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Author(s): Chad T. Hanson and Dennis C. Odion
Source: Natural Areas Journal, 36(1):8-19.
Published By: Natural Areas Association
DOI: http://dx.doi.org/10.3375/043.036.0106
URL: http://www.bioone.org/doi/full/10.3375/043.036.0106

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RESEARCH ARTICLE

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Historical Forest Conditions within the Range of the Pacific Fisher and Spotted Owl in the Central and Southern Sierra Nevada, California, USA

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Natural Areas Journal 36:8–19

ABSTRACT: There is significant debate about restoration targets for ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests in the Sierra Nevada, California, USA. On one side are recommendations to create both extensive open and park-like pine forests, and to reduce high-severity fire occurrence by mechanical thinning of forests. These recommendations drive current management. On the other side are recommendations to manage landscapes for both dense, old forest, and complex early-seral forest that is created by both high-severity and moderate-severity fires characteristic of historical fire regimes. Our research suggests that the latter approach may best maintain forest associated with two imperiled species that are top management concerns of federal agencies in the Sierra Nevada: the California Spotted Owl (*Strix occidentalis occidentalis*) and the Pacific Fisher (*Pekania pennanti*). We used spatially extensive US Forest Service forest survey data from 1910 and 1911, and synthesized research from other parts of this region for comparison, to assess reference conditions in low/mid-elevation Sierra Nevada forests. We found that historical ponderosa pine and mixed-conifer forests had a mixed-severity fire regime, with an average of 26% high-severity fire effects, and varied more widely in species composition and density than suggested by previous research. Our findings are contrary to other reports using a very small subset (~6%) of the available data from these same 1910 and 1911 surveys. Therefore, we suggest that historical reference conditions of forests in the Sierra Nevada range of these species are not like that reported previously in other studies, and that mixed-severity fire, and forests defined by strong contrasts and dynamic natural processes, were characteristic of historical ponderosa pine and mixed-conifer forests of the western Sierra Nevada. Our analysis indicates that managing for both dense, old forests, and protecting complex early-seral forest created by high-severity fire, will likely advance conservation and recovery of the Spotted Owl and Pacific Fisher, while current management direction may exacerbate threats.

Index terms: mixed-conifer, mixed-severity fire, Pacific Fisher, ponderosa pine, Spotted Owl

INTRODUCTION

Historical fire regimes of mixed-conifer and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forests of the northern Sierra Nevada and southern Cascades in California have been described as mixed-severity, and often included substantial portions of high-severity fire effects (Leiberg 1902; Show and Kotok 1924, 1925; Beaty and Taylor 2001; Bekker and Taylor 2001, 2010; Odion et al. 2014). However, the western slope of the central and southern Sierra Nevada has been less examined in this regard. Some recent articles have hypothesized that Sierra Nevada ponderosa pine and mixed-conifer forests had low/moderate-severity fire regimes historically (Stephens et al. 2013; Fulé et al. 2014), and a modeling study assumed very low high-severity fire levels in historical forests (Mallek et al. 2013). In contrast, an analysis of US General Land Office surveys from the mid/late-1800s found a mixed-severity fire regime and a wide range in forest density and composition (Baker 2014).

Two recent studies, using a subset of the 1911 portion of the "1910/1911 Forest Survey" conducted in this area (USFS 1910-1911), described generally open forest conditions hypothesized to have been maintained by frequent, low-severity fire, and noted that there was no clear evidence of high-severity fire occurrence (Scholl and Taylor 2010; Collins et al. 2011). These results were from 17 and 28 plots, respectively (combined, ~6% of the available data), in partially overlapping study areas of 2125 ha and 4000 ha on the western edge of Yosemite National Park (in an area that was, in 1911, part of Stanislaus National Forest); the subset of forest selected was not a statistical sample of the landscape. Mechanical thinning across much of the Sierra Nevada has been suggested by some to restore these open conditions, prevent higher-severity fire from affecting dense, old conifer forests, and increase the pine component (Stephens and Ruth 2005; North et al. 2009; Collins et al. 2011; Scheller et al. 2011).

However, two imperiled wildlife species native to this area, the California Spotted Owl (*Strix occidentalis occidentalis* de Vesey) and the Pacific Fisher (*Pekania pennant* Rhoads), are strongly associated with dense, mature/old forest with high canopy cover and abundant understory trees and snags for nesting/roosting (for Spotted Owls) and denning/resting (for Fishers) (Verner et al. 1992; Zielinski et al. 2005, 2006; Purcell et al. 2009; Underwood et al. 2010). The forests selected (selection, as manifested by preference—i.e., disproportional use relative to abundance: Hall et al. 1997) by these species tend to have a substantial component of ponderosa pine (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana* Dougl.), but are often dominated by white fir (*Abies concolor* Gordon & Glend.) and incense-cedar (*Calocedrus decurrens* Torr.) (Underwood et al. 2010). Recently, Fisher den sites were mostly found to occur in white fir and incense-cedar (R. Sweitzer, wildlife ecologist, The Great Basin Institute, unpubl. data: http://snamp.cnr.berkeley.edu/static/documents/2011/10/28/SNAMP_2011_Annual_Meeting_Presentation_AM.pdf).

Moreover, a radiotelemetry study in Sequoia National Forest found that, when distance from nest and roost sites was taken into account, California Spotted Owls in the McNally fire area selected unlogged high-severity fire areas—a condition most strongly distinguished by high snag basal area and shrub cover—for foraging (Bond et al. 2009). A radiotelemetry study of Northern Spotted Owls (*Strix occidentalis caurina* Merriam) by Clark (2007: Figure 6.2) found that, after fire, the owls foraged in unlogged moderate- and high-severity fire areas occurring in pre-fire nesting/roosting/foraging habitat (generally, pre-fire dense, old forest) more than expected based upon abundance, and foraged in post-fire logged areas less than expected. They noted that the limited foraging documented within post-fire logging units was generally in logging-exclusion zones, such as riparian areas. Roberts (2008) found 60% higher reproduction of California Spotted Owls in unlogged mixed-severity fire areas than in unburned forests, and Lee et al. (2012) found that mixed-severity fire, averaging 32% high-severity fire effects, did not reduce California Spotted Owl occupancy in a study of 41 territories. In territories with mostly high-severity fire, 63% were occupied 5–7 years post-fire (Lee et al. 2012). Similarly, Pacific Fishers selected mixed-severity fire areas over unburned forest when near fire edges, and the frequency of detections (scat) in dense, old forest that experienced moderate/high-severity fire was nearly identical to the detection frequency in dense, old unburned forest (Hanson 2013). The proportion of high-severity fire effects at detection locations within fire boundaries was also significantly higher than at random locations within fires (Hanson 2013).

