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California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes

Anu Kramer[a,*], Gavin M. Jones[a,b,1], Sheila A. Whitmore[a], John J. Keane[c], Fidelis A. Atuo[a,d], Brian P. Dotters[e], Sarah C. Sawyer[f], Sarah L. Stock[g], R.J. Gutiérrez[h], M. Zachariah Peery[a]

[a] *Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA*
[b] *USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA*
[c] *USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA*
[d] *Department of Biology, Southeast Missouri State University, Cape Girardeau, MO, USA*
[e] *Sierra Pacific Industries, PO Box 496014, Redding, CA, USA*
[f] *USDA Forest Service, Pacific Southwest Region, Vallejo, CA, USA*
[g] *Yosemite National Park, El Portal, CA, USA*
[h] *Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA*

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ABSTRACT

Wildland fire is a disturbance that shapes frequent-fire forest ecosystems and the life-histories of wildlife species that inhabit them. The California spotted owl (*Strix occidentalis occidentalis*) is an iconic old-forest species that evolved under a frequent-fire regime in western North America. While recent studies have focused on owl response to large, severe fire events, relatively little is known about how owls might respond to prescribed fires and wildfires managed for resource benefit. Therefore, understanding how owls use landscapes that are managed using fire may offer insight into how owls respond to fire management. We studied the breeding season nocturnal foraging habitat selection of 22 GPS-tagged California spotted owls in three national parks (Yosemite, Sequoia, and Kings Canyon) in the Sierra Nevada, California, USA where natural fires have largely been allowed to burn during the past 50 years and controlled burning has been used to target additional areas. Consistent with other studies of this species, owls selected forests dominated by medium and large trees and avoided areas with smaller trees within their home ranges based on step selection analysis. Owls neither selected nor avoided forests burned by low- and moderate-severity, or high-severity fires, yet avoided larger patches of severely-burned forest (odds of selection decreased by 20% for every 10 ha increase in severely-burned patch area). These results indicated the importance of patch characteristics, suggesting that larger patches reflected either lower quality foraging habitat or increased predation risk, even in these frequent-fire landscapes where “large” severely-burned patches were small compared to those common after megafires. Additionally, selection strength increased for areas burned recently by lower-severity fire and, to a lesser extent, by older fires (largely of lower severity) as the extent of these burned areas increased within individual home ranges. These results suggested that lower-severity fire benefitted spotted owls and that these benefits declined over time. Thus, our findings are consistent with the hypothesis that California spotted owls are adapted to historical frequent-fire regimes of overall lower-severity with small high-severity patches. We hypothesize that fire management, coupled with medium- and large-tree retention, likely maintains high quality spotted owl habitat and may contribute to the observed owl population stability in Sequoia and Kings Canyon National Parks, compared to declining populations on three national forests. Finally, our results indicated that fire management, as practiced in these national parks, could benefit owl conservation elsewhere if challenges to the reintroduction of frequent-fire regimes can be overcome.

Abbreviations: HRV, historical range of variability; DOP, dilution of precision; FRAP, CAL FIRE’s Fire and Resource Assessment Program; GNN, gradient nearest neighbor; GPS, global positioning system; SSF, step selection function; KDE, kernel density estimate; LEMMA Lab, Landscape Ecology, Modeling, Mapping, and Analysis Lab, Oregon State University; MTBS, Monitoring Trends in Burn Severity; VHF, very high frequency; VEGCLASS, vegetation class

[*] Corresponding author.
E-mail address: hakramer@wisc.edu (A. Kramer).

[1] Author made equal contributions as first author.

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1. Introduction

Wildland fire, ignited both naturally and intentionally by humans, has shaped ecosystems and the ecology of species living in them for millions of years (Clark, 1989; Bond and Keeley, 2005; Shakesby and Doerr, 2006; Johnstone et al., 2016). Despite the importance of wildland fires as a natural process, they can impact natural resources (e.g., trees, water) and environments (e.g., rural and urban areas) to such an extent that people have attempted to suppress them for many years and across many systems (Moritz et al., 2014; Kramer et al., 2019; Wood and Jones, 2019). Consequently, fire suppression has led to unnaturally high densities of vegetation in some areas (Parsons and DeBenedetti, 1979; Sugihara et al., 2006; Collins et al., 2011, 2017a). This situation is particularly true of dry forests in the western United States, such as those in California's Sierra Nevada forest ecosystems, where unnatural increases in vegetation density, warming and drying associated with climate change, and increasing human populations in the wildland-urban interface have increased both the size and severity of wildland fires (Gill et al., 2013; Abatzoglou and Williams, 2016; Westerling, 2016; Schoennagel et al., 2017; Stevens et al., 2017). Although many "fuels management" techniques are available to land managers to reduce the risk of large, severe fires in natural landscapes, some techniques (e.g., tree thinning and fire use) have been controversial partly because of their potential negative effects on sensitive wildlife species (Hanson et al., 2009; Collins et al., 2010; Stephens et al., 2019; Kuchinke et al., 2020). Thus, understanding wildlife responses to thinning and fire use intended to reduce high-severity wildfires, as well as wildlife responses to those severe fires themselves, will inform management decisions.

Managing dry forests with fire is considered an effective and economical method of mimicking historical fire regimes to restore forest resilience and reduce the risk of future severe fire (Hardy and Arno, 1996; Sugihara et al., 2006; van Wagtendonk, 2007; North et al., 2015; Stephens et al., 2019; Hiers et al., 2020). Both prescribed fire and managed wildfire are methods of fire use: prescribed fire refers to fires that are planned, ignited, and managed from start to finish (Stephens and Moghaddas, 2005; Stephens and Ruth, 2005; North et al., 2007; Hiers et al., 2020) and managed wildfires are naturally ignited fires that are allowed to burn if they are deemed to pose little or no threat to humans or ecosystems (Christensen et al., 1987; Parsons and van Wagtendonk, 1996; Parsons and Landres, 1998; van Wagtendonk and Lutz, 2007). Despite the benefits of fire use, this technique is not always compatible with management objectives, which differ among private landowners, non-profit organizations, and public land management agencies (Young et al., 2020). As a result, different groups often use different approaches to reduce the risk of severe fire. For example, mechanical "treatments" (thinning or harvesting trees and/or manually thinning the understory) may be used instead of or in combination with fire in order to offset the cost of fuel reduction treatments, to increase precision of treatment outcomes (by choosing the spatial pattern or altering species composition), or to avoid the liability and smoke associated with burning (Stephens and Moghaddas, 2005). Wildland fire size, severity, and frequency, as well as its socio-ecological impact, also vary across the western United States because of variation in management approaches, local climate, and ecosystems (Parsons and Landres, 1998).

The U.S. National Park Service has pursued a policy of encouraging the use of fire since the 1960 s to restore or maintain natural ecosystem processes across the large, often remote landscapes of national parks. In these settings, fire is a relatively cost-effective management tool. In Yosemite, as well as Sequoia and Kings Canyon (the latter two parks are under joint management and hereafter referred to as Sequoia-Kings Canyon), National Parks located in the Sierra Nevada, fire policy allows not only prescribed fire, but also managed wildfire (Christensen et al., 1987; Parsons and van Wagtendonk, 1996; Parsons and Landres, 1998; van Wagtendonk and Lutz, 2007). Thus, compared to other forest lands in this region managed under different guiding objectives, this policy has resulted in some national park landscapes that more closely resemble historical conditions and processes: more frequent fires burning at low- to moderate-severity with fewer and smaller patches of high-severity fire (Collins and Stephens, 2007; Collins et al., 2008; Stevens et al., 2017; Kane et al., 2019).

Within the seasonal dry forests of the western United States, some management-sensitive species like the spotted owl (*Strix occidentalis*) use forest conditions typical of both historical and fire-suppressed forests for nesting, roosting, and foraging if they contain large trees and dense canopies with available prey (Bias and Gutiérrez, 1992; Call et al., 1992; Jones et al., 2018; Atuo et al., 2019; Blakey et al., 2019). However, spotted owls can be negatively impacted by both large high-severity fires (Jones et al., 2016, 2020; Rockweit et al., 2017) and fuel reduction treatments, at least in the short term, that are designed to reduce fire risk (Stephens et al., 2014a; Tempel et al., 2014; Gallagher et al., 2019). Therefore, it is essential to understand the impacts and tradeoffs of wildfire, prescribed fire, and mechanical fuels treatments on spotted owls and other sensitive species to facilitate their conservation in the short and long term. How best to manage habitat for spotted owls, given the potential threat of "megafires" (fires with an area of at least ~ 40,500 ha; Stephens et al., 2014b), is complicated by research suggesting opposite effects of severe fire on spotted owls. Whereas some studies have reported negative effects of high-severity fire on spotted owls (e.g. Jones et al., 2016, 2019, 2020; Eyes et al., 2017; Rockweit et al., 2017; Lommler, 2019), others have reported no negative effects of high-severity fire on this species (e.g. Lee and Bond, 2015; Bond et al., 2016). Thus, the resolution of these different findings will require studies of owl response to prescribed, managed, and wildland fire to answer the following questions: what types and configurations of high-severity fire negatively impact owls and their habitats, and what types and configurations might not convey these negative consequences? Given such information, how can prescribed fire, managed wildfire, or even other vegetation management techniques be used to mitigate potential threats without also harming owls (Jones, 2019; Peery et al., 2019; Jones et al., 2020)?

California spotted owls (*S. o. occidentalis*) have been studied intensively for many years throughout the dry forests of the Sierra Nevada in California and only one of four populations studied on public lands (located in Sequoia-Kings Canyon National Parks) has shown a stable population trend (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). Although it is not known why this owl population has been stable while the three others on national forests have declined, it has been hypothesized that the presence of higher densities of large trees, differing prey resources, and the restoration of fire to this system through prescribed and managed wildfire may be contributing factors (Franklin et al., 2004; Blakesley et al., 2010; Jones et al., 2018). Additionally, and perhaps because of these differences in burning between these landscapes, prey type consumed by owls also differs between national parks and national forests, with the diet of spotted owls in national parks consisting of a higher proportion of (high-calorie) woodrats and pocket gophers compared to national forests (Hobart et al., 2019a). Therefore, the forest conditions that are maintained through restorative fire management in Yosemite and Sequoia-Kings Canyon National Parks provide a unique opportunity to understand owl habitat selection when prescribed and managed fire are used extensively within their home ranges. Indeed, a recent study in Yosemite National Park revealed neutral owl selection of recently burned territories when < 30% of the core area had burned at high-severity, indicating compatibility between owl occupancy and lower-severity fire (Schofield et al., In press). One explicit goal of restorative fire management is to reduce high-severity fire that has the potential to kill larger trees that are key features of both old-growth forests and owl habitat (Jones et al., 2018). The benefits of restorative fire also include a reduction in the size of patches of forest that burn at high-severity (Collins et al., 2008; Kane et al., 2014). Hence, conserving larger trees and reducing the size of high-severity fire patches are two outcomes of restorative fire management that we predict will benefit spotted owls.

It is against this background and existing knowledge gaps that we studied California spotted owls in forests where fire is regularly used as a management tool. We formulated our study based on the hypothesis that owls evolved in forests characterized by frequent-fire regimes, including a patchy burn pattern with small areas of high-severity fire (Safford and Stevens, 2017), and that they would respond in predicable ways to the occurrence of fire in their home ranges. We predicted that in fire-restored landscapes, where high-severity patch size and characteristics are likely to be more closely aligned with the historical range of variability (HRV), (1) owls would show neutral or positive overall response to high-severity fire and higher levels of pyrodiversity (a mix of different burn severities and unburned area in close proximity), (2) owls would show no selection for or against high-severity patch characteristics, such as patch size, and they would equally forage along edges and far into larger patches of high-severity fire, and (3) owls would show neutral or positive response to low- and moderate-severity fire. These predictions were based on the assumption that in this landscape, high-severity patches created by a frequent-fire regime would fall within the HRV and therefore not adversely affect owl populations. Nevertheless, we acknowledge that severe fire even within the HRV could render some areas unsuitable for foraging by individual owls without adversely impacting populations. In addition, we tested whether habitat selection changed as a function of habitat availability within the home range (i.e., functional response) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). Our intent in testing these predictions was to help answer critical questions about the potential effects of fire to inform spotted owl conservation efforts.

2. Methods

2.1. Study site

We studied California spotted owl nocturnal habitat selection during the breeding season within three national parks: Yosemite and Sequoia-Kings Canyon. All three parks are located in the southern Sierra Nevada, California, and have experienced 50 years of active fire management (Fig. 1). Although fire restoration is still relatively recent in national parks, and "restored" areas encompass only 0.3% of the Sierra Nevada, Jeronimo et al., (2019) found that nearly 80% of these areas "restored" to the HRV fell within Yosemite and Sequoia-Kings Canyon National Parks, covering 3.7% of the area within these parks. Our study area encompassed these three parks, which spanned approximately 652,000 ha from the foothills (~500 m elevation) to the crest of the Sierra Nevada (> 4000 m elevation). The climate was Mediterranean, with cool, wet winters and warm, dry summers. Vegetation varied by elevation with oak woodlands and chaparral predominant at lower elevations, grading to mixed-conifer forests at middle elevations, and subalpine forests at higher elevations (Mayer and Laudenslayer, 1988; Sugihara et al., 2006). Logging is prohibited in national parks, which has resulted in the preservation of large, old trees (Beesley, 1996). Fire suppression began in the region during the late 19th century and continued until the late 1960 s when new fire policies for national parks allowed the use of fire as a restoration tool (van Wagtendonk, 1991, 2007; Sugihara et al., 2006). Beginning in 1968 in Sequoia-Kings Canyon National Parks, and 1972 in Yosemite National Park, both prescribed and managed fire were used to facilitate restoration of historical fire regimes and to increase forest resilience within the parks (van Wagtendonk, 1991; Parsons and Botti, 1996).

2.2. Owl space use data

We captured 27 owls (males and non-nesting females) in the breeding season of 2018 (April and May) either by hand, pan trap, or using snare poles (Bull, 1987; Franklin et al., 1996). We then fitted owls with small (7–10 g) tail-mounted dual GPS/VHF (very high frequency) tags (Lotek Pinpoint VHF 120, Newmarket, Ontario, Canada; GPS/VHF tags hereafter as "GPS tags") that allowed remote downloading of onboard data. We recaptured owls to remove GPS tags when possible and expected tail-mounted tags of owls that we did not recapture to be shed during the next tail molt. We used the VHF capabilities to relocate tagged owls for recapture and GPS data retrieval, but in our habitat selection analyses, we used only the GPS locations. Accordingly, we programmed GPS tags to collect five hourly GPS locations per night (2200 to 0200), which we assumed primarily represented foraging activities because owls are nocturnal predators. However, owls engage in territory defense, resting, and returns to the nest at night that may also be reflected in these GPS locations (Forsman et al., 1984; Delaney et al., 1999).

2.3. Fire history and severity

We compiled fire history from CAL FIRE's Fire and Resource Assessment Program (FRAP) database, where we downloaded perimeters of all fires in our study area that were at least 10 acres in size (http://frap.fire.ca.gov/, accessed May 2, 2018). This dataset also included information on whether a fire was a wildfire or a prescribed fire. We compiled fire severity data using the Monitoring Trends in Burn Severity (MTBS) database and additional data maintained by each national park. MTBS severity data (http://www.mtbs.gov/, accessed February 14, 2018) accounted for all fires in our study area over 1,000 acres (405 ha) in size that burned between 1984 and 2017 (Eidenshink et al., 2007). However, for smaller fires (100–1,000 acres) including wildfires and prescribed burns, we used spatially explicit severity data provided by Yosemite (personal communication, K. van Wagtendonk; Lutz et al., 2011) and Sequoia-Kings Canyon (personal communication, K. Folger) National Parks that used the same methodology as MTBS. Although these additional datasets included fires that burned before 2003, many older wildfires in the smaller size class (100–1,000 acres) lacked data on severity. Therefore, we used 2003 as the oldest date to include fire severity in our analyses.

We used the FRAP database of fire perimeters to check that our fire severity dataset included all wildland fires that burned over 100 acres between 2003 and 2017, with at least 30 acres of that burned area within an owl's home range. We defined home range as the 95% kernel density estimate (KDE) from all filtered nocturnal GPS locations (see Habitat Selection Analysis section below for filtering methods) for each individual owl. However, a significant amount of fire severity data was missing for two owls, so we removed them from analysis. Four of 21 prescribed fires were missing information on fire severity, yet we found that only 1% of the area of the 17 prescribed fires in our dataset burned at high-severity. Thus, we assumed that these four prescribed fires only burned at low- and moderate-severity and that all fires smaller than 100 acres (for which we did not have information on fire severity) also burned at low- and moderate-severity. For fires that burned < 30 acres (12 ha) of an owl's home range (home ranges were 750 – 3,000 ha), we included severity information, where available, and assumed that the area burned at low- and moderate-severity in cases when this information was not available.

