surplus. All y-axes are set to a maximum of 700 trees/ha to emphasize differences in tree densities between burned and unburned plots. Error bars are ± 1 SE.

Table 4
Mean values for environmental variables in red fir plots from the Sierra Nevada and Cascade-Klamath. Burned and unburned plots within each region are pooled. Different letters denote significant differences between regions.

Variable	Sierra Nevada	Cascade-Klamath
Elevation (m)[1]	2283	1938
Slope (%)	17[a]	31[b]
Northness (cos(asp))	−0.23	−0.04
% Rock cover	5[a]	17[b]
% Bare ground cover	6[a]	10[b]
% Woody debris cover	14[a]	5[b]
% Litter cover	75	68
Parent material	Granitic	Volcanic
Snowpack (mm/yr)	437[a]	1023[b]
AET (mm/yr)[2]	285[a]	366[b]
CWD (mm/yr)[3]	521[a]	341[b]

[1] Elevation range is 2034–2594 m (Sierra Nevada) and 1739–2256 m (Cascade-Klamath).
[2] AET: Actual evapotranspiration.
[3] CWD: Climatic water deficit.

trees (<30 cm dbh), than unburned plots that had not experienced a fire in over 100 years (Fig. 2). Our findings are largely consistent with other studies demonstrating the effectiveness of fire in restoring red fir stand structure in southern Oregon and California by reducing the density of small trees (Chappell and Agee 1996, Becker and Lutz 2016, Collins et al. 2016).

Two limitations of our study include the lack of pre-fire stand structure data and the exclusion of high severity burned areas in our study design. Although our sampling did cover a wide array of fires (Table 1) across a broad geographic area of California (Fig. 1) and included VTM data for historical reference conditions, our ability to detect temporal changes in red fir forest structure is limited by the lack of recent pre-fire stand structure data. Additionally, we excluded high severity burned sites that did not meet our minimum forest cover criteria (≥10% tree cover) that could affect stand structural patterns. However, any influence of high severity burned sites were likely to be negligible, because stand replacing fire occurred in only a small proportion of our total potential sampling area (≤5% of sites based on the remaining site selection criteria) and inclusion of high-severity areas would only further emphasize the differences in stand densities between burned and unburned sites (M. D. Meyer, unpubl. data).

Although we found that reintroducing fire to red fir forests restored structural and fire regime attributes to within the historical range of variation (i.e., variation in ecological characteristics and processes over scales of space and time that are appropriate for a given management application; Romme et al. (2013) across a wide geographic range, the effect of fire was most evident in the Sierra Nevada (Fig. 2). The percent difference in total tree density between unburned and burned plots was significantly greater in the Sierra Nevada region (77% difference) than in the Cascade-Klamath (53% difference). In the Sierra Nevada, burned plots had significantly lower densities of both small (<30 cm dbh) and medium sized trees (30–60 cm dbh), while only the density of small trees (<30 cm dbh) was significantly lower in burned plots in the Cascade-Klamath. The stronger fire effects we observed in Sierra Nevada red fir forests may be related to greater departure from reference fire return intervals in this region. Although regional differences in FRID values in unburned plots were relatively small (69% in the Sierra Nevada and 61% in the Cascade-Klamath), they did equate to a departure rating of high in the Sierra Nevada, but only a departure rating of moderate in the Cascade-Klamath. Stronger fire effects observed in the Sierra Nevada may also be linked to greater departure from historical structural conditions in this region (Fig. 4). Although unburned plots in both the Sierra Nevada and the Cascade-Klamath regions had a surplus of trees in the smallest size classes (<30 cm dbh) relative to historical estimates, unburned plots in the Sierra Nevada also had significantly higher density of medium sized trees (30–60 cm dbh) relative to VTM data.

Climatic differences between regions may have also promoted higher severity fire effects in the Sierra Nevada, resulting in higher mortality of small and medium sized trees. Our analysis of climatic variables collected over a 30-year period at each of our plot locations show that snowpack was higher in the Cascade-Klamath study plots, while climatic water deficit was higher in the Sierra Nevada plots (Table 4). These results suggest warmer and drier conditions for red fir stands in the Sierra Nevada, one of the primary drivers of increased fire activity (Abatzoglou and Williams 2016) and severity (Keyser and LeRoy Westerling 2017). Red fir forests have often been considered “climate limited” systems, where sufficient fuel exists for fire occurrence, but fuel moistures are typically too high for combustion (Agee 1993, Steel et al. 2015). However, there is evidence that some red fir forests are becoming more “fuel limited” where warming and drying conditions have increased ignition probabilities and the flammability of fuels. For example, Taylor et al. (2008) examined the relationship between climate variability and fire extent in upper montane forests of the southern Cascades for the period of 1700 through 1900 and determined that widespread burning was strongly associated with dry and warm conditions in the year of the fire, and that the strength of this relationship also varied over time in response to climatic variation over longer multidecadal time scales. Other studies in higher elevation forests in the Sierra Nevada have found that areas where fire was historically limited by moist conditions are now burning more frequently and at slightly higher severity, likely as a result of increased temperature, decreased snowpack, and drier late season conditions (Miller and Safford 2012, Schwartz et al. 2015). Our results also suggest that red fir forests in the Sierra Nevada may have become more “fuel limited” and prone to higher severity fire effects as a result of climatic warming (Steel et al. 2015), while those in the Cascade-Klamath still experience wetter conditions that generally limit fire activity (Williams et al. 2019) and reduce fire severity (van Mantgem et al. 2018).