The association with mixed-severity fire areas by these two imperiled wildlife species is likely tied to the enhanced small mammal prey base in complex early-seral forests rich with snags, downed logs, montane chaparral, and dense pockets of natural conifer regeneration (Bond et al. 2013; Hanson 2013). Mechanical thinning has been found to adversely affect occupancy for California Spotted Owls (Seamans and Gutiérrez 2007). Owl populations have been declining in research study areas managed with extensive thinning on national forests (Conner et al. 2013; Tempel and Gutiérrez 2013), while they have been stable or increasing on protected national park lands (Conner et al. 2013). Likewise, Fishers have been found to avoid areas within 200 m of mechanically thinned areas in the Sierra Nevada (Garner 2013).

Thus, there is a need to better determine the historical reference forest conditions in the Sierra Nevada in general, and the forests inhabited by California Spotted Owls and Pacific Fishers in particular, to resolve the inconsistency between habitat currently used and theoretical historical conditions. On the one hand, these species select dense (Zielinski et al. 2006; Seamans and Gutiérrez 2007; Purcell et al. 2009), fir/cedar-dominated forests (Underwood et al. 2010), and forage in unlogged high-severity fire areas (Bond et al. 2009; Bond et al. 2013; Hanson 2013, 2015). On the other hand, some studies conducted at relatively small spatial scales indicate that historical forests were fairly open and sparse, with only lower-severity fire effects (Scholl and Taylor 2010; Collins et al. 2011), and were commonly dominated by ponderosa pine and Jeffrey pine, even at middle elevations (Collins et al. 2011).

The 1910/1911 Forest Survey (USFS 1910–1911) covered a combined area of 65,296 ha in the central and southernmost portions of the Stanislaus National Forest (including a small area that is now included within Yosemite National Park), and included data on understory structure (conifers <15.2-cm dbh, and shrub cover), as well as fire effects, and species composition. Thus, there is an opportunity to investigate a much larger portion of the historical landscape in ponderosa pine and mixed-conifer forests of the central and southern Sierra Nevada than in previous studies and to compare results with spatially limited assessments within the same landscape. The 1910/1911 surveys also allow an assessment of the extent of high-severity fire and vegetation conditions associated with potential for high-severity fire, such as shrub cover and conifer regeneration (Leiberg 1902; Show and Kotok 1924; Brown et al. 2003; Odion et al. 2010), in unlogged forests generally before the effects of fire suppression.

Our goal was to describe the historical fire regime and forest conditions over the whole landscape covered in the 1910/1911 Forest Survey data and compare these findings with those obtained from analyzing select, spatially limited areas within this landscape. Specific objectives in this study were to: (1) determine whether forests dominated by ponderosa pine had lower levels of high-severity fire than fir/cedar forests; (2) estimate the high-severity fire rotation interval; (3) determine whether forests dominated by ponderosa pine had lower understory (shrubs and conifer seedlings/saplings) density than fir/cedar forests, and whether ponderosa pine prevalence changed on wetter/cooler northerly slopes or at higher elevations within the mixed-conifer zone; and (4) determine whether live conifer density varied with differing levels of high-severity fire.

METHODS

Study Sites

The 1910 portion of the study area comprised 9328 ha of ponderosa pine and mixed-conifer forest in the central portion of the Stanislaus National Forest, ranging in elevation from 1221 to 2416 m (Figure 1). The 1910 survey included data on logging history, fire effects, and conifer species composition. The 1911 portion of the study area comprised 55,968 ha of ponderosa pine and mixed-conifer forest in