We classified each burn location as follows: (a) burned 41 to 65 years prior (1953–1977), (b) burned 16 to 40 years prior (1978–2002), (c) burned at low- and moderate-severity (up to 75% overstory mortality) up to 15 years prior (2003–2017), and (d) burned at high-severity (over 75% overstory mortality) up to 15 years prior (2003–2017; Table 1). We grouped low- and moderate-severity fire (henceforth "lower-severity") because others have shown that owl selection was similar between these areas (Bond et al., 2002; Eyes et al., 2017). We also used the definition of high-severity commonly used in other papers on spotted owls and wildfire (Jones et al., 2016; Eyes et al., 2017; Hobart et al., 2020), although we note that other thresholds for high-severity wildfire have been used (Bond et al., 2002;

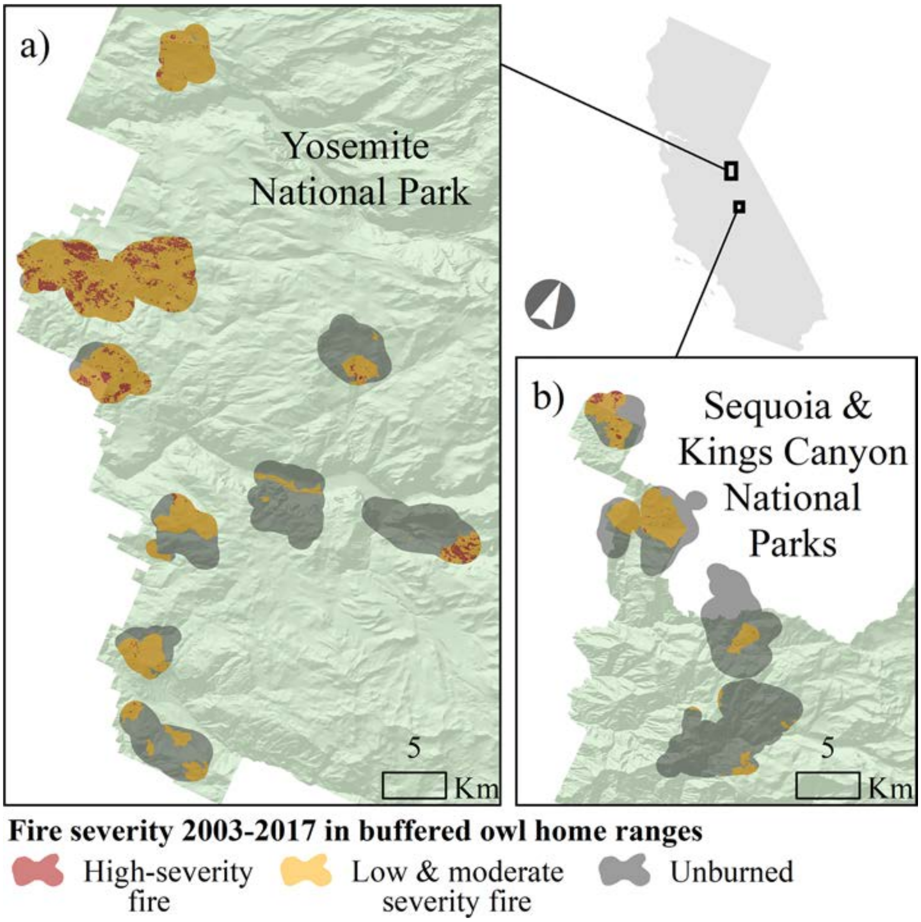

Fig. 1. Map of our California spotted owl study area in the Sierra Nevada, California, showing fire severity within buffered owl home ranges in (a) Yosemite National Park (n = 13 owls), and (b) Sequoia & Kings Canyon (n = 9 owls) National Parks. Home ranges represent the 95% kernel density estimate of all owl nocturnal GPS locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Lydersen et al., 2016; Collins et al., 2017b). If an area burned more than once between 2003 and 2017 (0.6% of assessment points in our analysis), we used the highest burn severity for that location for the classification because we expected high-severity fire to represent the predominant fire effects at that location. However, areas that burned in older fires were noted separately, such that an area could be coded as having burned during as many as three time periods, corresponding to the three time periods described above (e.g. an area that burned in 1967 and 1976, but not more recently would be coded as Burned $_{1953\text{-}1977}$ = 1, Burned $_{1978\text{-}2002}$ = 0, Lower-severity = 0, and High-severity = 0; Table 1).

Spotted owl foraging patterns have been shown to be correlated with the spatial characteristics of high-severity patches (Jones et al., 2020). Thus, we calculated the size of each high-severity fire patch, the "permeation distance" of each point (the distance from the point to the patch edge, conditional on the point occurring within a high-severity patch), and the patch complexity (perimeter-area ratio of the patch; Table 1). We also computed a pyrodiversity index using data from fires

Table 1

Covariates used to model California spotted owl habitat selection in Sequoia, Kings Canyon, and Yosemite National Parks California, including the variable description, class, type, and values. Continuous variables were scaled so that values fell between 0 and 1.The class of each variable links it to the three stages of analyses, where stage I corresponds to landscape and disturbance covariates tested in a step selection function (SSF), stage II uses only high-severity patch covariates in an SSF, and stage III utilizes disturbance and patch covariates to test for functional response. Acronyms used in the table include digital elevation model (DEM), gradient nearest neighbor vegetation estimates (GNN), quadratic mean diameter (QMD), and monitoring trends in burn severity (MTBS).

Variable	Description	Class	Type	Range of values
Elevation	Elevation (m) based on a DEM	Landscape	Continuous	1000–2800
Medium-large trees	Proportion of area where dominant trees have medium and large diameters (as determined by 2016 GNN; QMD ≥ 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Small trees	Proportion of area where dominant trees have small diameters (as determined by 2016 GNN; QMD < 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Lower-severity	The point burned at low- and moderate-severity in 2003–2017	Disturbance	Categorical	0 or 1
High-severity	The point burned at high-severity in 2003–2017	Disturbance	Categorical	0 or 1
Burned$_{1978\text{–}2002}$	The point burned from 1978 to 2002	Disturbance	Categorical	0 or 1
Burned$_{1953\text{–}1977}$	The point burned from 1953 to 1977	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon diversity of 3-class (unburned; low/mod -severity; high-severity) MTBS classification within 100 m buffer for fires in 2003–2017	Disturbance	Continuous	0–1.09
Patch area	Area (ha) of severe fire patch[1] that point falls in for fires in 2003–2017	Patch	Continuous	0–225
Patch complexity	Perimeter-to-area ratio of the severe fire patch[1] that a point falls in for fires in 2003–2017	Patch	Continuous	0–0.133
Permeation distance	Distance (m) from point within severe fire patch to edge for fires in 2003–2017	Patch	Continuous	0–265

[1] High-severity patches were smoothed to remove patches under 4 pixels (0.36 ha)

that burned between 2003 and 2017, where we calculated the Shannon diversity of unburned, lower-severity, and high-severity fire within a 100-m radius of each point (Table 1). Thus, an area composed entirely of a single class (unburned, lower-severity, or high-severity) would yield a pyrodiversity index equal to 0, whereas an area composed of multiple classes would yield a pyrodiversity index > 0.

2.4. Environmental variables

We determined the elevation at each point, which is related to spotted owl habitat preferences (Kramer et al., in revision). We also used Gradient Nearest Neighbor (GNN) maps of forest structure to classify the 2016 landscape into vegetation classes as follows: (i) forests where dominant trees were small in diameter (henceforth small trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was under 25 cm, (ii) forests where dominant trees were medium and large in diameter (henceforth medium-large trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was at least 25 cm, and (iii) open areas where canopy cover was under 40% (LEMMA Lab, Oregon State University, Corvallis, OR; using their *VEGCLASS* variable; Ohmann and Gregory, 2002). Note that we combined medium and large tree categories, given uncertainties in the accuracy of the GNN-based vegetation cover type classifications at fine scales. While there were two years between GNN habitat classification and bird tagging, there were minimal changes in forest structure to owl home ranges in our study area besides a few small fires (all under 10 acres between 2016 and when owl GPS data was collected in 2018), so we assumed these habitat classifications provided an acceptable representation of general forest structure.

2.5. Three stages of analysis

We used a three-part analysis to explore the effects of fire on spotted owl foraging habitat selection. In stage I of our analyses, we modeled selection relative to landscape and fire-related disturbance variables (Table 1) to examine how this broad range of environmental covariates shaped selection. In stage II of our analyses, we examined whether covariates related to the spatial characteristics of severely-burned areas could further explain patterns of selection related to the simple categorical severe fire effect from stage I. Therefore, we tested whether the spatial pattern and configuration of high-severity patches (area, complexity, and permeation distance; Table 1) influenced selection by owls. The third and final stage of analysis tested for a functional response in habitat selection to determine whether differing individual levels of exposure to the fire disturbance- and high-severity patch-related covariates (Table 1) also influenced habitat selection (see below) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). We examined these three stages of questions by developing models in each stage that allowed us to test and evaluate these questions.

2.5.1. Habitat selection analyses: Stages I and II

The analyses performed for stages I and II were similar, with the exception of the covariates used in the models. We examined patterns of habitat selection using a use-availability framework that compared habitat attributes at used locations to those at randomly generated available locations (Manly et al., 2002; Hooten et al., 2017). To improve spatial accuracy (to achieve median error of ~20 m) we only used GPS location points that had a dilution of precision (DOP) below five and whose coordinates were estimated by at least four satellites (Kramer et al., in revision). As a result, we excluded three individuals from analysis that had < 100 usable GPS points and two individuals that lacked sufficient fire severity data, which yielded an analysis sample of 22 individuals (13 from Yosemite and nine from Sequoia-Kings Canyon National Parks). Our sample owls had an average of 4.6 GPS points per night and 47 nights per individual. Because we eliminated an average of only 0.4 points per night per owl, we were confident that our data filtering process did not result in substantive bias, even though it was possible that more points under dense canopy were elimated due to fewer satellite hits (but see Frair et al., 2004).

We used a step selection function (SSF) to test for patterns in habitat selection (Duchesne et al., 2010; Fortin et al., 2005; Muff et al., 2020), where available habitat associated with a given owl location was conditional on where the individual occurred at the time of the previous GPS location during the same night (i.e. a "step"). While a "used" point refers to an owl GPS location, "available" points refer to 10 locations that were theoretically available for selection by that individual during that time period. For this reason, we calculated the position of these 10 available points by selecting random points that fit the spatial distribution of step lengths and step time intervals for any movement an owl made, while accounting for differences among individuals. Since some step intervals were 2–3 h long (because some GPS points were eliminated from analysis as described above), we created distributions of hourly, bi-hourly, and tri-hourly step lengths. All random points were located within a 400 m buffered 95% KDE. We used this buffer to avoid restricting the directionality of available steps near the edge of the owl's home range. Thus, turn angles were random and represented a uniform distribution, corresponding to non-directional random walks (Fortin et al., 2005).

We used mixed conditional Poisson regression models with stratum-specific intercepts, which are likelihood-equivalent to mixed conditional logistic regression models that yield equivalent parameter estimates and standard errors (Duchesne et al., 2010; Muff et al., 2020). We fitted the SSF using the Poisson formulation where the stratum-specific random intercept variance was fixed to a large value to avoid shrinkage, following Muff et al. (2020). By using conditional Poisson regression we were able to compare observed and available locations representing temporally correlated "matched pairs," as was the case with our data.

Our response variable was binary (1 = used, 0 = available). In the stage I analysis that examined landscape characteristics and fire-related disturbance, we fitted a model that included elevation, pyrodiversity (2003-2017), small trees, and medium-large trees as continuous fixed effects and $\text{burned}_{1953\text{-}1977}$, $\text{burned}_{1978\text{-}2002}$, lower-severity burn (2003-2017), and high-severity burn (2003-2017) as categorical fixed effects. In the stage II analysis that focused on high-severity patch characteristics, we added to the stage I model continuous variables related to features of high-severity fire patches: patch size (2003-2017), permeation distance (2003-2017), and patch complexity (2003-2017). Since these variables were moderately- to highly-collinear with one another, we did not include them in the same model, but ran three separate SSF models. Because a SSF matches available points in close proximity to each used point, we did not include a variable for the distance from the nest or activity center of these central place foragers (Rosenberg and McKelvey, 1999). We tested for correlation among all continuous predictor variables and none were highly correlated (correlation coefficient > 0.7). We rescaled all continuous variables so that they would range between 0 and 1. Although we did not formally test for variability among individuals, we adopted the advice of Duchesne et al. (2010) that individual (random) coefficients should be included to avoid bias in the population-level (fixed) effects, allowing for more robust population-level habitat selection estimates, given individual heterogeneity. We used the R package glmmTMB version 0.2.0 to conduct the step selection analysis (Magnusson et al., 2017).

2.5.2. Functional response analysis: Stage III

A functional response to an available resource by an animal is indicated by an estimate for selection of that resource that changes as that resource also becomes more abundant (available) to the animal in its home range (Hebblewhite and Merrill, 2008; Holbrook et al., 2019; Jones et al., 2020; Mysterud and Ims, 1998). We tested for functional responses in habitat selection in our stage III analysis by including an interaction term between the habitat covariate of interest and a term representing its availability within a given individual's home range,

Table 2
Coefficient estimates from a mixed-effect step selection analysis from stage I (estimating California spotted owl selection relative to disturbance and land cover in the Sierra Nevada) and stage II (estimating California spotted owl selection relative to high-severity fire patch-related covariates). Column abbreviations correspond to: β, population-level (fixed) coefficient; SE, standard error of the mean; LCL, lower 95% confidence limit; UCL, upper 95% confidence limit; p, p-value for the effect of the population-level coefficient; σ^2, variance of individual-level (random) effects for each parameter.

variable	β	SE	LCL	UCL	p	σ^2
stage I						
elevation	−0.46	0.71	−1.84	0.93	0.52	10.69
small trees	−2.43	0.93	−4.25	−0.61	0.01	13.94
medium-large trees	1.16	0.26	0.65	1.66	< 0.01	1.19
burned $_{1953\text{-}1977}$	−0.25	0.37	−0.97	0.48	0.51	1.47
burned $_{1978\text{-}2002}$	−0.30	0.17	−0.64	0.03	0.08	0.49
lower-severity	0.47	0.33	−0.17	1.11	0.15	1.59
high-severity	−0.50	0.41	−1.30	0.29	0.22	< 0.01
pyrodiversity	−0.91	0.35	−1.58	−0.23	< 0.01	1.65
stage II						
patch size	−4.52	2.15	−8.73	−0.31	0.04	12.18
permeation distance	−3.45	2.26	−7.89	0.99	0.13	9.64
patch complexity	1.18	0.92	−0.63	2.99	0.20	1.40

where availability was constant for each individual owl and represented the proportion of that resource among all available locations generated for the SSF within each individual's home range (Matthiopoulos et al., 2011; Aarts et al., 2013). We ln-transformed availability because functional responses are assumed to be non-linear (Mysterud and Ims, 1998; Beyer et al., 2010). In all three analyses, we gauged the importance of fixed effects based upon their direction, effect size, and uncertainty (using 95% confidence intervals). We used R version 3.6.0 for analyses.

3. Results

We obtained 4,815 usable nocturnal GPS locations for the 22 GPS-tagged owls we monitored in 2018 that was composed of four females (all paired, but not nesting), and 18 males (all paired, with nine nesting and nine not nesting). These GPS locations provided data for 3,765 used steps (i.e., the first GPS point on any given night was the reference for subsequent steps and was not treated as a step itself) ranging from 118 to 188 used steps per owl (Table 1). We generated 37,650 available step locations corresponding to the 10 available steps generated for each used step. Owl home ranges were composed of 59.8% medium-large tree forest, 5.6% small tree forest, and 34.6% bare area (Fig. S1). Among all owls, 47.6% of used locations (steps) were in areas that had burned in the previous 15 years (between 2003 and 2017), with 46.2% of all used points having burned at lower-severity and 1.4% at high-severity (Fig. S1). The distribution of available locations (steps) was similar, with 44.1% falling in burned areas but with fewer available points in lower-severity burned areas (40.3%) and more in severely burned areas (3.9%). Among high-severity patches used, patch size ranged between 0.36 and 225 ha with a median of 18 ha (Table 1; Fig. S2). The overall distribution of high-severity patches within owl home ranges was skewed toward smaller patch sizes, with a maximum patch size of 225 ha (Fig. S2).