Regional differences in other biophysical factors such as topography, soils, elevation, latitude, or geology may have also influenced the regional differences in fire effects and tree densities we observed at the plot scale (Meyer and North 2019, van Wagtendonk et al. 2018). For example, we encountered steeper slopes in the Cascade-Klamath than in the Sierra Nevada (Table 4), as well as a greater prevalence of volcanic soils in the Cascade-Klamath region and more granitic soils in the Sierra Nevada. Plots in the Cascade-Klamath region had higher cover of rock and bare ground, suggesting lower productivity and discontinuity of fuels. Variation in these and other biophysical factors have been shown to influence red fir stand structure and fire frequency (Parker 1992, Caprio and Graber 2000, Taylor 2000, Bekker and Taylor 2001, Caprio and Lineback 2002, Meyer and North 2019, Coppoletta et al. 2021).

We found that total tree density in burned plots was lower than historical density estimates in both regions, corresponding to a negative departure (indicating a lower amount than historically present) of −39% in the Sierra Nevada and −28% in the Cascade-Klamath (Fig. 4). The greatest departure was found in the smallest size classes (<30 cm dbh), corresponding to −54% lower density of small trees in the Sierra Nevada and −35% lower in the Cascade-Klamath relative to VTM data. Relatively lower densities of small trees in burned plots could be the result of higher severity fire effects from modern reintroduced fires that reduced smaller diameter tree density to below historical VTM values. Following a period of fire exclusion, reintroduction of fire may cause more tree mortality than historical fires or subsequent natural fires (Fulé and Laughlin 2007, Holden et al. 2007, Webster and Halpern 2010). For example, Becker and Lutz (2016) observed a significant reduction in red fir densities in the 10–30 cm dbh size class with a single-entry prescribed burn in the Sierra Nevada. Moreover, fire management approaches and outcomes may differ by region, with greater tolerance of more severe fire effects in the Sierra Nevada than the Cascade-Klamath, possibly due to greater opportunities to manage wildfires for resource objectives on National Park System lands or in larger wilderness areas in the southern and central Sierra Nevada (van Wagtendonk 2007, Meyer 2015, Miller et al. 2012).

Alternatively, the lower densities of small trees in burned plots relative to VTM plot data may also be a result of the timing and sampling methodology of the VTM study itself. Since fire suppression in California generally started around 1850 to 1870, by the time of the VTM study in the early 1930 s, many of the VTM plots may have already experienced between 60 and 80 years of fire exclusion (approximately two historical fire return intervals for red fir forests). This likely contributed to an increase in small and possibly some large (e.g., 60–90 cm dbh) size class tree densities in the VTM sampling compared with red fir forests with an intact fire regime within the historical range of variation. For example, small tree and total tree densities in burned plots from the Sierra Nevada (252 ± 159 and 92 ± 135 (mean ± SD) trees per hectare, respectively) were generally similar to the historical range of variation (260 ± 92 and 80 ± 49, respectively; Meyer et al. 2019, Meyer and North 2019); we suspected a similar pattern in the Cascade-Klamath, but there was insufficient historical stand data independent of this study for a robust comparison. This suggests that the extended period of fire exclusion preceding VTM plot data collection likely contributed to elevated small tree densities observed in this historical dataset, especially for the smallest 10–30 cm dbh size class.