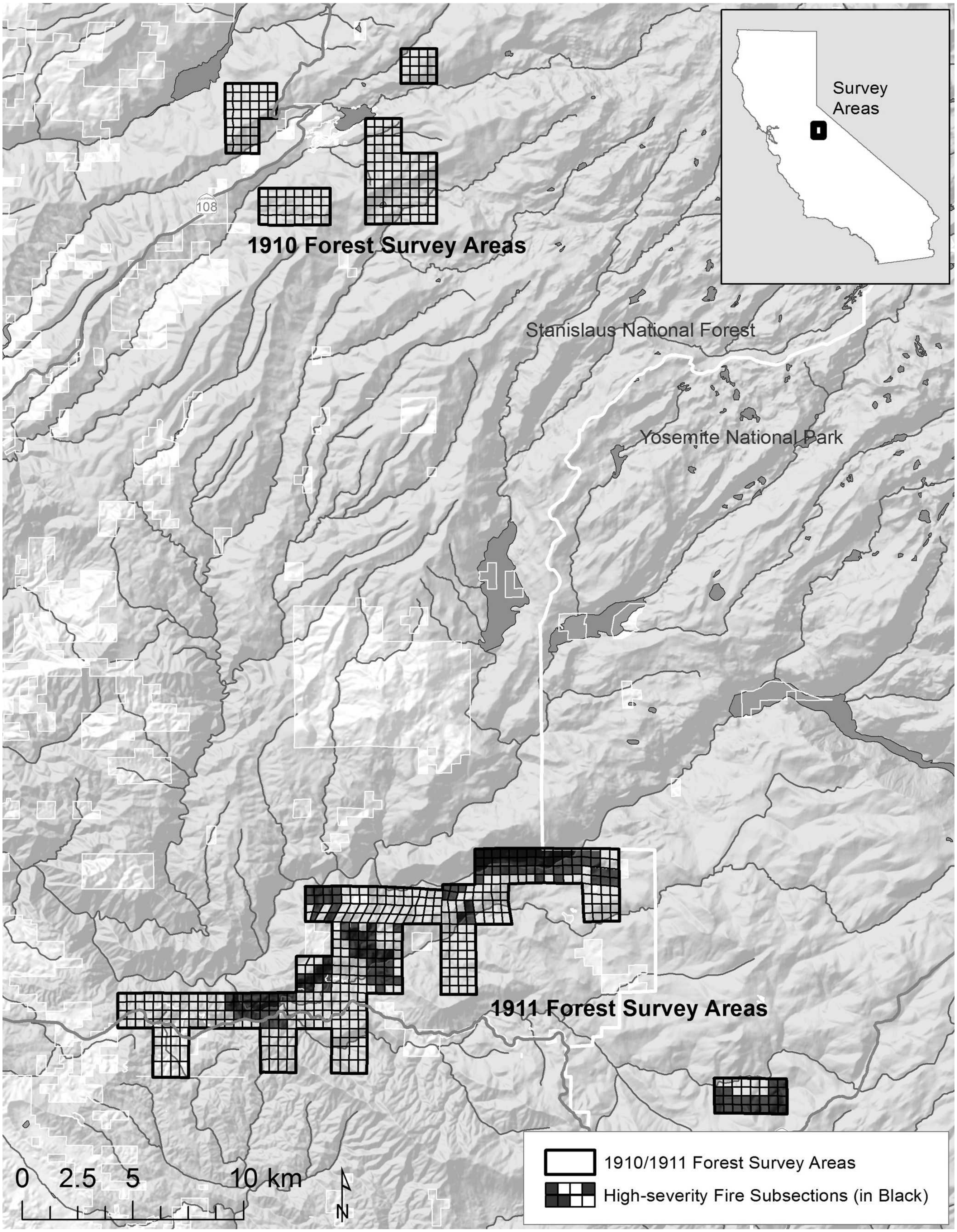

Figure 1. The 1910 and 1911 portions of the USFS forest inventory study area, western slope of the central and southern Sierra Nevada, California, USA.

the southern end of the Stanislaus National Forest, including the western edge of what is now Yosemite National Park (Figure 1). Plot locations with complete surveys in the 1911 study area ranged from 725 to 1989 m in elevation. Plot data included information on logging history, fire effects, conifer species composition, percent shrub cover, and density of conifer seedlings and saplings. Another distinct portion of the Stanislaus National Forest was surveyed in 1912, but there were no notes about previous logging history so we did not include this portion of the survey in the analysis. At the lower elevations of the study area, the forest is dominated by ponderosa pine, mixed with California black oak (*Quercus kelloggii* Newb.), canyon live oak (*Quercus chrysolepsis* Liebm.), and scattered gray pine (*Pinus sabiniana* Dougl. ex D. Don.); at the intermediate elevations, the forest is composed of a mixture of ponderosa pine, Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), sugar pine, incense-cedar, Douglas-fir (*Pseudotsuga menziesii* Franco), and white fir, with some California black oak and canyon live oak; and at the higher elevations of the study area, it is composed of white fir, incense-cedar, sugar pine, ponderosa pine, Jeffrey pine, a small amount of red fir (*Abies magnifica* Andr. Murray) and lodgepole pine (*Pinus contorta* Louden).

Surveys

Surveys were conducted at two scales: 1.6-hectare (ha) plots (belt transects) through each of the 16.2-ha subsections surveyed; and 259.1-ha (640-acre) sections. At the plot scale, the 1910/1911 Forest Survey recorded timber volume by conifer species, and also estimated percent shrub cover (except in the 1910 portion, which did not record shrub cover extent in subsections with merchantable timber). Only plots with merchantable timber were surveyed in the study area in 1910 and 1911.

At the 259.1-ha section scale, surveyors recorded average conifer seedling and sapling density in forested portions of each section in the 1911 portion, but not the 1910 portion. Saplings were trees <15-cm dbh. Seedlings were not explicitly defined, in terms of size, but the typical definition then, and now, for seedlings is a tree less than breast height (i.e., less than 1.37 m in height). In the 259.1-ha section surveys, for subsections with no merchantable timber, surveyors recorded cover type, noting whether subsections were comprised of montane chaparral and early-seral conifer regeneration, or other cover (e.g., rock outcroppings), and made explicit notes of fire effects in conifer forest, as well as whether any previous logging had occurred on a given section. There were very few sections in which logging had occurred in this area as of 1910 and 1911, and we excluded these from the analysis (which also excluded subsections and, therefore, plots, in which logging had occurred). In both portions of the study area, not all sections were surveyed. In some sections, surveyors did not record data for all subsections, or did not record fire effects on some subsections. We excluded these incomplete sections from our analysis.

Historical Fire Regimes

For the purposes of this study, we divided the forest into three strata: ponderosa pine (>85% ponderosa pine, by timber volume); mixed-conifer/pine (50–85% ponderosa pine); and mixed-conifer/fir (10–49% ponderosa pine).

We assessed high-severity fire occurrence in the study area based upon field notes in the 1910/1911 Forest Survey. This determination was made based on evidence, or lack of evidence, of high-severity fire across entire 16.2-ha subsections (surveyors did not make records of fire effects at finer spatial scales than this) in each of the three forest strata. The 1910/1911 Forest Survey field notes contained a required field on survey data sheets pertaining to fire effects, and surveyors included specific notes on fire severity, or lack of fire evidence.

To verify that any subsections recorded in 1910/1911 as conifer forests in which high-severity fire occurred actually represented potential conifer forest, we quantified the extent to which any such areas have regenerated back to conifer forest in recent times. For this we used the California Wildlife Habitat Relationships (CWHR) vegetation database (www.dfg.ca.gov/biogeodata/cwhr/) to calculate the proportion of the historical high-severity fire area that is currently vegetated with conifer forest.

We only recorded areas as forests that experienced high-severity fire if: (1) surveyors explicitly included notes about 'severe' fire in conifer forest; and (2) the affected subsections were recorded as having no merchantable timber at the time of the surveys, with surveyors noting dominance by brush and conifer seedlings/saplings. We compared the proportion of plots with no merchantable timber, resulting from high-severity fire effects in these conifer forests, among the three conifer forest strata, using a Chi-square test for trends in binomial proportions (Rosner 2000) to determine whether this proportion changed with increasing proportion of ponderosa pine. We also evaluated the results in the context of other previous studies examining the proportion of high-severity fire in these forest types (in historical data sets and current studies either analyzing historical data or using stand structure or age to estimate past high-severity fire effects) within the Sierra Nevada management region, which consists of the Sierra Nevada, the portion of the southern Cascades in California, and the Modoc Plateau (Miller et al. 2012).