3.1. Landscape and disturbance selection analysis: Stage I

Spotted owls in our study areas selected forests with medium and large-sized dominant trees ($\beta_{\text{medium-large trees}} = 1.16$, 95% confidence interval [0.65, 1.66]) and avoided forests where dominant trees were small ($\beta_{\text{small trees}} = -2.43$ [−4.25, −0.61]; Table 2; Fig. 2). There was no apparent selection relative to whether an area had burned in older fires ($\beta_{\text{burned 1953-1977}} = -0.25$ [−0.97, 0.48]; $\beta_{\text{burned 1978-}}$

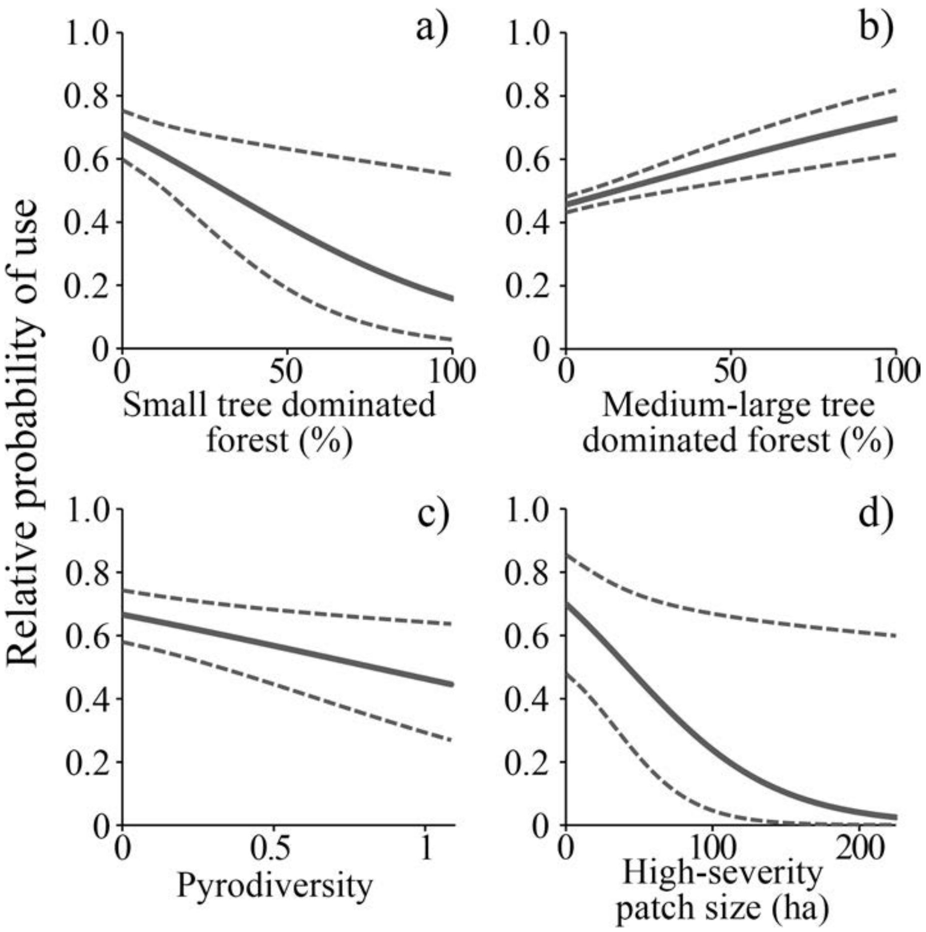

Fig. 2. Relative probability of use by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks plotted against (a) the proportion of small tree dominated forest within 100 m, (b) the proportion of medium-large tree dominated forest within 100 m, (c) the pyrodiversity of fires that burned between 2003 and 2017 within 100 m, and (d) the size of a given high-severity fire patch (that burned between 2003 and 2017). The probability of use is shown as a solid line and the 95% confidence interval is bounded by dashed lines.

$_{2002}$ = −0.30 [−0.64, 0.03]). There was also no apparent selection relative to the categorical effect of high fire severity ($\beta_{high\text{-}severity}$ = −0.50 [−1.30, 0.29]) or lower-severity fire ($\beta_{lower\text{-}severity}$ = 0.47 [−0.17, 1.11]) in more recent fires (Table 2). Owls selected areas that had lower pyrodiversity suggesting that, opposite to our prediction, they avoided areas that experienced a higher diversity of burn severities ($\beta_{pyrodiversity}$ = −0.91 [−1.58, −0.23]; Table 2; Fig. 2).

3.2. High-severity patch selection: Stage II

When we compared selection or avoidance of patch characteristics by owls within severely-burned areas, owls showed avoidance of larger patches ($\beta_{patch\ size}$ = −4.52 [−8.73, −0.31]) indicating that the odds of selection decreased by 20% for every 10 ha increase in severe fire patch size based on odds ratio and covariate scaling (Table 2; Fig. 2). Owls appeared to avoid traveling farther into severe fire patches ($\beta_{permeation\ distance}$ = −3.45 [−7.89, 0.99]) and appeared to select more convoluted patches ($\beta_{patch\ complexity}$ = 1.18 [−0.63, 2.99]), although the 95% CIs for both of these effects overlapped zero (Table 2).

3.3. Functional response analysis: Stage III

Owls selected areas that had burned in the past 16–40 years when this type of area was more abundant within their home range ($\beta_{burned\ 1978\text{-}2002\text{-}FR}$ = 0.48 [0.09, 0.87]; Table S1; Fig. 3A). Similarly, owl selection for areas that burned at lower-severity in recent fires (up to 15 years old) increased as this type of burned area became more abundant within their home range ($\beta_{lower\text{-}severityFR}$ = 0.55 [0.04, 1.05]; Table S1; Fig. 3B). There was no evidence for a functional response in the other six variables considered (see Table S1 and Fig. S3). Although Table S1 indicates weak evidence for a functional response to severe fire patch size (p = 0.06), inspection of the response curve indicates this effect was driven by a single owl that showed no change in selection based on patch size, while all other individuals showed relatively strong avoidance as patch size grew larger (Table S1; Fig. S3).

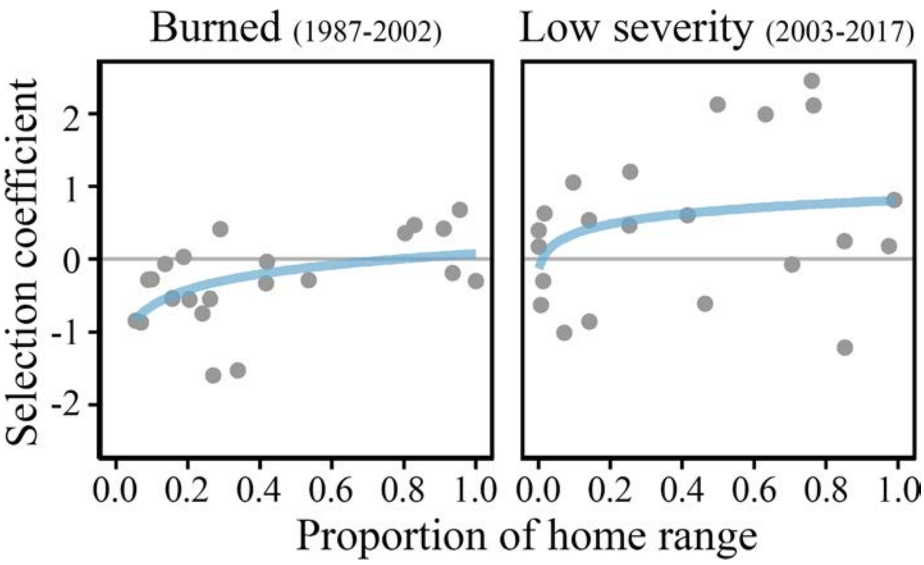

Fig. 3. Functional responses by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks when selecting areas burned within their home ranges that were significantly different from zero, including the proportion of owl territory (a) burned at any severity between 1978 and 2002 and (b) burned at lower-severity between 2003 and 2017, with each dot representing an individual owl, and blue lines indicating significant trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Discussion

We made two key discoveries about the way California spotted owls used burned forests in national parks that have significant implications for the conservation of this species in the Sierra Nevada and other frequent-fire forest ecosystems where they occur. First, spotted owls avoided larger patches of high-severity fire, a trend that was not apparent in our stage I analysis in which only a categorical effect of severe fire was explored. This demonstrated the importance of including high-severity patch size in analyses of spotted owl habitat selection, even in these landscapes with partially restored fire regimes and relatively small severely-burned patches (Jones et al., 2020). Second, although owls neither preferentially selected nor avoided areas burned recently at lower-severity and areas burned by older fires, their strength of selection for these areas became stronger as their prevalence within home ranges increased – this functional response in habitat selection was a finding novel to studies of spotted owls in burned landscapes. Collectively, these two results suggested that owls were resilient, and likely adapted, to the patchwork of fire effects that characterize these landscapes with frequent-fire regimes (primarily low- and moderate-severity intermixed with small high-severity patches). Our findings support the hypothesis that spotted owls are adapted to frequent-fire regimes and when coupled with the retention of medium-large trees, may explain in part why spotted owl populations were stable in Sequoia-Kings Canyon National Parks (Franklin et al., 2004; Blakesley et al., 2010). Our results also suggest that spotted owl habitat can benefit from the restoration of frequent fires.

3.5. Selection for forest type

Spotted owls avoided forests dominated by small trees and selected for forests dominated by medium- to large-sized trees, a finding that was consistent with previous studies of both California (Call et al., 1992; Gutiérrez et al., 1992; Roberts, 2017) and northern spotted owls (Solis and Gutiérrez, 1990; Gutiérrez et al., 1995). Thus, despite our broad characterization of medium-large forest (QMD ≥ 25 cm) that covered 59.8% of owl home ranges (Fig. S1), our results emphasize that this forest type constitutes important foraging habitat for spotted owls in fire-managed landscapes, as is the case in other forested landscapes. Although we did not evaluate specific structures likely important to owls such as large trees and dense large-tree canopies (Bias and Gutiérrez, 1992; North et al., 2017), higher resolution representations of forest type and structure (e.g., with LiDAR) and prey studies would further improve our understanding of the specific features used by owls for foraging in forests with frequent fire regimes.

3.6. Selection for burn severity class and patch characteristics

Owls avoided larger patches of severely-burned forest, suggesting that spotted owl selection/avoidance of forests burned at high-severity could only be adequately interpreted in light of severe fire patch size. We expected that the largest high-severity patches on these fire-managed landscapes would be relatively small in comparison to previous studies and would thus not be avoided by owls. Indeed, high-severity patches within owl home ranges in this study were heavily skewed toward smaller patches, with a median of 18 ha and the largest patch measuring 225 ha and highly convoluted in shape (Fig. S2; Fig. S3). This pattern was consistent with the HRV for Sierra Nevada yellow pine mixed-conifer forests, where high-severity patches rarely exceeded 100 ha (Safford and Stevens, 2017). In comparison, in the 2014 King fire (a megafire), where Jones et al. (2020) found that owls avoided larger patches and patch interiors, the largest high-severity burned patch was 8,818 ha. Severe fire patches in this study were smaller and more complex than the patches within the King Fire (Collins et al., 2017b; Stevens et al., 2017) (Fig. S4). Therefore, although owls may use smaller severely burned patches, owls tended to avoid larger patches within their home range (but see Fig. S3), even in landscapes where patches of this type remain relatively small and often highly convoluted (Jones et al., 2016, 2019, 2020; Eyes et al., 2017). Although these patches were recently burned, their age ranged between one and 15 years old, with varying amounts of vegetative ingrowth. Despite this variation, owls may have avoided large patches of high-severity fire for several potential reasons such as predator avoidance, low prey availability (little vegetation on recently burned areas may decrease prey abundance, and dense shrub ingrowth longer after a fire may hinder prey capture by owls, even if prey abundance is high), and insufficient perches to support their hunting strategy (Forsman et al., 1984; Gutiérrez, 1985). Consistent with our finding that spotted owls avoided large patches of severe fire, Schofield et al. (in press) found that owls were less likely to occupy territories in Yosemite National Park that experienced high severity fire across $>$ 30% of their core area. Thus, while owl populations may be relatively stable in landscapes with partially restored fire regimes, larger areas of high severity fire that make habitat less suitable for foraging also appear to have emergent effects that render territories less suitable for occupancy by owls in these landscapes.

Although confidence intervals for effects of permeation distance and patch complexity overlapped zero, our results suggested that owls may have selected more complex severe fire patches and may have avoided traveling further into severe fire patches (Table 2). The direction of the selection coefficient estimates were consistent with Eyes et al. (2017), who found that owls frequently foraged along the edges of severely burned patches, as well as Jones et al. (2020), who showed that spotted owls rarely traveled over 100 m into a severely-burned patch. Similarly, the maximum distance traveled into severely burned patches in our study was 169 m, and only 6% of locations that occurred within severely burned patches (0.08% of all locations) were farther than 100 m from the patch edge. Thus, our ability to detect significant effects may have been constrained by the small patches in this study. Even though we did not detect a significant effect of permeation distance, owls appeared to avoid making deep forays into larger patches of severe fire, regardless of tree size, in areas burned by both megafires (in the case of the King fire referenced above) and fires resembling historical regimes (reflected by our results for this study).

There has been disagreement in the literature about the effect of high-severity fire on spotted owls (Peery et al., 2019) because some studies have detected positive effects while others have detected negative effects (Ganey et al., 2017; Lee, 2018; Jones et al. In press). However, mounting evidence suggests these contrasting results could be explained in part by the spatial pattern and configuration of severely burned areas (Jones et al., 2020; this study). Our results indicated that owls avoided larger high-severity patches, even in a landscape where larger high-severity patches were relatively small, suggesting the importance of these characteristics to owl selection. Additionally, recent work on the King fire showed that while owls used some areas that burned at high-severity, they avoided both larger patches of severe fire and avoided traveling deep into those patch interiors, even after accounting for the potential effects of salvage logging (Jones et al., 2019, 2020). Thus, the size and configuration of high-severity patches may determine the direction and strength of owl habitat selection. The absence of these high-severity patch characteristics in earlier studies (e.g., Bond et al., 2009, 2002) may potentially explain why adverse effects of high-severity fire were not detected, which would be similar to our results of neutral selection in our stage I analysis where we did not consider the characteristics of high-severity patches.

Questions have also lingered about the potentially confounding effects that salvage logging of severely burned areas could have on spotted owl response to high-severity fire. Although salvage logging was explicitly accounted for by Jones et al. (2020), who found avoidance by spotted owls of both salvage logging and large patches of severe fire after the King fire, there is strong interest in studies of owl response to severe fire in areas where salvage logging operations have not occurred at all (Bond et al., 2009; Lee and Bond, 2015). Our study in national park landscapes (also see Roberts et al., 2011, Eyes et al., 2017, and Schofield et al., in press) provided such an opportunity to formally examine the response of owls to severe fire in the absence of salvage logging while also accounting for patch characteristics that were not considered in many previous studies (e.g. Bond et al., 2009, 2016; Lee and Bond, 2015). Thus, our results suggested that in the absence of salvage logging (though we note the possibility of the occurrence of small areas of hazard tree removal along roads and other areas where hazard trees could endanger park visitors) spotted owls avoided larger patches of severely-burned forest, yet this relationship was only apparent when high-severity patch size was included in the analysis.

3.7. Selection for lower-severity burned areas

Our results supported our prediction that spotted owls are resilient to lower-severity fire, as well as older burned areas, the majority of which were likely of lower-severity (similar to trends in more recent fires). Owls in this study neither selected for nor against areas burned by recent lower-severity fire (within 15 years) or older fire (that burned 16–40 years before), each of which covered about 40% (with overlap) of owl home ranges in our study. Our results were supported by other studies that have shown spotted owls to be resilient to low- and moderate-severity fires (Bond et al., 2002; Ganey et al., 2017), perhaps partially due to their broader range of habitat use when foraging (Verner et al., 1992; Williams et al., 2011; Eyes et al., 2017; Hobart et al., 2019b).

Although owls exhibited neutral overall selection for recent lower-severity fire, the strength of selection for these conditions increased as the area of lower-severity fire increased within owl home ranges (Fig. 3). Indeed, a heterogeneous landscape of lower-severity burned and unburned areas likely promotes small mammal community diversity (Roberts et al., 2015) and could increase the abundance and availability of key prey species such as woodrats, pocket gophers, and flying squirrels – with emergent benefits to spotted owl populations (Hobart et al., 2019a, 2020). However, it could be that prey using lower-severity burned areas require larger areas of habitat to persist and maintain stable populations, especially as owls deplete those populations, making these areas beneficial to owls only if they cover a sufficiently large portion of an owl's home range. Alternately, small pockets of prey created by less overall burned area within an owl's home range may be less energetically efficient for an owl to find and utilize. Our functional response analysis also revealed a significant effect of the amount of older burned areas (which likely burned primarily at lower-severity) within an owl's home range on selection of those areas. Owls with little older burned area available to them avoided these older burned areas, whereas owls with greater amounts of older burned area showed neutral selection for those areas (Fig. 3). Together, these results suggest that the benefits of lower-severity fire may attenuate over time, and that frequent, low-severity fire events might benefit owl populations and perhaps their prey.

The owl's use of lower-severity burned areas could also explain why owls avoided more pyrodiverse areas. Avoidance of pyrodiverse areas was in contrast to our prediction that owls foraging in heterogeneous landscapes shaped by fire would exhibit neutral or positive selection for areas with high pyrodiversity (Franklin et al., 2000; Franklin and Gutiérrez, 2002). Indeed, the most pyrodiverse locations were those containing a mix of burn severity classes (unburned, lower-severity, and high-severity fire), whereas areas of low pyrodiversity were those composed entirely of a single class of these three categories. Therefore, the composition of areas with low pyrodiversity becomes important for determining the direction and magnitude of owl selection. For instance, owls appeared to show weak selection for areas with high pyrodiversity in the King fire (Jones et al., 2016, 2020). However, areas of low pyrodiversity in the King fire predominately occurred in the large high-severity patch that owls avoided (and would have driven selection for greater pyrodiversity). In comparison, areas with low pyrodiversity in this study were most often composed of lower-severity or unburned area. Thus, neutral selection for lower-severity and unburned areas in our study may have resulted in an apparent avoidance of pyrodiversity unlike the owls in the King fire study (Jones et al., 2020; Fig. S5). Furthermore, the diversity of forest structure in unburned areas also may play a role in selection for pyrodiversity. Selection for more pyrodiverse areas may be more pronounced if pre-fire forest conditions are homogeneous, such that increased pyrodiversity might create structural heterogeneity preferred by owls, as may be the case on national forests and areas burned by the King fire (Jones et al., 2020). Regardless of the specific mechanism, our results suggest the importance of characterizing both pyrodiversity and structural diversity of unburned areas, especially when comparing selection for or against pyrodiversity among fires with different patterns of severity.