Lower densities of small trees in burned plots in both regions may be adaptive in the future as climate change increases moisture stress, so that densities at or below the lower end of the historical range of variation may make red fir forests more resilient to predicted future climatic conditions. Although historical references provide insight into ecological patterns and processes that occur over long time frames (Safford et al. 2012), it is important to adjust the management implications of these references in light of current and predicted future conditions (Millar and Woolfenden 1999). The composition, distribution, and structural attributes of red fir forests managed with reintroduced fire regimes may diverge from historical conditions to allow them to persist well into the future (Lutz et al. 2010, Becker and Lutz 2016). Most red fir forests in our study area will be outside of their present climatic envelope by the end of the century, with pronounced reductions in geographic extent predicted by 2070–2100 (Meyer and North 2019, Coppoletta et al. 2021). Several models also project a relatively higher degree of climate vulnerability for red fir forests within the southern extent of their geographic distribution, at lower elevations, and in isolated populations (Meyer and North 2019). Despite these ominous model projections, red fir forests may persist in or adapt to areas of moderate climate exposure, potentially by maintaining lower density and more open canopy stands than were historically present during Euro-American settlement. Reestablishing natural fire regimes is considered one of the primary ways that forests can be managed to persist under future climate scenarios, specifically by reducing stand densities and reinstituting a key ecological process that builds adaptive capacity in forest ecosystems (van Mantgem et al. 2016, Stephens et al. 2020).

In both the Cascade-Klamath and Sierra Nevada regions we found that large trees (>90 cm dbh) were retained in burned plots and had positive departure values (indicating a surplus) relative to VTM data (Fig. 4). Although some studies have found that prescribed burning can cause high mortality rates among larger trees (Perrakis and Agee 2006, Dolanc et al. 2014), our results support other findings that reintroducing fire can, in some circumstances, reduce small tree density without killing large trees (Holden et al. 2007, van Mantgem et al. 2011, Becker and Lutz 2016). Large diameter trees have been lost from many modern forests (Lutz et al. 2009, Dolanc et al. 2014), potentially as a result of drought, insects and diseases, historic logging practices, and competition for limited resources in high-density forests generated through more than a century of fire exclusion (Das et al. 2011, van Mantgem et al. 2018, Fettig et al. 2019, Steel et al. 2021). Maintaining large trees is critical to provide structural heterogeneity (Franklin et al. 2002, Lutz et al. 2013), carbon sequestration (Stephenson et al. 2014), seed production (Keeton and Franklin 2005), wildlife habitat (Le Roux et al. 2018, Meyer et al. 2005) and moderation of the forest canopy microclimate (Rambo and North 2009). The retention of large trees in our burned study plots suggests that low and moderate severity fire can effectively maintain this critical component of red fir forest ecosystems across a broad geographic range. On the other hand, we observed lower numbers of large trees relative to VTM values in our unburned plots, particularly in the Cascade-Klamath region where the deficit of large trees (>90 cm dbh) was −40% (Fig. 4). This discrepancy may be a consequence of climate change (Dolanc et al. 2013, 2014) and its potential interaction with long-term fire exclusion (Lutz et al. 2009). Even under historical conditions, there were significantly fewer large trees in the Cascade-Klamath than in the Sierra Nevada region (Fig. 3), a pattern consistent with the statewide analysis of VTM data by McIntyre et al. (2015).

We found that departure from reference fire return intervals followed a similar pattern to departure from historical tree density in both of our study regions (Table 3, Fig. 4). Unburned plots were 61% departed from reference fire return intervals in the Cascade-Klamath and 69% departed in the Sierra Nevada. In these same plots, departure from VTM total tree density estimates were 37% in the Cascade-Klamath and 44% in the Sierra Nevada. These results confirm that estimates of departure based on a reference fire return interval generally correspond to estimates of departure based on historical structural conditions, such as tree density. Although the relationship between fire frequency and tree density is often assumed (Agee 1993, van Wagtendonk et al. 2018), our results suggest that incorporating information about departure of historical structural conditions may provide a more detailed and comprehensive evaluation of forest conditions than using departures of fire return intervals alone. For example, percent departure of total tree density in comparison to historical VTM data indicate that total trees per hectare were relatively similar in the Sierra Nevada and Cascade-Klamath regions. However, when we evaluated the departure of individual size classes separately, we were able to detect differences that were not apparent in total tree density data alone (Fig. 4).

In this study, we used departure metrics of regional fire return intervals and historical stand densities by diameter class to help explain differences in fire effects between red fir forests in the Sierra Nevada and the Cascade-Klamath regions. Further refinement of regional differences in fire return interval, both for red fir forests and other vegetation types, could lead to a more refined assessment of departure in specific areas, particularly in ecosystems with highly variable historical fire return intervals. In addition, using historical references for structural conditions (e.g., VTM data) in combination with regional fire return interval estimates, contributes to a more complete understanding of reference conditions and departure at both local and regional scales.

CRediT authorship contribution statement

Kyle E. Merriam: Investigation, Project administration, Writing – original draft. **Marc D. Meyer:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Project administration. **Michelle Coppoletta:** Investigation, Formal analysis, Writing – original draft. **Ramona J. Butz:** Investigation, Writing – review & editing. **Becky L. Estes:** Investigation, Writing – review & editing. **Calvin A. Farris:** Project administration, Writing – review & editing. **Malcolm P. North:** Conceptualization, Writing – review & editing.

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.

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