Next, we estimated the high-severity fire rotation interval (years divided by the proportion of forest area affected by high-severity fire) in these forests. We restricted this analysis to forests of the west side of the central and southern Sierra Nevada (south of the Middle Fork of the American River) that had not been previously logged (Wilderness Areas, Inventoried Roadless Areas, National Parks, and Wild and Scenic River Corridors) to avoid any potentially confounding effect of past timber removal. Since the surveyors for the 1910/1911 Forest Survey recorded high-severity fire areas as nonmerchantable if dominant trees were <31-cm dbh, we used US Forest Service Forest Inventory and Analysis (FIA) data to determine the time required for dominant and codominant trees to reach 31-cm dbh (rounding up to the nearest decade, to be conservative), and also determined whether there was a correlation between diameter and age to check the validity of this approach. FIA records various metrics in fixed plots, with approximately one plot for every 2400 ha (http://www.fia.fs.fed.us/tools-data/). The high-severity fire rotation interval was defined as the time period in years, t (here, the number of years for trees to reach 31-cm dbh after stand initiation), divided by the proportion of forest experiencing high-severity fire, p_h (here, the proportion of subsections with high-severity fire and no remaining merchantable timber): t / p_h.

Historical Forest Structure and Composition

To determine whether shrub cover changed with increasing proportion of ponderosa pine, we used a Chi-square test for trends in binomial proportions (Rosner 2000) to compare the proportion of 259.1-ha sections (within merchantable conifer forest as of 1911 surveys) above and below the mean percent shrub cover in all conifer forest. Similarly, to determine whether conifer seedling/sapling density changed with increasing proportion of ponderosa pine, we again used a Chi-square test for trends in binomial proportions to compare the proportion of 259.1-ha sections (within merchantable conifer forest as of 1911 surveys) above and below the mean conifer seedling/sapling stems/ha in all conifer forest.

We used a Chi-square 2 × 2 contingency test (Rosner 2000) to determine whether southerly slopes had a greater relative abundance of pines (*Pinus* spp.) than did northerly slopes. We conducted the analysis within the elevation band analyzed in Collins et al. (2011): 1460–2130 m, where pines, firs and cedar tend to intermix in today's forests. Following Underwood et al. (2010), northerly slopes were defined to represent the cooler and wetter aspects, centered on an aspect of 45° (north and east), and southerly slopes were defined to represent the warmer and drier aspects, centered on an aspect of 225° (south and west). Northerly slopes had ≥50% of the area in the plot on north- and east-facing slopes, while southerly slopes had >50% of the area in the plot on south- and west-facing slopes. Plots were categorized as primarily pine (ponderosa, Jeffrey, and sugar pine, with occasional small amounts of lodgepole pine at higher elevations) if ≥50% of the conifer timber volume was comprised of *Pinus* species, and were categorized as primarily non-pine if <50% of the conifer timber volume was comprised of *Pinus* species (white fir, incense-cedar, Douglas-fir, and some red fir at higher elevations).

We used a Spearman's rank correlation test (Rosner 2000) to determine whether the higher elevations (in 50-m increments) correlated to higher proportions of non-pine conifers in terms of timber volume (board feet). We restricted this analysis to the same elevation band (1460–2130 m) in mixed-conifer forests.

Last, we conducted an a posteriori analysis using a t-test for two independent samples with unequal variances (Rosner 2000) to determine whether the mean plot-scale timber volume was different between the 1910 and 1911 portions of the study area. The former had no evidence of large high-severity fire patches (i.e., covering entire subsections), whereas the latter had extensive evidence of such high-severity fire. We restricted this analysis to the overlap in elevation between the two portions of the study area: 1221–1989 m.

RESULTS

Historical Fire Regimes

There were 166 subsections available for this analysis in the 1910 portion, and 480 subsections in the 1911 portion, which yielded a total of 646 plots. The 1910/1911 Forest Survey field data contained extensive evidence that a mixed-severity fire regime in ponderosa pine and mixed-conifer forests occurred on the western slope of the central/southern Sierra Nevada prior to modern fire suppression, as described below. Surveyors often explicitly recorded in their data forms (in the required field regarding fire effects) that "severe" fire had killed all of the timber in many subsections within a given section such that there were many areas in 1910/1911 that were characterized by brush and young (nonmerchantable) conifer regeneration. Within the 7773 ha of forest with complete surveys (representing 480 plots) in the 55,968-ha 1911 portion of the study area, 6640 ha were recorded as either conifer forest, or early-seral conditions resulting from high-severity fire in conifer forest (i.e., excluding montane chaparral areas that did not clearly result from high-severity fire). Within this 6640-ha area, 37% (2429 ha) was recorded as having been affected by high-severity fire, such that there was no merchantable timber in the subsections (Figure 1). None of the subsections in the 2688-ha forested area with complete surveys in the 1910 portion of the study area were affected by high-severity fire (Figure 1) across the forest subsections (i.e., at least some merchantable timber remained in every forest subsection). All areas included in this analysis were unlogged, according to field notes.

Where there was no clear evidence of past high-severity fire in subsections vegetated by montane chaparral, surveyors recorded cover type and evidence of previous fires, but did not describe such past fire as being severe fire that killed the merchantable timber across entire subsections. In addition, surveyors did not record data in sections without merchantable timber, so there may have been some larger areas of high-severity fire—covering one or more entire 259.1-ha sections—that were not recorded in the 1910/1911 Forest Survey (Figure 1). Therefore, our results regarding high-severity fire occurrence are likely conservative. Subsections recorded in 1910/1911 as having montane chaparral from high-severity fire in previously mature conifer forest currently have 62% conifer forest cover (oak/shrubs dominate the remainder).

Our results were not consistent with the hypothesis that lower levels of high-severity fire characterized forests dominated by ponderosa pine in the Sierra Nevada. We found no evidence of a significant trend toward decreasing high-severity fire proportion as the amount of ponderosa pine in stands increased ($\chi^2 = 2.45$, $P = 0.294$, df = 2, $n = 410$ plots). High-severity fire proportions in the 1911 survey area were 67%, 22%, and 48% in mixed-conifer/fir, mixed-conifer/pine, and ponderosa pine forests, respectively, and averaged 37% overall. We used only the 1911 portion for this analysis because: (1) it was unclear how differing high-severity fire levels in the three forest strata could be assessed in the 1910 portion when there was no high-severity fire recorded across any individual subsection in that portion of the study area; and (2) only a portion of the elevation bands of the 1910 and 1911 parts of the study area overlapped, and an even comparison using the overlapping portion of the elevation band would have eliminated most of the high-severity fire records in ponderosa pine forest, undermining the analysis. The combined proportion of recorded high-severity fire effects, including both the 1910 and 1911 portions of the study area, was 26%. These results are within the range of those from previous studies of mixed-conifer and ponderosa/Jeffrey-pine forests in other portions of the USFS Sierra Nevada management region (Table 1).