4. Conclusions and implications for using fire for owl conservation

Our study supports the long-held hypothesis that spotted owls are adapted to frequent-fire regimes, characterized by low- to moderate-severity fire with small patches of severe fire, such as those that have been reintroduced to the national parks that comprised our study area (Verner et al., 1992; Gutiérrez et al., 2017). Conversely, natural fire regimes on Sierra Nevada national forests have been altered by fire suppression, which has resulted in very different forest structures between the national parks we studied and other public lands in the Sierra Nevada. Hence, our study supports earlier speculation that the difference in management between these two general landscapes (fire managed and fire suppressed) may account for the difference in owl population trajectories – stable in Sequoia-Kings Canyon National Parks and declining on national forests (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). We do not know the mechanism(s) that confer higher fitness in fire-managed landscapes, but we propose that the benefit is conferred by (1) a positive influence of frequent low- and moderate-severity fire on prey habitat, (2) the change in forest structure that reduces the impact or spread of high-severity fires, and (3) the interaction of large trees and fire because large trees are relatively fire resistant and have helped facilitate the reintroduction of frequent lower-severity fire regimes. Therefore, we conclude that the effect of a natural fire regime is complex with positive benefits conferred on owls, the maintenance of forest systems, and reduction in high severity fire.

The habitat selection patterns revealed by owls in our study suggest that prudent use of fire, as practiced in the Sierra Nevada national parks we studied, could benefit spotted owl conservation in fire-suppressed landscapes such as national forests as previously proposed (Bond et al., 2002; Roberts et al., 2011; Eyes et al., 2017). However, the positive functional response owls exhibited to low-severity fire and the apparent attenuating benefits of lower-severity fire over time that we found suggest that restoration of frequent fire regimes, rather than discrete (nonrepeating) fire treatments, will be needed to continue achieving benefits for owl foraging habitat. Hence, increasing the amount and frequency of lower-severity fire would serve a dual purpose of (1) reducing surface and ladder fuels that contribute to the large, high-severity fires that negatively affect owls and (2) promoting prey habitat for owls (Jones et al., 2016; Hobart et al., 2019a).

The extensive reintroduction of frequent lower-severity fire on national forests and other fire-suppressed areas within the range of spotted owls is constrained by social (e.g., air pollution, fear of escaped fire), economic (e.g., high cost), and ecological (e.g., escaped fire, unintended negative impacts on wildlife habitat) considerations (Collins et al., 2010; Young et al., 2020). In areas lacking frequent, lower-severity fire, mechanical treatments intended to remove surface and ladder fuels may serve as an intermediate step to the restoration of fire regimes, although they are also constrained by concerns of stakeholders – that logging to remove smaller trees may also have negative effects on spotted owls and other wildlife (Wood and Jones, 2019). Note that our study was limited to national parks, where such treatments do not occur, and so our results cannot provide direct insight on mechanical treatments. Nevertheless, if mechanical treatments are applied with rigorous guidelines designed to maintain key habitat features (e.g., retention of large trees and dense canopy of tall trees) of old forest ecosystems and sensitive species like spotted owls, fishers (*Pekania pennanti*), and others, the benefits of reducing severe fire through mechanical thinning may outweigh the adverse effect on spotted owl habitat, yet these areas need to be closely monitored because of high scientific uncertainty (Verner et al., 1992; Schwilk et al., 2009; Tempel et al., 2015; Jones, 2019). Increasing the use of fire as a management tool in fire-suppressed forests may increase the feasibility and spatial extent of restoration efforts compared to mechanical treatments alone (North et al., 2012). However, fire used in combination with mechanical treatments (e.g., removal of small and medium-sized trees) may be more effective in restoring vegetation structure with lower fuel loads than currently present, particularly in forests where the risks from prescribed or managed fire are now high (Schwilk et al., 2009). Thus, while much uncertainty and many obstacles remain, our study reinforces previous findings that owl conservation may benefit from restoration of frequent fire regimes in dry forests (Roberts et al., 2011; Jones et al., 2016, 2020; Eyes et al., 2017; Stephens et al., 2019).

5. Ethics approval and consent to participate

University of Wisconsin Institutional Animal Care and Use Protocol # A005367

6. Consent for publication

Not applicable.

7. Availability of data and materials

General data is available on request, but because of the sensitive status of these owls, specific owl locations will not be released.

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CRediT authorship contribution statement

Anu Kramer: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Gavin M. Jones:** Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.

Sheila A. Whitmore: Data curation, Writing - review & editing. **John J. Keane:** Writing - review & editing, Project administration. **Fidelis A. Atuo:** Conceptualization, Methodology, Writing - review & editing. **Brian P. Dotters:** Data curation, Writing - review & editing. **Sarah C. Sawyer:** Project administration. **Sarah L. Stock:** Writing - review & editing, Project administration. **R.J. Gutiérrez:** Writing - original draft, Writing - review & editing. **M. Zachariah Peery:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Funding acquisition.

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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Appendix A. Supplementary material

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Cover of tall trees best predicts California spotted owl habitat

Malcolm P. North[a,b,*], Jonathan T. Kane[c], Van R. Kane[c], Gregory P. Asner[d], William Berigan[e], Derek J. Churchill[c], Scott Conway[f], R.J. Gutiérrez[e,g], Sean Jeronimo[c], John Keane[a], Alexander Koltunov[f,k], Tina Mark[h], Monika Moskal[c], Thomas Munton[i], Zachary Peery[e], Carlos Ramirez[f], Rahel Sollmann[j], Angela White[a], Sheila Whitmore[e]

[a] *USFS PSW Research Station, Davis, CA 95618, United States*
[b] *John Muir Institute, University of California, Davis, CA 95616, United States*
[c] *College of the Environment, University of Washington, Seattle, WA 98195, United States*
[d] *Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, United States*
[e] *Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, United States*
[f] *US Forest Service Region 5 Remote Sensing Laboratory, McClellan, CA 95652, United States*
[g] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Minneapolis, MN 55455, United States*
[h] *Tahoe National Forest, Nevada City, CA 95959, United States*
[i] *USFS PSW Research Station, Fresno, CA 93710, United States*
[j] *Dept. of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, United States*
[k] *Center for Spatial Technologies and Remote Sensing (CSTARS), University of California, Davis 95616, United States*

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ABSTRACT

Restoration of western dry forests in the USA often focuses on reducing fuel loads. In the range of the spotted owl, these treatments may reduce canopy cover and tree density, which could reduce preferred habitat conditions for the owl and other sensitive species. In particular, high canopy cover ($\geq 70\%$) has been widely reported to be an important feature of spotted owl habitat, but averages of stand-level forest cover do not provide important information on foliage height and gap structure. To provide better quantification of canopy structure, we used airborne LiDAR imagery to identify canopy cover in different height strata and the size and frequency of gaps that were associated with owl nest sites, protected activity centers (PACs), and territories within four study areas and 316 owl territories. Although total canopy cover was high in nest stands and PAC areas, the cover in tall (> 48 m) trees was the canopy structure most highly selected for, while cover in lower strata (2–16 m) was avoided compared to availability in the surrounding landscape. Tall tree cover gradually decreased and lower strata cover increased as distance increased from the nest. Large ($> 1000\ \text{m}^2$) gaps were not found near nests, but otherwise there was no difference in gap frequencies and sizes between PACs and territories and the surrounding landscape. Using cluster analysis we classified canopy conditions into 5 structural classes and 4 levels of canopy cover to assess the relationship between total canopy cover and tree size within nest sites, PACs, and territories. High canopy cover ($\geq 70\%$) mostly occurs when large tree cover is high, indicating the two variables are often confounded. Our results suggest that the cover of tall trees may be a better predictor of owl habitat than total canopy cover because the latter can include cover in the 2–16 m strata – conditions that owls actually avoid. Management strategies designed to preserve and facilitate the growth of tall trees while reducing the cover and density of understory trees may improve forest resilience to drought and wildfire while also maintaining or promoting the characteristics of owl habitat.

1. Introduction

Historically dry western forests, on average, had lower tree densities, canopy cover and fuel loads than forests today largely due to the absence of frequent, low-severity fire for much of the 20th century (Knapp et al., 2013; Collins et al., 2015; Stephens et al., 2015; North et al., 2016). To increase resistance and resilience to current high-intensity wildfire and increasingly frequent and severe drought conditions (Graumlich, 1993; Asner et al., 2016; Margulis et al., 2016), managers often use mechanical thinning and managed fire to create

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[*] Corresponding author at: USFS PSW Research Station, Davis, CA 95618, United States.
E-mail address: mnorth@ucdavis.edu (M.P. North).

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some semblance of these historic stand conditions (Agee et al., 2000; Agee and Skinner, 2005; North et al., 2009). Such treated forests, however, often lack some of the structural features that have been linked with old-growth associated species such as the spotted owl (*Strix occidentalis*), fisher (*Martes pennanti*) and northern goshawk (*Accipiter gentillis*) (McClaren et al., 2002; Lee and Irwin, 2005; Purcell et al., 2009; North et al., 2010; Truex and Zielinski, 2013; Tempel et al., 2014; Sweitzer et al., 2016). In particular, throughout much of the western U.S., managing for the high canopy cover and tree density conditions of preferred spotted owl habitat may conflict with reducing ladder and canopy bulk density fuels, and stem density to improve a forest's fire and drought resilience (Zabel et al., 1995; North et al., 1999; Stephens et al., 2014; Jones et al., 2016; Stephens et al., 2016). The uncertainty about the effect of forest treatments on owls has often led to forest plans that separate landscapes into distinct restoration (i.e., managed to reduce fuels and stand density) and owl habitat zones (managed to preserve and increase high canopy cover) (Ager et al., 2007; Carroll and Johnson, 2008).

High (≥70%) levels of canopy cover within both owl territories and their core use areas (120 ha management designated Protected Activity Centers [PACs]) have been associated with greater owl occupancy and survival (Tempel et al., 2014; Tempel et al., 2015), and higher reproduction at nest sites (North et al., 2000). High canopy cover is commonly used to identify potential habitat areas and determine management options. Yet, canopy cover can be a difficult management target because estimates significantly vary depending on how many measurements are taken, the observer's viewing angle (i.e., closure vs. cover sensu Jennings et al., (1999)) and whether estimates are derived from direct field measurements (ex. spherical densiometer, densitometer, or 'moosehorn'), indirect interpretation (i.e., using aerial photographs or Landsat imagery) or modeled from non-spatial plot data (i.e., such as the Forest Service's estimates using the Forest Vegetation Simulator) (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009). Field plots are used to record tree size and foliage characteristics, but sample size is often small, which makes it difficult to extrapolate across the large, diverse forest conditions used by owls.

Canopy cover estimates using Landsat imagery or interpreted aerial photographs can sample larger areas, but neither method can be used to identify the tree size or height of foliage cover, and must be categorized (e.g., 0–39%, 40–69% and ≥70%) to meet the wide variety of ages and structures of forests (Tempel et al., 2016). Given the challenges of measuring canopy cover, both managers and researchers have often resorted to coarse classifications such as the widely used California Wildlife Habitat Relationships (CWHR) classes (Tempel et al., 2014) that are known to simplify and only roughly correlate with patterns of actual animal use (Purcell et al., 1992; Block et al., 1994; Howell and Barrett, 1998). Regardless of how it is estimated as a stand-level characteristic, canopy cover does not provide information on the height and distribution of foliage or the size and frequency of forest gaps (Jennings et al., 1999). Consequently, it is unclear how foliage and gaps are either distributed within owl use areas, or how best to assess and then establish management objectives for sustaining and enhancing owl habitat.

In this study we use airborne LiDAR data to measure canopy structure both intensively and accurately within all owl territories (n = 316 territories within a cumulative 420,478 ha) found in four large study areas having a variety of management histories in the central and southern Sierra Nevada. Three of these locations are long-term owl demographic study areas, and include an area in Sequoia/Kings Canyon National Park (SEKI) where the only logging occurred 75–120 years ago in localized, limited areas. SEKI includes forests with restored fire regimes, and has the only known non-declining population of spotted owls that have been studied in California. The fourth site, Tahoe National Forest, while not a demographic study area, did survey owl occupancy and reproduction over an extensive area for which LiDAR data was collected. The LiDAR data allowed us to map forests in high fidelity, measuring total canopy cover, the distribution of cover by height strata, and opening sizes and frequencies. We analyzed habitat at three scales for each owl pair: nesting area (~4 ha), the surrounding Protected Activity Center (~120 ha), and the encompassing territory (~400 ha). Using the data on tree cover in different height strata and how they are associated, we used cluster analysis to identify common forest structural conditions. We then compared structural conditions between owl use areas and the surrounding forest with a complete LiDAR sampling of the landscape within a 5 km radius.

The goal of this study was to use our large sample size and high fidelity measurements over large areas to examine which attributes of forest structure are most strongly associated with California spotted owl habitat. Using LiDAR measures of forest structure, we examined the following specific questions:

- Which canopy structures are most strongly associated with different scales of owl habitat use, focusing on the nest, PAC and territory?
- How does the percentage of overstory tree canopy area in different height strata and gap sizes compare between owl use areas and across study areas?
- How strongly selected are different canopy attributes at nests compared to the available landscape and how does that change with distance from the nest?
- How are structure classes distributed between different owl use areas and what is the relationship between these structure classes and total canopy cover?

2. Methods

2.1. Study areas

The four study areas are located on the western slopes of California's Sierra Nevada Mountains in predominantly ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests, and extend over a range of 3^0 latitude or about 320 km (Fig. 1). The Tahoe study area (311,930 ha) encompasses most of the Tahoe National Forest and is dominated by ponderosa pine, incense cedar (*Calocedrus decurrens*) and black oak (*Quercus kelloggii*) on drier, lower elevation locations, and a combination of ponderosa and sugar pine (*P. lambertiana)*, incense cedar, Douglas-fir (*Pseudotsuga menziesii*) and white and red fir (*Abies concolor* and *A. magnifica)* generally above 1300 m in more mesic conditions. At higher elevations (generally > 2000 m) and in the eastern-most portion of the owl use area, red and white fir and Jeffrey pine (*P. Jeffreyi*) dominate forest composition. Areas of the Tahoe NF are checkerboarded with private ownership and much of the forest has been heavily selectively logged over the last century, resulting in scattered large individual trees and small pockets of old growth (Taylor, 2004). Since about the 1930s almost all fires have been suppressed leaving forests often in a fuel-loaded condition with high stem density and canopy cover.

The Eldorado Study Area (40,549 ha) includes an owl demographic study area on the Eldorado National Forest (Tempel et al., 2016). It is located east of Georgetown on steep terrain surrounding the Rubicon and middle Fork of the American rivers between 300 and 2500 m elevation. It is primarily mixed conifer with occasional black and canyon live oaks (*Quercus chrysolepis*), tanoak (*Notholithocarpus densiflorus)* and bigleaf maple (*Acer macrophyllum*). At higher elevations some of the study area includes red fir and lodgepole pine (*Pinus contorta*). The Eldorado National Forest was logged selectively, often removing the largest trees, and fire suppressed through much of the last century (Darr, 1990). Portions of the demographic study area have a checkerboard of private land ownership, much of which is owned by SIMORG Forests LLC. About 50% of the owl study area burned, much of it at high severity, in the 2014 King Fire (Jones et al., 2016). The LiDAR data we use is from an acquisition completed before 2014.