There was a significant correlation between the diameter and age of dominant/codominant trees ($r = 0.74$, $t = 41.94$, $P < 0.001$, df = 1439, $n = 1441$ trees) (Figure 2). Based on this regression, the time required from stand initiation to 31-cm dbh was 60 years. The high-severity fire area (2429 ha) divided by total forest area (1910 and 1911) with complete surveys (9328 ha) yielded a proportion of 0.26. Thus, the estimated high-severity fire rotation interval in ponderosa pine and mixed-conifer forests in the study area was 60/0.26 = 231 years.

Historical Forest Structure and Composition

We found no trend in decreased shrub cover as the amount of ponderosa pine in stands

Table 1. Historical high-severity fire proportions in mixed-conifer and ponderosa/Jeffrey-pine forests in various portions of the Sierra Nevada management region of California (Sierra Nevada, southern Cascades in California, and Modoc Plateau) and nearby regions.

Study	Location	High-severity fire proportion
Leiberg (1902)	Northern Sierra Nevada	>8% (ponderosa pine) and >20% (mixed-conifer) [a]
Show and Kotok (1925)	California, including the Sierra Nevada	14% [b]
Minnich et al. (2000)	Northern Baja California, Mexico	16% [c]
Beaty and Taylor (2001)	Southern Cascades	18–70%, depending on slope aspect
Bekker and Taylor (2001)	Southern Cascades	52–63%
Beaty and Taylor (2008)	Eastern Sierra Nevada	7–36%, depending on slope position
Baker (2012)	Eastern Cascades, Oregon	16% (ponderosa pine) and 23% (mixed-conifer)
Baker (2014)	Western Sierra Nevada	31–39%

[a] Hanson (2007) used digitized versions of Leiberg's mapping of high-severity fire areas in unlogged forests (areas mapped as logged were excluded), overlaid with forest type, to determine high-severity fire percentages in patches >32.4 ha. Because these percentages do not include patches <32.4 ha, they are underestimates (Hanson 2007). Leiberg (1902) explicitly noted that if high-severity fire patches <32.4 ha were included the amount of high-severity fire would be "considerably increased" (Leiberg 1902: p. 41). Mallek et al. (2013: Table 5) referenced this study with regard to 8% high-severity fire effects. However, this figure was based only on the narrowest subset of high-severity fire effects: areas with 100% tree mortality (Leiberg 1902: p. 41). Leiberg specifically mapped areas of 75–100% timber volume mortality (in patches >32.4 ha), corresponding to high-severity fire areas, and such areas comprised a much larger acreage than the areas of 100% mortality (Leiberg 1902: Plate VII; Hanson 2007).

[b] Show and Kotok (1925: p. 3, footnote 2) noted that one acre out of every seven, on average, was montane chaparral habitat resulting from previous high-severity fire. Mallek et al. (2013: Table 5) referenced this study with regard to 5% high-severity fire effects in ponderosa pine-dominated forests. However, the reference to this proportion (5%) was in regard to the percent of timber volume typically killed in "surface fire," not crown fire, and even for typical fires the authors estimated an ultimate timber volume mortality level of 14% (Show and Kotok 1925: p. 3).

[c] Mallek et al. (2013: Table 5) referenced this study with regard to 4–8% high-severity fire effects. However, Minnich et al. (2000) used "stand-replacement" fire, defined as 90–100% mortality of overstory trees, as the highest fire severity category, which comprised 16% of all fire effects. The standard, and most currently accepted, definition of high-severity fire is RdNBR values (from satellite imagery) >641 (Miller and Thode 2007), and this corresponds to approximately 70% basal area mortality, based upon field validation plots (Hanson et al. 2010: Table 1). Thus, the 16% figure from Minnich et al. (2000) is likely an underestimate of the high-severity fire proportion.

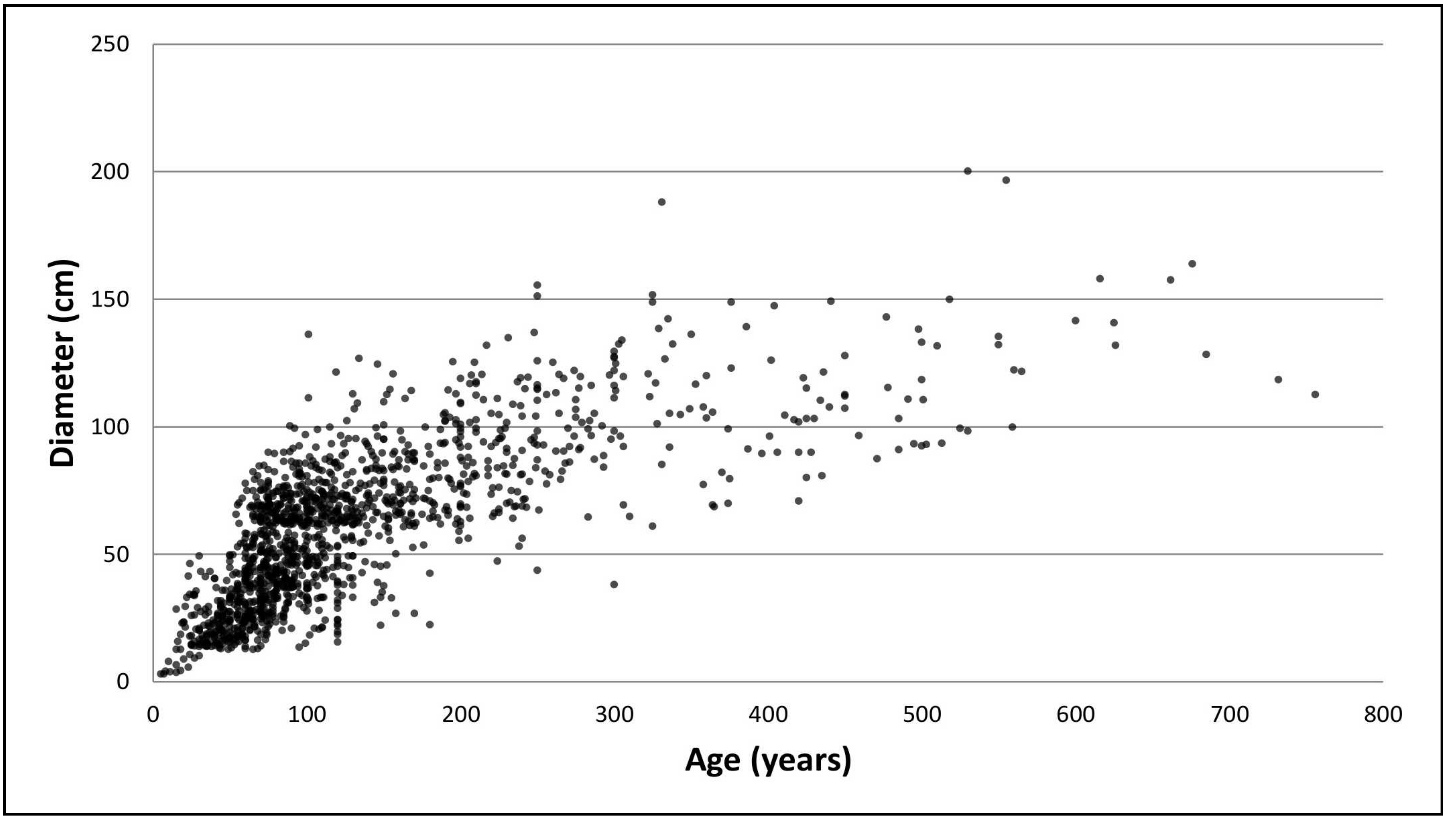

Figure 2. Diameter (cm dbh) and age (years) of dominant and codominant trees in ponderosa/Jeffrey-pine and mixed-conifer forests of the west side of the central and southern Sierra Nevada in unlogged forests.

increased ($\chi^2 = 1.13$, $P = 0.568$, df = 2, n = 30 sections) in the 1911 portion of the study area (as discussed above in the Methods, surveyors did not record shrub cover in the 1910 portion of the study area). Shrub cover comprised 40%, 29%, and 75% of the area in mixed-conifer/fir, mixed-conifer/pine, and ponderosa pine forests, respectively, and these forest strata combined had 34% shrub cover in merchantable conifer forest (range = 6–80%).

Similarly, we found no trend in decreased conifer seedling/sapling density as the amount of ponderosa pine in stands increased in the 1911 portion of the study area ($\chi^2 = 0.13$, $P = 0.937$, df = 2, n = 30 sections) (as discussed above in the Methods, surveyors did not record mean conifer seedling/sapling density in the 1910 portion of the study area). Conifer seedling density averaged 673/ha (range = 37–4081/ha), and sapling density averaged 164/ha (range = 7–1386/ha) in the three conifer strata combined.

In mixed-conifer forests, at 1460–2130 m in elevation, there was a significant relationship between aspect and pine dominance, where south-facing slopes had more than twice as many (59 versus 26) pine-dominated plots ($\chi^2 = 6.31$, $P = 0.012$, df = 1, n = 162 plots). However, contrary to our expectations, plots dominated by fir and cedar did not show an effect of aspect, with approximately the same number on southerly slopes as on northerly slopes (40 on southerly slopes, and 37 on northerly slopes). Overall (southerly and northerly slopes combined), pine and fir/cedar plots were nearly evenly split in mixed-conifer forests, at 52% and 48%, respectively.

The proportion of timber volume comprised by pine decreased significantly with increasing elevation within the mixed-conifer zone, 1450–2150 m ($r_s = -0.82$, $P < 0.001$, df = 12, n = 14; elevation increments of 50 m). Dominance shifted from primarily pine to primarily fir and cedar at approximately 1850 m in elevation (Figure 3). Our review of historical data sets (including modern analyses of historical data) in the mixed-conifer zone of the western Sierra Nevada also indicates a high proportion of surveyed areas were dominated by non-pine conifers, mostly white fir and incense-cedar (Table 2).

Finally, within the overlap of elevation between the 1910 and 1911 portions of the study area (1221–1989 m), the mean timber volume (board feet/ha) was significantly higher in the 1910 portion (75,141 bf/ha, SD = 42,466, n = 105 plots), which did not have evidence of extensive high-severity fire, than in the 1911 portion (31,658 bf/ha, SD = 19,735, n = 103 plots), which had substantial occurrence of high-severity fire ($t = 9.50$, $P < 0.001$, df = 148).

DISCUSSION

Based on evaluation of all forest inventory data conducted in 1910 and 1911 by the US Forest Service, we found considerable evidence for substantial portions of large areas affected by high-severity fires

Table 2. Historical conifer species composition in ponderosa pine and mixed-conifer forests of the Sierra Nevada.

Study	Location	Composition (trees/ha)
Leiberg (1902)	Western Sierra, northern	In four unlogged watersheds:[1]
		35% pine, 63% non-pine conifer, 3% oak
Cooper (1906)	Western Sierra, northern	
	761–1218 m elevation	50% pine, 40% non-pine conifer, 10% oak
	1371–1523 m elevation	33% pine, 62% non-pine conifer, 5% oak
	Western Sierra, southern	
	1218 m elevation	61% pine, 34% non-pine conifer, 5% oak
	1523 m elevation	33% pine, 66% non-pine conifer, 1% oak
Hodge (1906)	Western Sierra, northern	
	761–1218 m elevation	50% pine, 40% non-pine conifer, 10% oak
	1371–1523 m elevation	44% pine, 52% non-pine conifer, 4% oak
	Western Sierra, central	
	1523 m elevation	26% pine, 74% non-pine conifer
	Western Sierra, southern	
	1218 m elevation	61% pine, 34% non-pine conifer, 5% oak
	1523 m elevation	38% pine, 60% non-pine conifer, 2% oak
	~1800–2000 m elevation	24% pine, 76% non-pine conifer
Stephens (2000)[2]	Central/northern Sierra	
	"average" mixed-conifer	51% pine, 43% non-pine conifer, 6% oak
	"large" mixed-conifer	20% pine, 80% non-pine conifer
North et al. (2007)	Southern Sierra	
	1900–2600 m elevation	49% pine, 51% non-pine conifer
Lydersen et al. (2013)	Central Sierra	
	1740–1805 m elevation	17–25% pine, 75–83% non-pine conifer
Baker (2014)	Northern Sierra	30% pine, 38% non-pine conifer, 29% oak
		2% other species
	Southern Sierra	46% pine, 28% non-pine conifer, 22% oak,
		3% other species

[1] Feather River, South Fork, between Lexington Hill and Strawberry Valley; Yuba River; American River, North Fork; American River, Middle Fork.