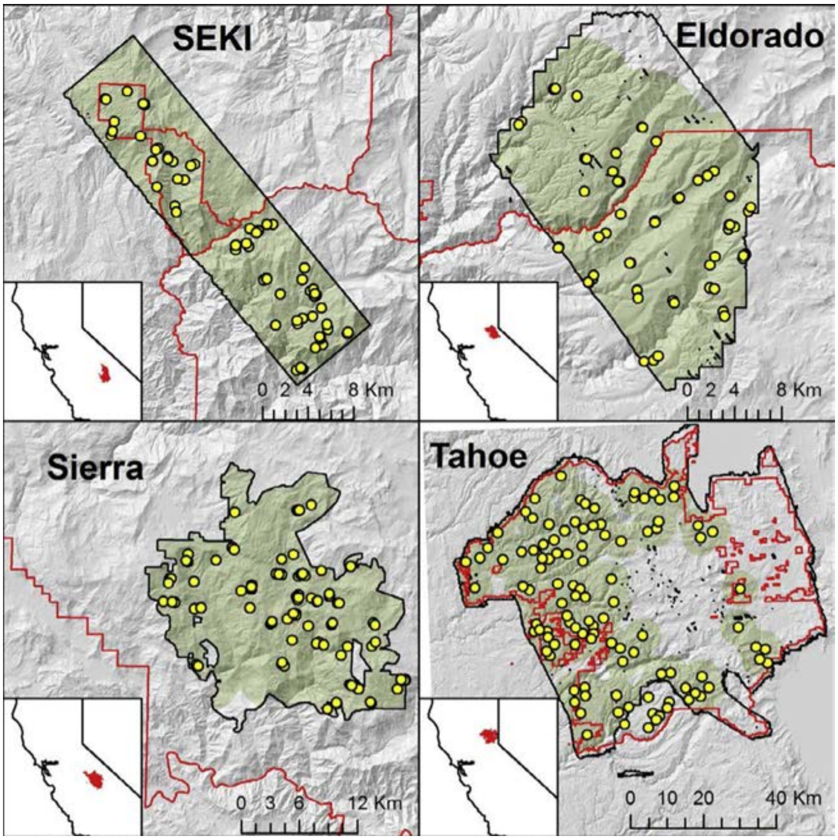

Fig. 1. The location in California (inset) of each of the four study areas. The black line shows the area of the LiDAR acquisition, circles indicate owl nest sites and green shading indicates the study area analyzed (i.e., within a 5 km radius of the PAC nests centroid). The background grey shading indicates the topography of the area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The Sierra Study Area (41,080 ha) is on the Sierra National Forest, east of Fresno between 300 and 2900 m elevation. Both the Sierra study area and the nearby Sequoia-Kings Canyon study area (SEKI) are drier than the Tahoe and Eldorado areas (North et al., 2016). The Sierra study area is dominated by mixed-conifer forests, but on lower and drier sites includes ponderosa pine, interior live (*Quercus wislizeni*) and canyon oaks. Higher elevations include red fir, lodgepole pine and western white pine (*Pinus monticola*) (North et al., 2002). Most wildfire has been suppressed on the Sierra National Forest for decades but the forest was not as extensively logged as the more northern study areas (North et al., 2005). Many large, old trees remain in stands that were selectively logged and areas of old growth remain on steeper slopes because topography limited access for mechanical logging (North et al., 2015).

The Sequoia/King Canyon (SEKI) area (26,919 ha) is located on the western side of the two national parks of the same name and is mostly comprised of ponderosa pine and mixed-conifer forest types between 425 and 3050 m in elevation. Within the mixed-conifer zone there are several giant sequoia (*Sequoiadendron giganteum*) groves. With the exception of localized hazard tree removal and small areas of late 19th century logging (Stohlgren, 1992), these forests have not been logged (Vankat and Major, 1978). In addition, although many fires were suppressed in the first half of the 20th century, fire has been restored throughout much of the study area beginning in the 1970s (Parsons et al., 1986). Of California's four demographic study areas, SEKI is the only owl population that has been stable to expanding (Franklin et al., 2004; Blakesley et al., 2010; Conner et al., 2013; Tempel et al., 2014; Tempel et al., 2016). Therefore in our analyses we often compare SEKI forest structure to the three other study areas because it may provide more favorable habitat relative to the more heavily logged and fire-suppressed areas on the national forests.

2.2. Spotted owl data

The three study areas (Eldorado, Sierra, and SEKI) that encompass California spotted owl demographic studies had similar survey methods (Blakesley et al., 2010), whereas slightly different owl survey methods were used in the Tahoe study area. For the three demographic areas, owls were annually surveyed from at least 1993 to the present (Tempel et al., 2016). All three areas contained a core zone that was completely surveyed (i.e., known territories as well as areas not containing owls). Some individual owl territories were added over time that surrounded core areas to increase sample size for demographic analysis, while a portion of SEKI was deleted in 2006 due to funding limitations. Surveys were conducted from April 1 to August 31 in the Eldorado study area and from March 1 to September 30 in the Sierra and SEKI study areas. SEKI was not surveyed in 2005 due to budget limitations that year. Spotted owl vocalizations were used as vocal lures and broadcast at designated survey stations or while walking survey routes. The sex of owls was initially determined by the pitch of territorial 4-note calls (Forsman et al., 1984). If owls were detected during nocturnal surveys, diurnal surveys were conducted as a follow up to band unmarked birds, re-sight marked birds, assess reproduction, locate nesting/roosting areas, and band fledglings (Franklin et al., 1996).

Owl surveys in the Tahoe National Forest were conducted for at least two years before and two years after in areas where management treatments (e.g., thinning to reduce fuel loads) were conducted. As such the Tahoe area did not have a core study area that was continually sampled but instead had focal surveys that shifted with management activities. However, owl survey methods were similar to those used on the owl demographic study areas.

In each study area, our analysis focused on confirmed owl pair nest sites that were occupied for at least one year. To insure that the LiDAR assessed forest conditions relevant to owl use, we only used 2001–2013 owl nest sites. We conducted our analysis at four different scales related to owl use and management. The nest site was considered a four-hectare area immediately surrounding each nest tree or snag. The size of the area around a nest that may influence owl selection has not been assessed but several studies have suggested canopy cover and microclimate conditions may be factors in nest site selection (LaHaye et al., 1997; LaHaye and Gutierrez, 1999; North et al., 2000). We used four hectares as a conservative estimate for the area over which forest structure might influence microclimate (Ma et al., 2010). The protected activity center (120 ha or 300 ac) has been a forest management construct designed to approximate a core area that receives heavy use (Verner et al., 1992). In practice, agencies define these areas as a polygon of the best available habitat (often related to tree size and disturbance history) around a nest location (Verner et al., 1992; Tempel and Gutierrez, 2013) that often approximates a circle. Without knowing the exact shape of each PAC, for our analysis we defined this area as a circle of 120 ha (300 ac) immediately around the centroid of all nests belonging to an individual owl (Berigan et al., 2012). To estimate forest characteristics within a territory, we used territory sizes within the three study areas that were delineated as 400 ha, 302 ha and 254 ha for the Eldorado, Sierra and SEKI studies, respectively (Tempel et al., 2016). We did not have similar information for the Tahoe study area. Thus we fitted a regression line of territory size against latitude using the three demographic studies areas, as well as a fourth demographic study area on the Lassen NF (639 ha), which resulted in an approximated territory size of 437 ha for the Tahoe study area.

To estimate availability in the surrounding landscape, we used a circle 5 km in radius from the calculated activity center of each territory. To evaluate how forest conditions may differ with potentially different owl uses (e.g., nesting vs foraging and the influence of a central place forager), we removed the PAC area from territory calculations. In contrast, we did not remove the nest areas from each PAC, because studies have shown that owls select multiple nest and roost locations throughout a PAC (LeHaye et al., 1997).

2.3. Analysis of canopy structure

LiDAR data was acquired over our study areas between 2010 and 2015 (Table 1). We used the digital terrain models prepared by the acquiring vendor or organization. We processed the LiDAR data using the USDA Forest Service's Fusion software package (version 3.60, http://forsys.cfr.washington.edu/fusion/fusionlatest.html) (McGaughey, 2016) to produce metrics describing the canopy structure. In the processing, we normalized all laser returns to height above the digital terrain models. There were no major disturbances such as large high severity fire on our study areas between the time of the collection of the owl field data and the acquisition of the LiDAR data.

We used several strategies to generate the widest possible range of canopy structure measurements. We used the FUSION gridmetrics utility to produce 30 m resolution rasters of statistical measures of the vertical distribution of LiDAR return heights. This provided measurements of percentile return heights (e.g., 95th percentile height is the height at which 95% of returns fall below), standard deviation of return heights, and skew and kurtosis of return heights. These quantify canopy structures that have been associated with owl use: tall tree height, the variability in tree heights and how evenly or skewed tree heights are, respectively. We calculated these statistical descriptors excluding returns < 2 m to exclude returns representing the ground, shrubs, and saplings. The gridmetrics utility also produced a measurement of canopy cover calculated as the count of returns above 2 m divided by the count of all returns.

Researchers are beginning to analyze forests as clumps of trees and openings (e.g., Larson and Churchill, 2012). We developed methods for this study to do this using the LiDAR data. Several studies have found that characteristic tree clump and opening patterns emerge at scales of 0.5–1 ha (Harrod et al., 1999; Larson and Churchill, 2012; Knapp et al., 2012; Lydersen et al., 2013). We therefore analyzed these patterns at a 90 m (0.81 ha) scale. We created a canopy surface model with a grid cell size of 0.75 m^{-2} and assigned the height above the digital terrain model of the highest return to each grid cell. We used the canopy surface model to identify tree approximate objects (TAOs) using the watershed segmentation algorithm implemented in the TREESEG utility in the FUSION package (Fig. 2). The TREESEG utility provided a raster map of the modeled canopy area of each TAO with the maximum height of each TAO assigned to the entire canopy area for that TAO (Fig. 3a). We then reclassified each TAO into the following height strata: 2–16 m, 16–32 m, 32–48 m, and > 48 m so that clumps of overstory trees with similar heights could be identified. Areas with no canopy > 2 m were considered openings. We measured the area in each strata using a moving 90 by 90 m window with measurements centered at 30 m spacing to match the raster cells of the statistical and canopy cover measurements (Fig. 3b). The use of an overlapping moving window had the practical effect of smoothing the measurements of tree clump and opening areas. We report metrics as the area in each stratum for each grid cell.

We also investigated whether the presence and density of larger gaps that might affect microclimate and protective cover conditions for the owls, as well as providing foraging opportunities for the owl, were negatively associated with owl habitat. We defined gaps following methods (Lydersen et al., 2013) that set a minimum size of 112 m^2, the approximate crown area of a dominant tree. We binned gaps larger than this minimum size into categories suggested by research on forests that have frequent fire regimes (Harrod et al., 1999; Larson and Churchill, 2012) and operational sizes often used by managers in thinning prescriptions (Knapp et al., 2012; North and Rojas, 2012; Stine and Conway, 2012). We reported the percentage of area and frequency for gaps in the categories 112–1000 m^2, 1000–5000 m^2, 5000–10,000 m^2, and > 10,000 m^2 (Fig. 3c).

2.4. Statistical analysis

To identify canopy variables most strongly associated with owl use, we initially used three statistical approaches to compare structures at nest sites against the surrounding landscape: niche overlap modeling, general linear models and random forest. All three approaches produced similar results and hereafter we base inference on niche overlap modeling because it provides a quantitative measurement of distinction

Table 1
Attributes of owl territories and LiDAR data used for the four study areas.

Owl data	Tahoe	Eldorado	Sierra	SEKI
No. of nests	64	58	63	131
Area (ha) of coverage within 5 km of a nest	311,930	40,549	41,080	26,919
Elevation range within 5 km of a nest	292–2673	711–2190	390–2961	835–2643
Year(s) data acquired	2013 & 2014	2012	2010 & 2012	2015
Acquirer	NCALM[a]	NCALM[a]	Watershed Sciences[b]	Carnegie Institution for Science
Instrument family	Optech	Optech	Leica	CAO[c]/Optech
# of returns/m[b]	10.3	8.1	12.3	14

[a] National Center for Airborne LiDAR Mapping.

[b] Now part of Quantum Spatial.

[c] Carnegie Airborne Observatory modification of Optech (see Asner et al., 2012).

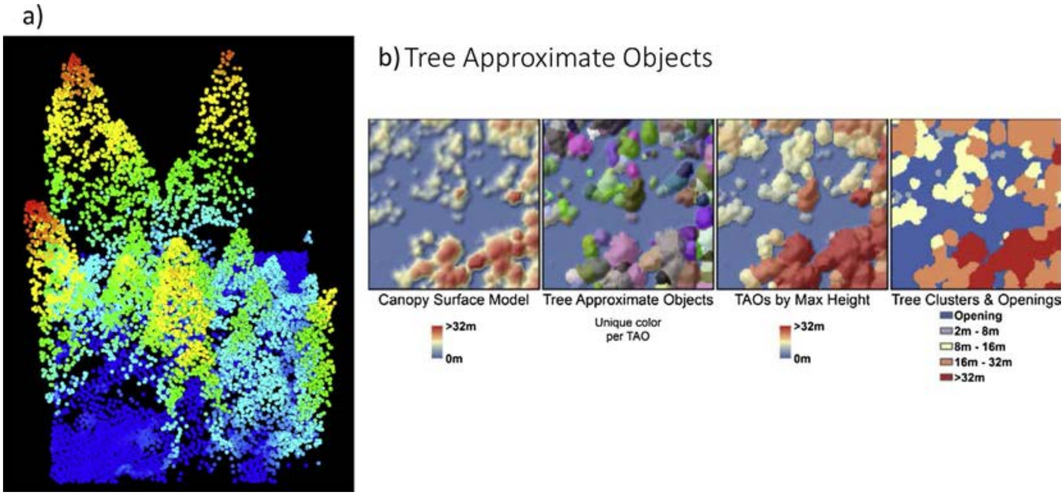

Fig. 2. Example of (a) a LiDAR point cloud where returns are color-coded by height; and (b) how tree approximate objects (TAOs) and gaps are derived from the point cloud data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between two distributions (Mouillot et al., 2005; Broennimann et al., 2012). Niche overlap compared the distribution of values of a structural variable across a landscape ('availability') relative to a specific location ('selection'). Smaller overlaps indicated that areas used by owls were more distinct from what was available across the landscape and by inference was selected by the owls (Fig. 4a).

Focusing on the canopy and gap attributes with the highest niche model ranks (Supplemental Table 1), we calculated the median, and standard deviation of each attribute as four different scales; nest sites, PACs, territories and the surrounding landscape within each study area. We then tested for significant differences between study areas using Student's post hoc ANOVA.

Spotted owls are central place foragers (Carey and Peeler, 1995), suggesting that canopy structure may change with distance from core locations (i.e., nesting and roosting sites). To evaluate changes in canopy conditions with distance from the nest, we assessed the niche decay function using annuli that expanded by 30 m per step. For highly ranked niche model variables, we plotted the percentage of niche overlap as a function of distance from owl nests for each of the four study areas.

Forests are often a complex assemblage of foliage in different strata. To quantify and describe how multiple canopy structures may commonly occur together, we created structure classes combining three core attributes of forest structure: tree height distribution, total canopy cover, and cover in different strata. These variables were analyzed using hierarchical clustering with the Ward method and the hclust

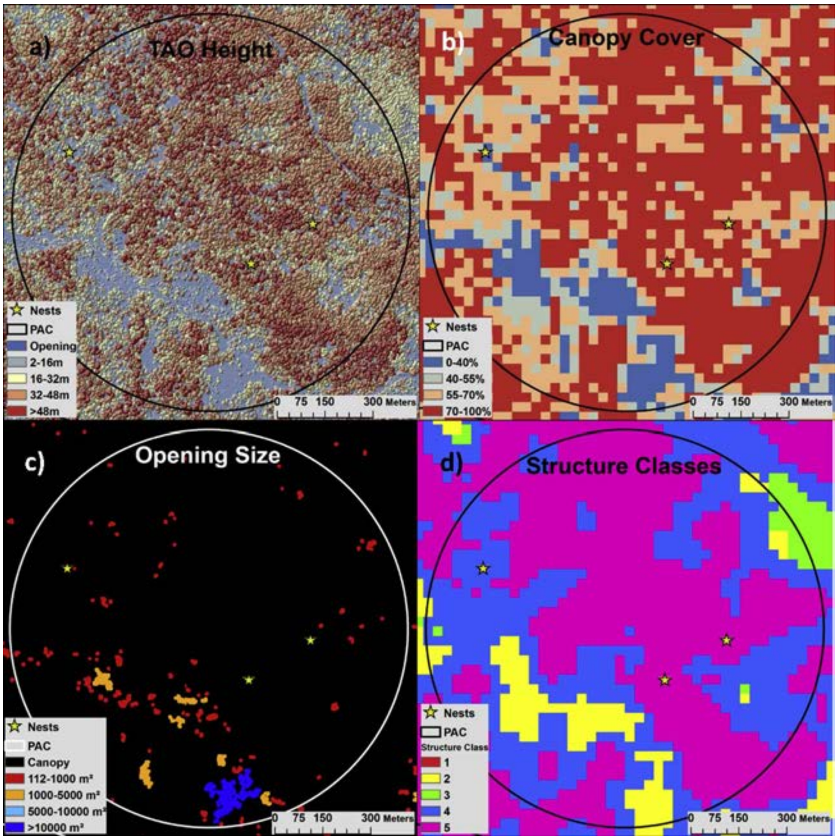

Fig. 3. Example of the distribution of (a) TAOs by height class; (b) total canopy cover; (c) opening size; and (d) structure class for the same PAC area (black circle) in the Eldorado study area. Stars indicate nest locations.