[2] These data were synthesized from plot data gathered by George B. Sudworth of the US Geological Survey in 1899 (Stephens 2000).

(Figure 1). Moreover, it was clear that mixed-severity fire regimes were characteristic of ponderosa pine and mixed-conifer forests of the western slope of the central and southern Sierra Nevada before fire suppression. Therefore, our findings were contrary to hypotheses articulated in North et al. (2009), Collins et al. (2011), Fulé et al. (2014), Stephens et al. (2013), and recent modeling (Mallek et al. 2013) that high-severity fire was relatively rare in forest in this mountain range before fire suppression, and ranged from 4–13% (Mallek et al. 2013). Some other recent studies, overlapping portions of our study area, also reported low levels of historical high-severity fire (Collins et al. 2015; Harris and Taylor 2015), but were based upon 1911 survey forms (Form 321a) pertaining only to stands of merchantable timber, and did not include the abundant records of merchantable timber stands entirely killed by high-severity fire that were contained on different forms (Form 322) in the same 1911 Stanislaus National Forest data set. Another recent study, Stephens et al. (2015), also used 1911 survey forms pertaining only to stands of merchantable timber, and did so in an area (a small area of the Greenhorn Mountains, about 235 km south of our study area) where 1911 surveyors simply did not address the issue of stands completely killed by fire in their

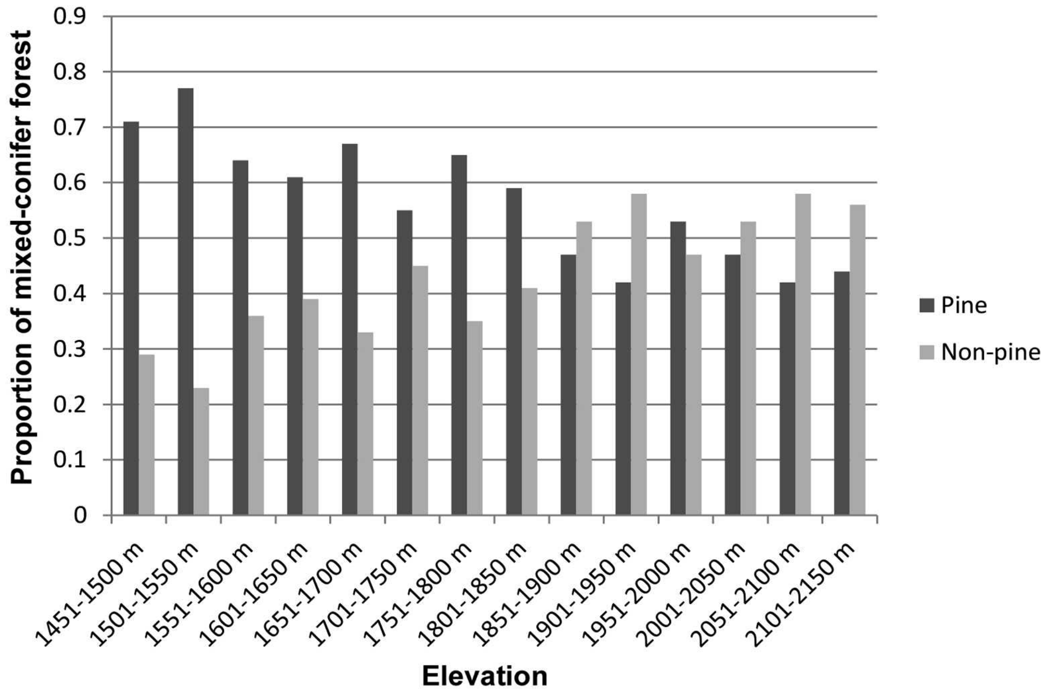

Figure 3. Proportions of pine and non-pine conifers with increasing elevation in mixed-conifer forests from the 1910/1911 survey data, western slope of the central and southern Sierra Nevada, California, USA.

survey notes. However, immediately after those 1911 surveys, US Forest Service surveyors issued a report noting that, in the 1870s, that area of the Greenhorn Mountains experienced a "wide spread and destructive fire" that burned for months and killed much of the timber in that area (Childs 1912).

In our analysis, we found a range of 7–63% high-severity fire, based upon historical sources and reconstructions, and most values were ~15–30% (Table 1). In the 1910/1911 study area, the proportion of high-severity fire averaged 26%, including both the 1910 and 1911 portions, consistent with other data in this region (Table 1). Also, our estimated high-severity fire rotation interval of 231 years was consistent with some research (Hanson and Odion 2014), and moderately shorter than rotations in other research (Baker 2014). Furthermore, there was a high correlation between tree diameter and age, which was contrary to the hypothesis advanced by Fulé et al. (2014). Although Miller et al. (2012) hypothesized that high-severity fire rotations in the range of 200–250 years might be too short to maintain old forest on the landscape, data on stand age distributions resulting from fire indicate that, with a 200-year high-severity fire rotation, ~25% of the forest would be 100–199 years old, ~17% would be 200–299 years old, and ~16% would be ≥300 years old, unlike the distribution for a 200-year-rotation clearcut logging cycle, which would result in zero stands over 200 years old (e.g., see Cyr et al. 2009).

The forests of the study area also had high variability in both density and species composition, with a denser structure associated with old forest areas that had not experienced high-severity fire for a long time. Pine was generally dominant at lower elevations within mixed-conifer forests, although substantial proportions of non-pine conifers still occurred there; fir and cedar dominated mixed-conifer forests at upper elevations (>1850 m) at this latitude (Figure 3). This was also consistent with other historical data sets for these forests (Table 2). Understories were also highly variable, but were generally dense, with shrub cover averaging 34% and conifer seedling/sapling density averaging 837/ha within forested areas.

Spatial scale was an important issue in our results. Had we analyzed only the smaller 1910 portion of our study area, or a small subset of the 1911 portion, as had been done previously (Scholl and Taylor 2010; Collins et al. 2011), we might also have reached overly narrow conclusions that would not have corresponded to the full range of variability of historical fire effects, forest structure, and tree species composition. Curiously, we found explicit notes about extensive high-severity fire effects that were made by 1911 surveyors about the subsections analyzed by Collins et al. (2011) (USFS 1910–1911, e.g., T2S, R20E, Sections 4 and 5), yet they drew the opposite conclusion. Our results also underscore the episodic nature of historical high-severity fire, such that one portion of the study area (1911) evidences extensive high-severity fire occurrence while another (1910) does not at a particular point in time (Figure 1). Thus, data from larger landscapes are essential, and landscape-level inferences should not be extrapolated from spatially limited studies.