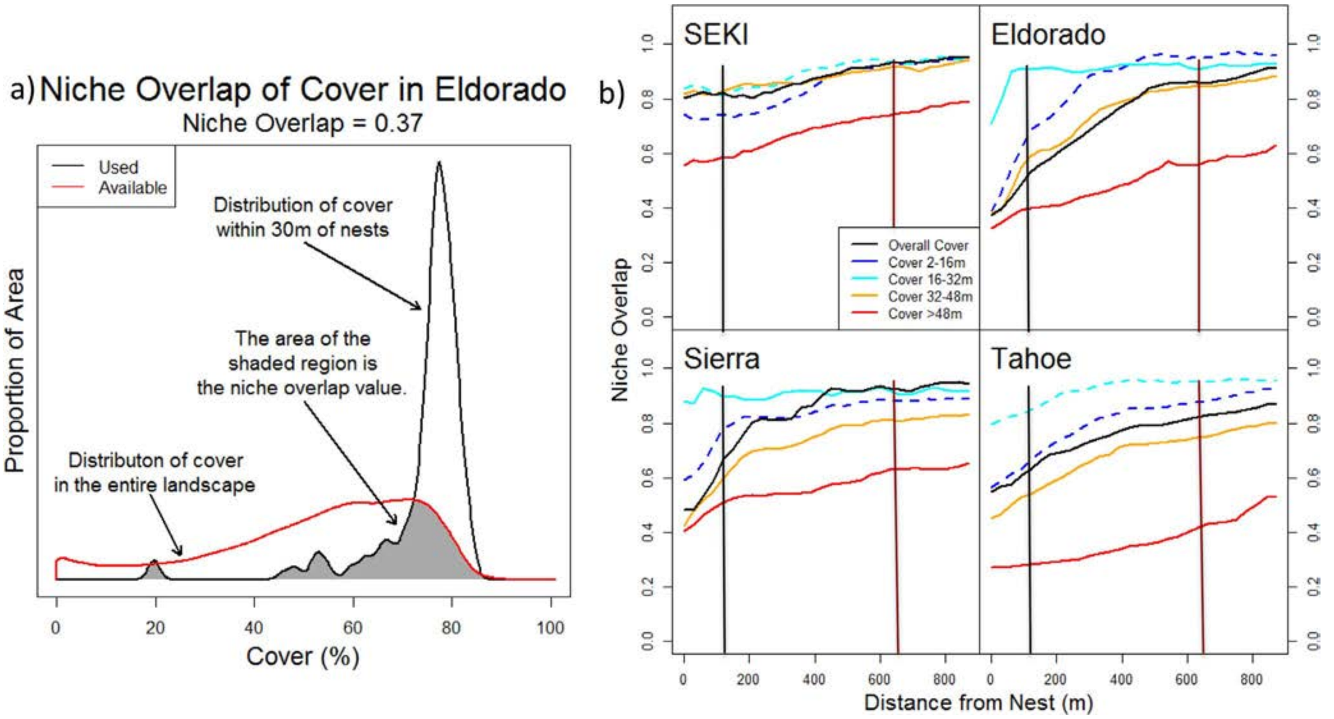

Fig. 4. (a) An annotated example of how niche overlap is calculated; and (b) graphs of niche overlap for total canopy cover and cover in four different height strata in each of the four study areas with distance (m) from the owl nest. Dashed lines are canopy structures that have lower values near the nest than in the surrounding landscape. Vertical lines indicate the distance defining the nest (black) and PAC (brown) areas.

function of the R statistical package (Team, 2013). Using dendrograms derived from 30,000 samples and structural characteristics of trial classes, we parsed conditions into five canopy structure classes that was the most parsimonious grouping that retained most (> 70%) of the original information (McCune and Mefford, 1999) (Supplemental Fig. 1). Within each of the five structure classes, we divided samples into four different canopy cover classes that previous research has suggested may be important thresholds to spotted owls; 0–39%, 40–54%, 55–69% and ≥70% canopy cover (Tempel et al., 2015, 2016). Therefore, we derived the percent area of each combination of canopy structure and canopy cover classes for nest, PAC, territory, and landscape areas.

3. Results

3.1. Canopy attributes associated with owl use

To determine which forest conditions were most distinct in areas used by owls versus the surrounding landscape, we evaluated 75 canopy structural attributes (Supplemental Table 1). The area of TAO canopy > 48 m was the most distinct metric for all study areas. The strongest nest and PAC selection for tall tree cover was in the Eldorado and Tahoe study areas presumably because both National Forests have been extensively logged and large, tall trees are rarer (Table 2). Area of TAO canopy 32–48 m, canopy cover, and measures of canopy height from LiDAR returns were moderately distinct from the surrounding landscape. Total area in gaps and gaps in different size ranges were among the least distinct. However, in the Tahoe study area, there were fewer small gaps (112–1000 m^2) within PACs compared to the surrounding landscape (Table 2).

Across all four study areas, median values for total canopy cover and cover in trees > 48 m were highest at nest sites, and consistently decreased as area expanded to PACs, territories and then the surrounding landscape (Table 3). We also found a similar trend of decreasing values from nest sites to landscape for the 32–48 m strata on the three National Forest study areas but not at SEKI. We found a reverse trend for cover in the 2–16 height strata with the lowest cover values near nest sites and increasing through larger scales. We did not find a consistent trend with changes in scale for cover values for the 16–32 m strata.

Across the entire study area, 20–40% of LiDAR returns were penetrating below 2 m indicating substantial area in openings. However, few of these openings were aggregated enough to reach the 112 m^2 threshold we used to define a ‘functional’ gap (an opening approximately equal to the canopy space occupied by a dominant tree). Gaps 112–1000 m^2 were rare within nest areas, and only accounted for 0.17–1.45% of the area in PACs and territories. Larger gaps were not found in nest areas. The area in gaps of 1000–5000 m^2 within PACs and territories ranged from 0.05 to 1.21% and we only found gaps > 5000 m^2 in the Sierra and Tahoe study areas (Table 3).

We found differences in canopy and gap conditions among the four study areas (Table 3). SEKI had lower canopy cover at nest sites, higher cover of tall trees (> 48 m) within nest sites, PACs and territories, and higher cover in the 32–48 m strata in territories. The Eldorado had greater cover than other areas in the 2–16 m cover in PACs and territories. The Sierra had lower total canopy cover in PACs and territories, and more gaps of all sizes, particularly those > 1 ha, in PACs and territories. The Tahoe had no distinguishing canopy cover conditions but did have high cover in gaps of all sizes at the territory scale (Table 3).

3.2. Changes in canopy structure with habitat scale

We examined spatially-explicit relationships by evaluating how niche overlap values changed with distance from the owl nest using a moving window and comparing each canopy attribute to its abundance in the surrounding (5 km) landscape (Fig. 4b). For all four study areas, the cover in tall (> 48 m) trees was the most distinct canopy attribute (i.e., the least niche overlap) starting at the nest site (the y intercept) and remained the most distinct over the 1000 m distance evaluated. The slope of the line for the cover of trees > 48 m continued to rise over 1000 m from the nest, suggesting that selection for tall trees may continue beyond the bounds of the PAC (618 m radius). Total canopy

Table 2
Niche values for different canopy structure attributes in four study areas and their overall mean comparing PAC and landscape habitat conditions. Bold values have low niche overlap (≤0.6) suggesting a structure selected for within PACs compared to the landscape. Metrics in italics are negative (i.e., have lower values in PACs compared to landscape). Metric type indicates the data used to calculate the structure value and pixel size indicates the dimension of the pixel used in the calculation. Canopy cover was calculated as the proportion of LiDAR returns greater than 2 m in height above the ground divided by all returns. Gap area was calculated as the area of the 0.75–2 m canopy surface model with no returns > 2 m.

Metric	Eldorado	SEKI	Sierra	Tahoe	Mean	Metric type/Pixel size
Canopy area TAO's > 48 m	**0.49**	0.66	**0.6**	**0.37**	**0.53**	TAO/90 m
Canopy area TAO's > 32–48 m	0.75	0.87	0.75	0.71	0.77	TAO/90 m
95th percentile lidar return height	0.81	0.75	0.79	0.76	0.78	Returns/30 m
75th percentile lidar return height	0.81	0.75	0.8	0.76	0.78	Returns/30 m
50th percentile lidar return height	0.81	0.75	0.81	0.77	0.78	Returns/30 m
Std Dev. of lidar return heights	0.83	0.79	0.8	0.77	0.8	Returns/30 m
25th percentile lidar return height	0.81	0.76	0.83	0.79	0.8	Returns/30 m
Canopy area TAO's 2–16 m	0.8	0.76	0.84	0.82	0.81	TAO/90 m
Canopy cover from lidar returns	0.75	0.88	0.87	0.78	0.82	Cover/30 m
Total gap area	0.75	0.89	0.88	0.77	0.82	TAO/90 m
Area in gaps 112–1000 m^2	0.91	0.91	0.94	**0.56**	0.83	Gap/90 m
Area in gaps 5000–10,000 m^2	0.9	0.77	0.88	0.88	0.86	Gap/90 m
Area in gaps > 10,000 m^2	0.81	0.88	0.86	0.89	0.86	Gap/90 m
Area in gaps 1000–5000 m^2	0.96	0.89	0.86	0.85	0.89	Gap/90 m
Canopy area TAO's 16-32 m	0.93	0.81	0.91	0.94	0.9	TAO/90 m

Table 3
Median percent cover of total canopy cover, cover by height strata and cover of different gaps by size class in owl nests, PACs, territories and the surrounding landscape in four study areas. Comparing values within the same scale (ex. all nests), **bold** values are significantly higher and ***italic bold*** values significantly lower than the values in the other three study areas ($p < 0.05$, post hoc ANOVA). Landscape values are medians calculated from the whole landscape area and as single values are not included in the ANOVA analysis.

		Total and by Stratum Canopy Cover (%)					Cover (%) in Gaps by Size Class			
Area	Scale	Total CC	> 48 m	32–48 m	16–32 m	2–16 m	112–1000 m^2	1000–5000 m^2	5000–10,000 m^2	> 10,000 m^2
SEKI	Nest	***67.9***	**23.7**	26.6	19.4	6.7	0.02	0	0	0
	PAC	66.8	**20.6**	29.3	***20.8***	9.3	0.46	0.2	0	0
	Terr	63.9	**16.6**	**30.5**	23.3	11.6	0.59	0.31	0	0
	Land	65.9	3.2	24.1	26.4	11.7	0.82	0.54	0.18	0.42
Eldo.	Nest	76	14.7	38.1	31.8	5.1	*0*	0	0	0
	PAC	67.6	8.3	25.6	35.8	**16.9**[b]	0.17	0.05	0	0
	Terr	61.8	4.8	20.8	36.7	**25.7**[b]	0.39	0.26	0	0
	Land	55.8	0	9.9	32.4	22.2	0.73	0.57	0.22	1.7
Sierra	Nest	75.9	9.4	30.4	24.2	6.2	0.20	**0**[a]	0	0
	PAC	***59.6***	9.2	27.4	24.8	7.7	0.88	**1.03**	0	**0.60**
	Terr	***52.3***	5.5	22.6	25.2	9.1	1.45	1.21	0.3	1.57
	Land	55.7	0	14.9	22.8	9.4	1.51	1.28	0.55	4.18
Tahoe	Nest	73.7	12.5	41.5	25.6	3.6	0.01	0	0	0
	PAC	67.2	6.9	31.6	32.7	9.9	0.72	0.51	0	0
	Terr	62.2	4.3	22.6	35.4	12.1	1.16	0.81	0.21	0.71
	Land	46.2	0	2.4	26.9	10.1	1.93	1.43	0.51	4.07

[a] Although all the cover values for gaps 1000–5000 m^2 at nest locations are zero due to rounding, the Sierra value is significantly higher than the values at the other three study areas.

[b] The high percentage of cover in the 2–16 m stratum on the Eldorado is influenced by a checkerboard of private ownership lands, many of which contain young plantations in this height class.

cover continued to rise across the 1000 m measured, but had the lowest niche overlap values between 0 to approximately 500 m on the Eldorado, Sierra and Tahoe study areas. In contrast, canopy cover at SEKI was not a selected canopy attribute except right at the nest site (Table 3).

3.3. Structure classes and canopy cover

Using the percent cover of TAOs in different height strata within over 30,000 pixels (each 30 by 30 m), hierarchical cluster analysis produced a dendrogram that had five structure classes retaining > 70% of the information (McCune and Mefford, 1999) (Supplemental Fig. 1). Understory (class 1) is dominated by tree cover in the 2–16 m strata, Openings (class 2) has low total canopy cover and more large gaps, Ladders (class 3) by cover in the 16–32 m strata, Co-dominants (class 4) by cover in the 32–48 m strata and Tall Trees (class 5) by cover in the > 48 m strata (Fig. 5).

Taking each of the classes and subdividing them into four canopy cover classes (0–39%, 40–54%, 55–69% and ≥70%), we examined how the percentage of total area of each structure/canopy cover class changed between nest sites, PACs, territories, and landscapes in each of the four areas (Fig. 6). Canopy cover conditions ≥70% (right slant hatching in Fig. 6) was dominated by the Tall Tree structure class (purple bars in Fig. 6) indicating that tall trees and high canopy cover co-vary. The Co-dominant structure class was dominated by canopy cover categories ≥55%, as the Understory and Ladders structure classes had fairly equal canopy cover distributions, while the Openings structure was dominated by 0–40% canopy cover. Nest sites and PAC areas were dominated by the Tall Tree and Co-dominant structure classes with high canopy cover (i.e., > 55%), but territories and landscapes had a much more even distribution of structure classes suggesting greater heterogeneity of forest conditions at these larger scales. Trees > 32 m, and especially > 48 m, were almost always associated with high canopy cover in large part because the large canopy area of these trees created high canopy cover. Locations with high canopy cover but without tall trees were not associated with owl nest sites or PACs.

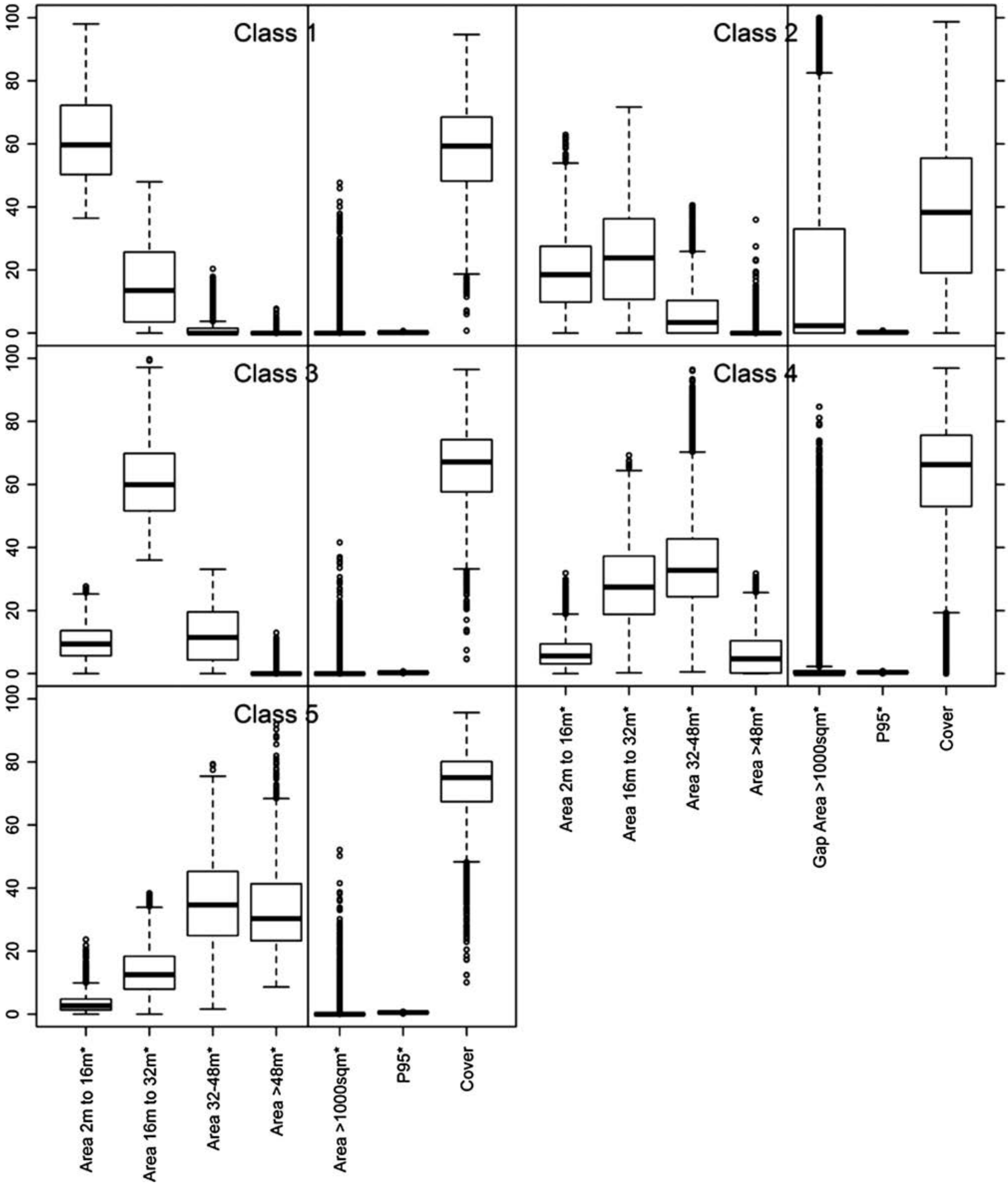

Fig. 5. Boxplots of canopy attribute values for each of the five identified structure classes. The boxplot contains the 25–75% range of values and the interior line is the median value. Whiskers show the range from 10 to 90% and dots are outliers. Gap area > 10,000 m^2, P95 (maximum height recorded from 95% of returns) and canopy cover are shown for reference but were not used in the cluster analysis to determine the structure classes.

4. Discussion

We found that the height of canopy cover matters, and the retention and promotion of large trees and the cover they provide may more directly benefit owl habitat than high levels of total cover from any canopy strata. Median values of total canopy cover were higher in nest and PAC areas than territories and the surrounding landscape, but the most distinct niche selection was cover of trees > 48 m. Tall tree cover is rarer on national forest lands (Table 3), and yet what is available is consistently found in nest and PAC areas. Our structure class analysis indicated that > 70% total canopy cover rarely occurred except when cover of Tall Trees and Co-dominants was high (classes 4 and 5 in Fig. 6), suggesting these two variables were often confounded. This covariance may explain why canopy cover, which is easier to measure

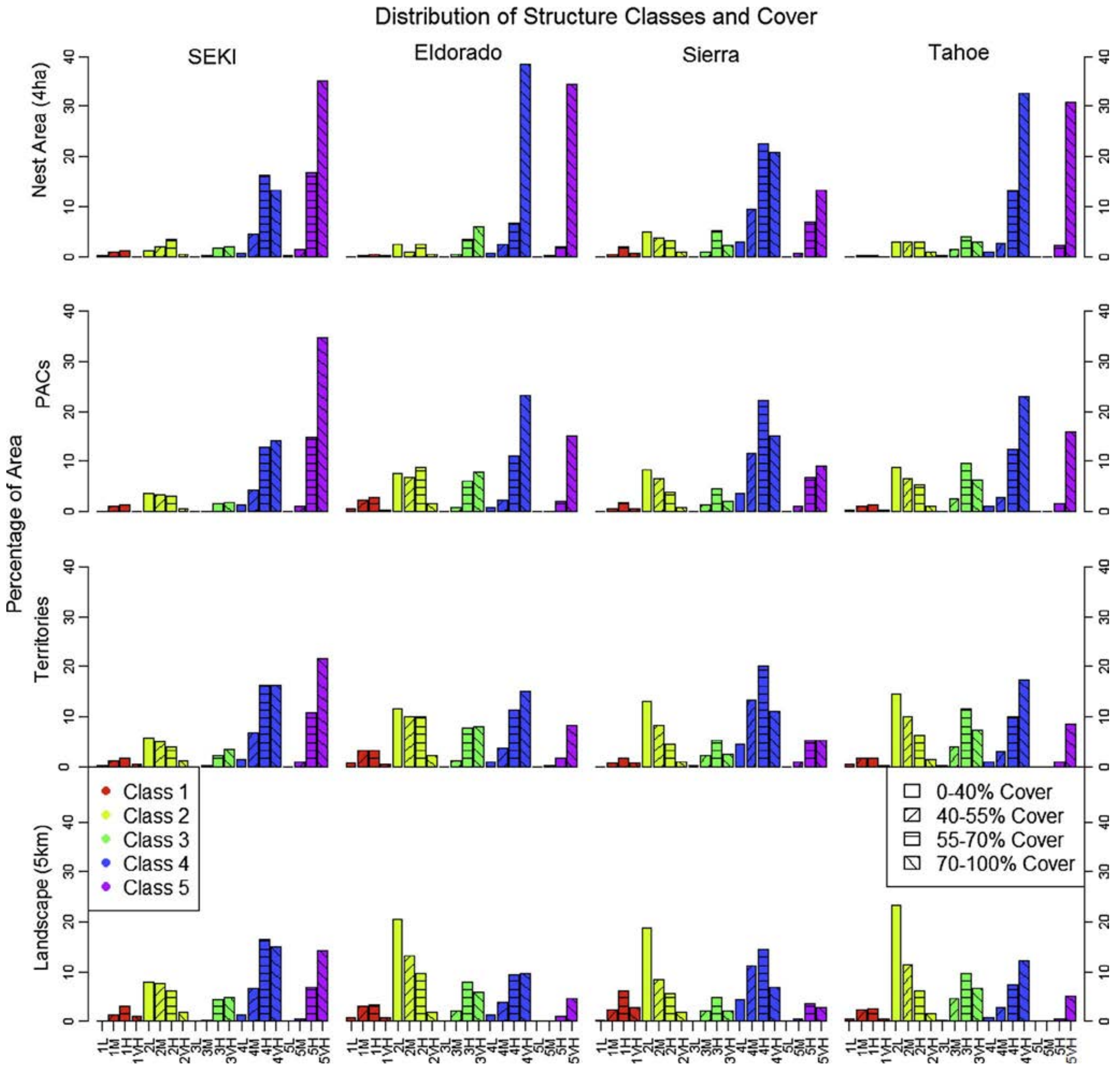

Fig. 6. Frequency distribution (% of total area) for each of the structure classes by nest, PAC, territory and surrounding landscape for each of the study areas.

and often recorded, has been reported as the forest condition associated with spotted owls rather than the cover in tall trees. Furthermore, although cover in the 2–16 strata can contribute to total canopy cover values, our analysis indicates nest sites and PACs actually have less cover in this stratum than is present in territories and the surrounding landscape, suggesting owls avoid this condition.

4.1. Large trees and canopy cover

Spotted owl research has consistently shown that owls are associated with large trees and total canopy cover (Call et al., 1992; Verner et al., 1992; North et al., 2000; Tempel et al., 2014; Tempel et al., 2016), but research has rarely parsed canopy structure into different height strata or assessed gap conditions. Our results confirm some widely reported owl habitat characteristics (Hunsaker et al., 2002; Blakesley et al., 2005; Seamans and Gutierrez, 2007), using larger sample sizes and a more quantitative measure of canopy structure than previous ground-based plot sampling and aerial photograph interpretation (although see Garcia-Feced et al., (2011)). Owl nest sites are in areas of high canopy cover that are dominated by a high percentage of cover in tall trees and few canopy gaps. Several studies of California spotted owl nest stands have also reported a selection for areas with high levels of canopy cover and groups of large (>75 cm dbh) trees (LaHaye et al., 1997; Blakesley et al., 2005).

The high canopy cover levels associated with spotted owl use areas has suggested that gaps were generally avoided or might reduce habitat quality. We found that gaps of any size, even as small as those in our 112–1000 m^2 category were rare in nest sites. Few studies have measured or discussed gap size and their frequency near nests, although one paper reported that owls generally avoided nesting in gap areas in fire-restored forests in Yosemite (Roberts, 2008; Roberts et al., 2011). At larger scales (PACs and territories) gaps were still rare in the SEKI and Eldorado study areas (Table 3), and sparse in the Sierra and Tahoe areas, but we did not find any pattern suggesting their abundance or size class distribution was significantly different from conditions in the surrounding landscape. Owl tolerance of gaps is difficult to infer from our data because gaps of at least a dominant tree crown area or larger are rare in our study areas. Since spotted owls persisted in historic forests that had much lower canopy cover and more gaps than modern forests, a better understanding of owl response to gaps may require telemetry location data.

We found the cover in tall trees was the most important canopy feature in PACs from the surrounding landscape (Table 2). In contrast, several studies have found the percentage of moderately high (> 50%) and high (> 70%) levels of canopy cover were most associated with owl occupancy and reproduction (Berigan et al., 2012; Tempel and Gutierrez, 2013; Tempel et al., 2014; Tempel et al., 2015; Tempel et al., 2016). Across our four study areas, PAC canopy cover averaged 67.6% (Table 2), and on the three national forest study areas PAC canopy cover ranged from 3.9% (Sierra) to 21% (Tahoe) higher than the surrounding landscape (Table 3). However, our niche overlap analysis showed that the canopy structure that was most distinct (i.e., lowest niche overlap scores of 0.49–0.68) was the cover in tall trees (Table 2). Canopy cover had much higher niche overlap values (0.75–0.88) than other attributes. The confounding of high-levels of canopy cover with the cover of tall trees may explain why other studies that did not account for tree height have generally reported total canopy cover as the most significant feature of PAC habitat.

4.2. Variation in canopy conditions from nest site to landscape

While we found that total canopy cover was generally higher within about 500 m of nests (Fig. 4b) compared to the surrounding landscape, the area in tall trees continued to be the most distinct canopy structure (lowest niche overlap) as distance from the nest sites increased over the 1000 m from nests we assessed. This suggests that the cover in tall trees could also be beneficial to owls when foraging because they often travel away from the nest to forage (Irwin et al., 2007; Williams et al., 2011). However, without telemetry we were unable to assess how owls used different forest conditions for foraging. Several studies have suggested heterogeneous forest conditions, particularly edges between cover types, may influence foraging behavior or reproductive success (Franklin et al., 2000; Eyes et al., 2017). Some degree of vertical structure seems to be important for owl foraging (Call et al., 1992) but it's unclear whether owls respond to canopy layering produced by adjacent forest patches of contrasting height or multi-layer foliage within the same stand. New technologies such as lightweight GPS tracking devices could be used to pinpoint foraging locations and improve our analysis of vertical layering.

4.3. Study area differences in large tree abundance

We found that > 70% canopy cover was usually only achieved when there were tall trees present. Canopy cover in modern Sierra Nevada forests typically averages between 40 and 60% depending on several factors including forest type, site productivity and disturbance history (Lydersen and North, 2012; Miller and Safford, 2017). Forests with canopy cover > 70% are not rare, but they usually occur in mixed-conifer forest types and require a combination of high site productivity and/or a long period of fire suppression (Collins et al., 2011). The owl's documented association with high canopy cover conditions has raised one hypothesis that owls have benefited from fire suppression and may presently have more high-quality habitat than would have been present under active-fire forest conditions (North et al., 2017; Peery et al., 2017). However, if the preferred canopy characteristic of nest and PAC conditions is an abundance of tall trees, then large tree harvest, such as National Forests have experienced, may have reduced the quality and/or extent of favorable habitat on Forest Service lands.

We did not find significantly higher canopy cover levels in SEKI, the only owl study population that is not declining, but we did find significantly higher cover of tall trees. The covariance of many structural attributes in forests (i.e., old forests often have large trees, big snags and logs, etc.) makes it difficult to partition individual attributes as the most significant habitat variable. Cover of tall trees may directly benefit owls by providing overhead predator protection or microclimate modification or indirectly by being associated with other age, size, and dead wood structural attributes that often occur when tall trees are present (Gutiérrez et al., 1995). Our research shows that tall tree cover is correlated with owl habitat, but identifying the particular benefits will require further study.

4.4. Implications for future research

We acknowledge several limitations of our research that constrain our understanding of California spotted owl habitat but that might be addressed with future research. While our LiDAR analysis provides a large sample size and precise quantification of the forest canopy, it cannot provide information on snags and logs, either of which may influence habitat selection (Call et al., 1992; Verner et al., 1992; LaHaye et al., 1997). Methods are being developed to accurately assess snags using LiDAR, and understory conditions, including coarse woody debris, can be measured with ground-based LiDAR (Hopkinson et al., 2004). Ground-based methods will have smaller sample sizes than aerial LiDAR, however, stratified sampling of different structure classes may overcome these limitations.

We focused on partitioning elements of canopy conditions that usually co-vary. This required a large dataset of owl locations and their delineated PACs. A next step building upon our analysis would be to weight these locations either by their frequency of use (accounting for years of observation) or reproductive output. We also did not have spatially-explicit data of owl habitat use such as that derived from radio telemetry and therefore, beyond the nest site, we used general scales of PAC and territory. However, as a central place forager and as several telemetry studies have shown, owl use decreases with distance from nests or roost (Call et al., 1992; Carey and Peeler, 1995; Rosenberg and McKelvey, 1999; Blakesley et al., 2005; Irwin et al., 2007; Williams et al., 2011; Williams et al., 2014). We hypothesize that telemetry would likely show that owls typically have many areas within their territories that are lightly used or completely avoided (Carey et al., 1992). This would greatly refine an analysis of forest structural conditions associated with owl territories, which are predominantly used for foraging. The structural heterogeneity of forests that some studies have suggested may benefit owl foraging (Eyes et al., 2017) could be examined with a much better understanding of which parts of the territory areas are most heavily used. Better insight into owl territory use would also greatly benefit from a spatially-explicit sampling of small mammal abundance, particularly common prey species such as the dusky-footed woodrat (*Neotoma fuscipes*) and northern flying squirrel (*Glaucomys sabrinus*) (Ward et al., 1998; Smith et al., 1999; Meyer et al., 2005a; Innes et al., 2007; Meyer et al., 2007a) and how these prey species are affected by common forest treatments (Meyer et al., 2005b).

Finally, we do not infer what may constitute 'optimal' owl habitat. In three of our four study areas, forests have been extensively altered by past timber management and fire suppression. We have attempted to identify favorable habitat using areas in SEKI without timber harvest and having recently (i.e., since the 1970s) restored fire regimes. However, even these forests have higher density and canopy cover from pre-1970 tree ingrowth that is now large enough to survive re-introduced surface fire (Lydersen and North, 2012; Collins et al., in press). Our analyses may help identify favorable habitat under current conditions but this may be different from historical forests.

4.5. Management implications

Research on characterizing the structure of owl habitat has been constrained by both technological (aerial photography and landsat imagery) and logistical (ground-based vegetation measurement) issues. Early remote sensing efforts in owl studies has been limited to estimation of area, spatial configuration, and canopy cover whereas ground-based sampling provided limited estimates of density and sizes of habitat attributes at small spatial scales. All this previous research has linked spotted owls to a combination of high canopy cover and large trees at both nest and roost sites (Verner et al., 1992; Gutiérrez et al., 1995; Tempel et al., 2014, 2016). One consequence of these studies has been that managers have tended to focus on canopy cover as the metric of interest for conserving spotted owl habitat.

Two lines of evidence, one historical and one derived from our findings in this study, suggest that a focus on preserving patches of large trees rather than canopy cover per se may be more effective. Historical data sets and forest reconstruction studies from the Sierra Nevada consistently suggest active-fire forests on average were dominated by large trees and stands generally had low canopy cover (17–41%) and tree densities (60–328 trees/ha or 24–133 tree/ac) (Lydersen et al., 2013; Collins et al., 2015; Stephens et al., 2015). The range in these values suggests forest conditions likely varied with topography and disturbance history (North et al., 2009; Lydersen and North, 2012; Kane et al., 2014; Kane et al., 2015). More mesic sites likely burned less frequently and intensely, and higher productivity resulted in bigger trees in larger patches than more xeric sites. Fuels were able to accumulate more rapidly on more productive sites, especially when fires "skipped an area", making them more prone to patchy crown fire (Innes et al., 2006). Variability in topography and soils combined with the inherent variability of fire created and maintained high levels of heterogeneity at small to large spatial scales in historical frequent fire landscapes (Meyer et al., 2007b; Kane et al., 2015).

Management based on canopy cover targets creates significant challenges in restoring this multi-scale heterogeneity. Canopy cover is generally used as a stand average measurement of forest conditions and as such does not account for the group/gap horizontal distribution of trees that is a defining characteristic of frequent-fire forests (Larson and Churchill, 2012). Furthermore, because high canopy cover can occur under a wide variety of stand ages, levels of productivity, and disturbance histories, it does not incorporate important habitat components such as vertical structure, snags, downed logs, and large trees. Forests with high canopy cover, particularly those with continuous cover over large areas, are at greater risk from high-severity wildfire and drought-induced mortality. An additional challenge is that while canopy cover estimates of forest conditions are widely available, their calculation from ground-based measurements, aerial photo interpretation or model estimates such as FVS, based on tree diameters and density, can be widely variable and inaccurate (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009).

In contrast, the association of owl nests and PACs with the cover in tall trees has more tractable forest management implications. Managing for the protection and production of large trees can be accomplished while still reducing potential fire intensity (through surface and ladder fuel reduction) and drought stress (lowering overall leaf area by removing small trees). Furthermore, PACs in our study had low canopy cover in the 2–16 m strata suggesting treatment of these potential ladder fuels may not adversely affect owl habitat. Reduction of subcanopy and intermediate-size trees may reduce water competition increasing large tree resilience to beetle attack while opening up more growing space to accelerate tree growth (Fettig et al., 2010a; Fettig et al., 2010b). Managing for landscapes that contain tall trees, which are more fire resilient, may reduce the loss of owl habitat that is increasingly occurring in an era of rising wildfire severity. In landscapes where patches of tall trees are rare, managers might identify the tallest tree areas and seek to reduce their vulnerability to drought and wildfire mortality through density reduction so the trees can grow to become anchors of more suitable habitat.

As a sensitive species with declining populations, forest managers should consider approaches to retain and improve California spotted owl habitat. Retaining current use areas is important to guard against further population declines. In the long-term an effective strategy may be to focus management on cultivating tall trees in more productive areas (i.e., wetter areas, drainage bottoms, lower slopes) of the landscape (Underwood et al., 2010) that can better support large tree biomass and that may be more resistant to fire and drought stress. This may take several decades and will require strategies that maintain current owl areas until new, more resilient forest locations develop large tree cover through growth and succession. To maintain selected habitat in the near-term, management may need to take a more active role reducing stem density in the 2–16 m class and surface fuels in tall tree areas to make these stands more resistant and resilient to drought and high-severity wildfire that can significantly reduce local owl populations (Jones et al., 2016). With climate conditions changing, managing for the retention and creation of large trees may benefit both owls and forest resilience to increasingly common wildfire and drought events.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.019.