The 1910/1911 Forest Survey data did not support the hypothesis of relatively homogeneous, open, pine-dominated forests and sparse understories that were maintained by low-severity fire across this Sierra Nevada landscape. Rather, the data describe forests that were characterized by strong contrasts and dynamic natural processes. These historical patterns were also consistent with the widely contrasting habitat associations reported for California Spotted Owls and Pacific Fishers in terms of very dense, old forest for nesting/roosting and denning/resting habitat (Gutiérrez et al. 1992; Zielinski et al. 2006; Purcell et al. 2009; Underwood et al. 2010; Hanson 2015), and complex early-seral forest, created by moderate/high-severity fire, for foraging (Bond et al. 2009; Bond et al. 2013; Hanson 2013). These were forests that could sustain not only the full range of habitat requirements for California Spotted Owls and Pacific Fishers, but could also provide abundant habitat for other rare species that are narrowly associated with high-severity fire in dense, old conifer forest, such as the Black-backed Woodpecker (*Picoides arcticus* Swainson) (Hanson and North 2008). Leiberg (1902: page 171) observed this juxtaposition of dense, old forest and high-severity fire patches in numerous mixed-conifer forest locations in the Sierra Nevada: "All the slopes of Duncan Canyon from its head down show the same marks of fire—dead timber, dense undergrowth, stretches of chaparral, thin lines of trees or small groups rising out of the brush, and heavy blocks of forest surrounded by chaparral."

In the mixed-conifer forest plots surveyed by Hodge (1906), stands were consistently dominated by small (<30.5-cm dbh) and small/medium-sized trees (<48.3-cm dbh), and density ranged from 185 to 2322/ha; these trees were comprised primarily of white fir and incense-cedar. Historical basal area of trees also ranged widely in mixed-conifer forests, with mature/old forests often exceeding 50 m^2/ha (North et al. 2007), and sometimes reaching levels >100, or > 200 m^2/ha (Stephens 2000; Lydersen et al. 2013). Such stand structure likely would have provided excellent denning and resting habitat for Pacific Fishers based on the historical USFS data collected in 1910/1911 (Zielinski et al. 2006; Purcell et al. 2009; Lofroth et al. 2010), as well as nesting/roosting habitat for California Spotted Owls (Gutiérrez et al. 1992).

Collins et al. (2011) suggest that the relatively low forest densities in their spatially limited (i.e., low sample size) study area be extrapolated to the larger Sierra Nevada landscape, and that extensive mechanical thinning operations could be used to greatly reduce forest density in order to restore forests and to prevent high-severity fire in the future. Given our analysis of all the data available in the 1910/1911 surveys, we believe this is an unjustified recommendation because the historical conditions indicated the widespread presence of high-severity fire, mixed-severity fire landscapes, and a heterogeneous landscape comprised of different forest conditions with high structural and floristic variability. Moreover, the widely contrasting habitat associations of California Spotted Owls and Pacific Fishers for nesting/roosting and denning/resting habitat, respectively, as compared to foraging habitat, suggest the Collins et al. (2011) approach would result in unnaturally homogenized forest conditions that would lead to further losses of not only high quality nesting/roosting habitat (California Spotted Owl) and denning/resting habitat (Pacific Fisher), but also foraging habitat for both species, which is characterized by high snag densities and high shrub cover following fire (Bond et al. 2009; Hanson 2013)—conditions that mechanical thinning generally seeks to reduce or prevent. This is of significant conservation concern, because the Pacific Fisher is a candidate for listing under the Endangered Species Act (ESA), and the California Spotted Owl is declining throughout the forested regions of the Sierra Nevada that have been managed by extensive mechanical thinning and fire suppression, while the owl is not declining in forests protected from mechanical thinning and post-fire logging (Conner et al. 2013; Tempel and Gutiérrez 2013). A recent analysis found a 43% loss of California Spotted Owl occupancy after mechanical thinning and group selection logging (Stephens et al. 2014). Pacific Fishers in the Sierra Nevada have been found to avoid mechanically thinned areas (Garner 2013).

Moreover, high-severity fire remains heavily suppressed in these forests currently, relative to its natural, historical occurrence (Odion and Hanson 2013; Hanson and Odion 2014; Odion et al. 2014). Some analyses, reporting increases in fire severity, have used vegetation data that post-dates the time series analyzed (Mallek et al. 2013). However, this approach has been found to create false trends of increasing fire severity, and the most comprehensive analysis to date indicates fire severity is not increasing in the Sierra Nevada (Hanson and Odion 2014). Thus, more active managed wildland fire will be needed to effectively restore fire to these ecosystems.

Concurrently, the rate of old forest growth greatly outpaces the rate of high-severity fire in old forest (Odion and Hanson 2013). Consequently, old forest would remain heavily dominant on the landscape, spatially, even if high-severity fire was restored to the levels before fire suppression (Odion and Hanson 2013). Complex early-seral forest created by high-severity fire supports high levels of native biodiversity and many wildlife species that are found predominantly, or almost exclusively, in post-fire landscapes (Hanson and North 2008; Donato et al. 2009; Burnett et al. 2010; Swanson et al. 2011; DellaSala et al. 2014). Thus, restoration of more active fire regimes would benefit many species.

CONCLUSION

Our analysis underscores the importance of data from larger spatial scales when using historical surveys to draw inferences about landscape-level reference conditions, and also highlights the problems that can result due to extrapolating from a small number of plots (Collins et al. 2011; Lydersen et al. 2013) to infer desired landscape-level forest structure, composition, and fire regimes. Our results also indicate that current plans by the US Forest Service to create, through logging, a landscape dominated by open pine forests maintained by lower-severity fire would result in novel, overly homogeneous conditions that could exacerbate risks to California Spotted Owls and Pacific Fishers.

ACKNOWLEDGMENTS

We thank the peer reviewers and the editorial staff of *Natural Areas Journal* for numerous suggestions that improved the manuscript significantly. We also thank Tim Sinnott at GreenInfo Network for the GIS analysis to produce the study area map.

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