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Effects of fire on spotted owl site occupancy in a late-successional forest

Susan L. Roberts[a,*], Jan W. van Wagtendonk[a], A. Keith Miles[b], Douglas A. Kelt[c]

[a] US Geological Survey, Western Ecological Research Center, Yosemite Field Station, El Portal, CA 95318, USA
[b] US Geological Survey, Western Ecological Research Center, Davis Field Station, University of California, One Shields Avenue, Davis, CA 95616, USA
[c] Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

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ABSTRACT

The spotted owl (*Strix occidentalis*) is a late-successional forest dependent species that is sensitive to forest management practices throughout its range. An increase in the frequency and spatial extent of stand-replacing fires in western North America has prompted concern for the persistence of spotted owls and other sensitive late-successional forest associated species. However, there is sparse information on the effects of fire on spotted owls to guide conservation policies. In 2004–2005, we surveyed for California spotted owls during the breeding season at 32 random sites (16 burned, 16 unburned) throughout late-successional montane forest in Yosemite National Park, California. Our burned areas burned at all severities, but predominately involved low to moderate fire severity. Based on an information theoretic approach, spotted owl detection and occupancy rates were similar between burned and unburned sites. Nest and roost site occupancy was best explained by a model that combined total tree basal area (positive effect) with cover by coarse woody debris (negative effect). The density estimates of California spotted owl pairs were similar in burned and unburned forests, and the overall mean density estimate for Yosemite was higher than previously reported for montane forests. Our results indicate that low to moderate severity fires, historically common within montane forests of the Sierra Nevada, California, maintain habitat characteristics essential for spotted owl site occupancy. These results suggest that managed fires that emulate the historic fire regime of these forests may maintain spotted owl habitat and protect this species from the effects of future catastrophic fires.

1. Introduction

Fire is an essential and dynamic process in many terrestrial systems throughout the world (Dickman and Rollinger, 1998). Whether on a 5-year or 200-year return interval, fire structures and maintains ecosystems (Wright and Bailey, 1982; Minnich et al., 2000). In western North America, fire regimes are so strongly correlated with the habitats they shape that it is difficult to ascertain whether fire regimes drive patterns in vegetation or vice versa (Agee, 1993; van Wagtendonk and Fites-Kaufman, 2006). The severity of fire can be quantified as a function of changes in vegetation after an area burned (van Wagtendonk, 2006). Attempts to exclude fire from these systems through a century of suppression have not been completely successful because continuing fuel accumulation (Kilgore, 1973; Vankat and Major, 1978; Agee et al., 2000) has led to more extensive high-severity fires (Skinner and Chang, 1996). While it is clear that unchecked wildfires in these forests are not an acceptable management option (Weatherspoon et al., 1992), van Wagtendonk (1996) suggested the best tool for restoring and protecting these forests is carefully planned prescribed fire.

One species that is dependent on old-growth and late-successional forests is the spotted owl (*Strix occidentalis*) (Forsman et al., 1984; Gutiérrez and Carey, 1985; Gutiérrez et al., 1992; Verner et al., 1992a). Spotted owls are strongly associated with old forests, but are threatened by habitat loss and fragmentation (Bart and Forsman, 1992; Noon and Blakesley, 2006), the recent expansion of barred owls (*Strix varia*) into the range of spotted owls (Olson et al., 2005), and climate change (Glenn et al., 2010; Carroll, 2010). The old, and often dense, forests favored by spotted owls are economically desirable (Thomas et al., 1990; Verner et al., 1992a), but are at risk to stand-replacing fires due to heavy fuel loading (Agee et al., 2000). A century of fire exclusion and various management activities has transformed much of this forest into even-aged, early-successional forests that often contain large amounts of understory fuels (Husari et al., 2006; Stevens and Sugihara, 2006). This accumulated dead and down woody debris acts not only as fuel to carry the fire horizontally through the forest, but also vertically into the upper canopy (Weatherspoon and Skinner, 1995; Tappeiner and McDonald, 1996). Such high fuel loading and spatially continuous ladder fuels place adjacent

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[*] Corresponding author. Tel.: +1 209 375 9557.
E-mail addresses: susan_roberts@usgs.gov (S.L. Roberts), jan_van_wagntendonk@usgs.gov (J.W. van Wagtendonk), keith_miles@usgs.gov (A.K. Miles), dakelt@ucdavis.edu (D.A. Kelt).

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old-growth forests at greater risk of catastrophic fire (Weatherspoon et al., 1992; Agee, 1993; Wright and Agee, 2004). The combination of logging and large-scale conversion of forests to human communities has resulted in dramatic declines in the extent and continuity of old-growth forests throughout western North America, causing concern for the persistence of spotted owls (Thomas et al., 1990; McKelvey and Weatherspoon, 1992). In the fire-adapted forests of the Sierra Nevada where California spotted owls (*S. o. occidentalis*) live and reproduce, habitat loss from wildfire also is a concern as the risk of catastrophic fire steadily increases in the absence of periodic low to moderate severity fire (Miller et al., 2009). Skinner and Chang (1996) estimated that prior to Euro-American settlement, montane forests in the Sierra Nevada experienced low to moderate severity fires every 2–20 years.

In montane forests of the Sierra Nevada, California spotted owls typically nest and roost in stands with high canopy cover ($\geqslant 75\%$) and forage in stands with moderate ($\geqslant 40\%$) to high canopy cover (Call et al., 1992; Zabel et al., 1992). These owls use stands for nesting and roosting that have multilayered canopies and an abundance of large trees (>60 cm diameter at breast height [dbh]) (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). We wanted to determine if the low to moderate severity fires that reduce fuels would sustain functional spotted owl habitat by maintaining specific forest characteristics necessary for nesting and roosting. To do this, we investigated site occupancy patterns by California spotted owls within burned and unburned montane forests in Yosemite National Park. We had three primary objectives. First, we wanted to determine whether burned and unburned forests contained sufficient nesting and roosting habitat elements (e.g., canopy closure, basal tree area) for spotted owl site occupancy. We predicted that spotted owl occupancy would be positively influenced by canopy closure and tree basal area, and that these characteristics would be maintained in forests burned at low to moderate severity. Yosemite has a large area of relatively contiguous, mixed-conifer forest, leading us to predict that the density of spotted owl pairs would be higher in the park than in other mixed-conifer forest in the Sierra Nevada. Our second objective was to develop a model that land managers could use to accurately predict spotted owl site occupancy in a particular forest stand based on fire history and vegetation characteristics. Our final objective was to estimate spotted owl density within Yosemite. This was to provide baseline information in late-successional forests experiencing a frequent fire regime and not confounded by the effects of past forest management practices. To date, population estimation for this subspecies has been almost exclusively limited to National Forests in California that have experienced decades of fire exclusion and intensive timber harvest.

2. Methods

2.1. Study area

Located in the central Sierra Nevada, Yosemite National Park encompasses 3027 km^2, of which approximately 1580 km^2 was relatively contiguous montane forest (van Wagtendonk and Lutz, 2007) and potential habitat for spotted owls. This habitat occurred between 1000 m and 2500 m elevation on the western slope of the range and supports a diverse fauna (Graber, 1996). White fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*) dominated the lower montane forests. Red fir (*Abies magnifica*), white fir, sugar pine, and Jeffrey pine (*Pinus jeffreyi*) dominated the upper montane forests. The most prevalent forest type in our study area consisted of white fir with a mix of Jeffrey pine (at higher sites) or ponderosa pine (at lower sites). More than half of the precipitation occurred from January through March, primarily as snow (van Wagtendonk and Fites-Kaufman, 2006). Between 1989 and 2004, 466 km^2 of the 1580 km^2 montane forest burned at least once.

At the time of this research, managers recognized three types of wildland fires, prescribed, wilderness, and wildfire. Mangers purposefully set prescribed fires in order to meet defined objectives. In 1970, Yosemite National Park developed a prescribed burning program to reduce fuels and lower the risk of stand-replacing fires while conserving the selection pressures that fire historically imposed on these ecosystems (van Wagtendonk et al., 2002). Wilderness fires were naturally occurring lightning fires and since 1972, the park's wildland fire use program managed them under prescribed conditions. Since 1972, as long as these conditions were met, wilderness fires were typically not suppressed in Yosemite. Yosemite's Fire Management Program suppressed all wildfires, including human caused fires and wildland fires that did not meet management objectives. Researchers dated, mapped, and digitized for use with geographic information system (GIS) software all fires that occurred within Yosemite since 1930 (van Wagtendonk et al., 2002). Yosemite Park personnel also developed a digital vegetation map consisting of polygons of dominant overstory and understory vegetation types with cover classes assigned to each vegetation type polygon (National Park Service, 1997). Although our study area experienced all three types of fire, we did not have a large enough sample size to perform separate analyses on each type. Therefore, a "burned" forest in our study could have experienced any of the three fire types.

2.2. Data collection

2.2.1. Plot selection

Spotted owls in the Sierra Nevada rarely use forests with <40% canopy cover (Call et al., 1992; Gutiérrez et al., 1992; Zabel et al., 1992); therefore, we used 40% canopy cover as our cutoff criterion for mapping potential owl habitat. We used ArcMap 9.1 (ESRI, Redlands, California) and the digital vegetation map to delineate montane forest stands with >40% canopy cover within the park. We overlaid the digital fire history map onto the vegetation map to delineate all fires in the montane forest zone that burned since 1989, and had post-fire canopy cover >40%. By this method, we delineated 466 km^2 of burned forest and 1113 km^2 of unburned forest, and we focused our surveys within these forests. We restricted our efforts to areas burned between 1989 and 2004 because this 15-year interval falls within the range of historic fire return interval (2–20 years) for these forest types (Skinner and Chang, 1996). We then generated 200 random points across that defined landscape (100 in burned, 100 in unburned areas) and selected the first 16 points in each stratum (total of 32 survey areas) that met logistical constraints of accessibility ($\leqslant$2 days travel, including driving and hiking) and crew safety (Fig. 1).

2.2.2. Owl surveys

We used acoustic-lure and live-lure surveys (Reid et al., 1999) and mark-recapture methods (Franklin et al., 1996) to survey owls during the breeding season (April–July) in 2004 and 2005. We sampled each survey area at night three times during the breeding season and separated surveys by at least two weeks. We surveyed each site for only 1 year; 16 survey areas in 2004 and 16 different survey areas in 2005. Because these owls exhibit extreme site fidelity, we assumed if owls were present at a site in 1 year, they would continue to occupy that site until their death. To support this assumption, we conducted follow up diurnal visits (to observe annual reproduction) at each occupied site we located in the previous year and found all sites occupied by both or one of the same owls in

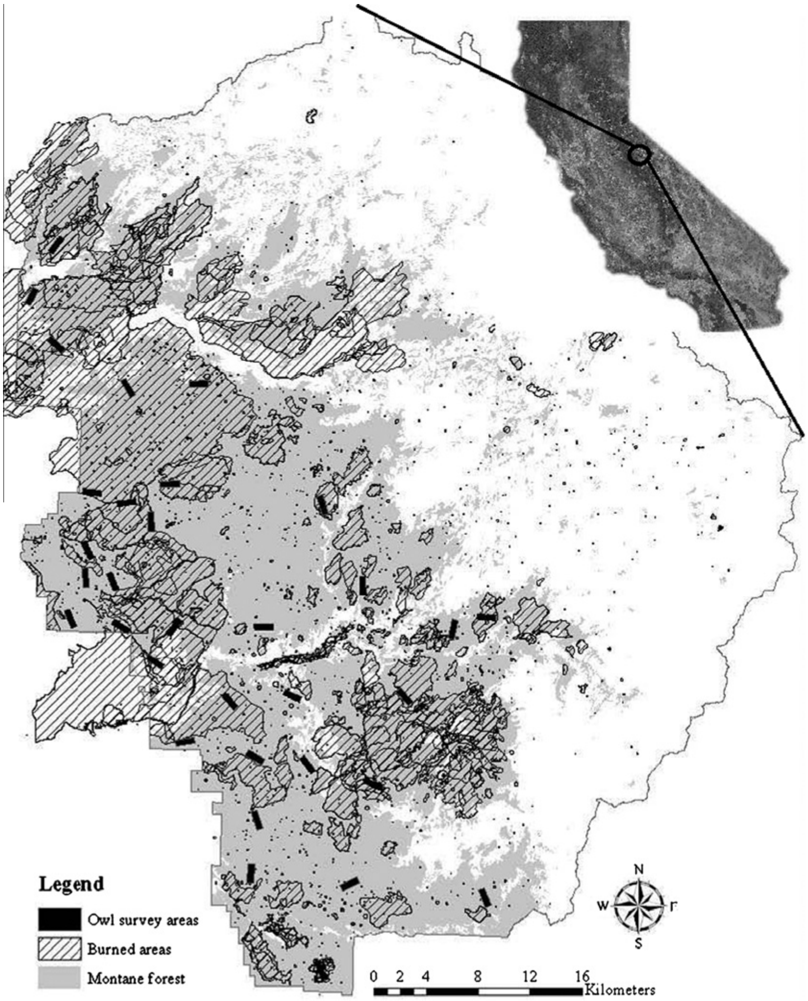

Fig. 1. Locations of 16 burned and 16 unburned California spotted owl survey areas (2004–2005) in Yosemite National Park, California. Burned areas experienced wildfires, managed wildland fires, or managed prescribed fires between 1989 and 2004.

repeated years (i.e., all sites occupied in 2004 were occupied in 2005). Therefore, we based our occupancy analyses on only the initial survey year and our results are not confounded by annual effects. Each survey area consisted of a rectangular grid with eight (four on each side) calling stations 500 m apart. We centered the grids on the 32 random points and thoroughly examined the entire survey area during grid establishment to ensure each survey area contained only one type of sampling strata (burned or unburned). We assumed that the effective sampling area was a 500 m wide buffer around each grid (Forsman, 1983) which converted to a sampling area of 3.75 km^2. In the rugged and remote terrain within the park, this was the largest area we could reasonably expect a field crew to survey in a single night. The combined area of the 32 transects we surveyed during the 2-year period was 120 km^2. We conducted systematic nocturnal surveys by vocally imitating spotted owl calls and listening for responses for 10 min at each station (Forsman, 1983; Franklin et al., 1996). Because spotted owls defend their territories by responding to "intruders" with hooting, we assumed owls responding to our vocally imitated calls were territorial (Forsman, 1983). We recorded the time, location (elevation and UTM [NAD27, Zone11 N]), sex, and species of all owl responses.

We identified, located, and captured spotted owls using the methods and protocols that were originally developed and published by Forsman (1983) and Franklin et al. (1996). When we detected spotted owls at night, we returned to the same locations the next morning to try to determine the nest or roost location of each owl. We marked non-juvenile owls with a plastic colored leg band on one leg, and a numbered aluminum US Geological Survey Bird Banding Laboratory band on the other leg. To locate nests, we offered up to six live house mice (*Mus musculus*) to each pair and then observed what the owls did with each mouse. Reproductively active owls usually took mice to the nest or juvenile(s), allowing us to identify individual owls (band re-sighting), and locate nests or roosts (Reid et al., 1999). Through our diurnal band re-sighting, we were able to determine whether a particular owl pair's territory overlapped >1 survey area. To avoid pseudoreplication, we only included one (chosen at random) of these overlapping survey areas. This situation occurred only once across the entire study area.

2.2.3. Habitat sampling

Following owl surveys each year, we measured spotted owl nesting and roosting habitat characteristics at all sites. We categorized owl activity sites as nests, roosts, or night survey observations ("night response"), and defined the geographic center for each site as the nest or roost tree used by the owls. Survey areas that did not yield spotted owl responses during nocturnal surveys we termed "no-response sites." For no-response sites, we defined the geographic site center of the vegetation plot as the random point we used to locate the owl survey area during plot selection. At each site center, we recorded elevation (using Suunto wrist altimeters) and location (UTM coordinates in NAD27 Zone11 N). To characterize locations where we found owls, we compared the vegetation at those locations to vegetation at a random point at the no-response sites. We sampled vegetation at owl activity and no-response sites using nested circular plots oriented around the owl nest or roost tree (activity sites) or the largest tree closest to the random point (no-response sites). To measure the characteristics at the local stand level, we recorded tree species, diameter at breast height (dbh), and status (live tree or snag) in three concentric, nested, circular plots (0.05 ha, 0.1 ha, 0.2 ha) with the plot size expanding to quantify larger aspects of the habitat (i.e., larger trees) (Spies and Franklin, 1991; North et al., 1999, 2000). Within the plots, we measured all trees and snags in three size classes: 10–49 cm, 50–79 cm, and ⩾80 cm dbh, respectively. We estimated the cover of downed coarse woody debris (CWD; logs ⩾ 20 cm in diameter and ⩾2 m long) using a 35.6 m line transect through the middle of the 0.1-ha plot. We measured shrub (>0.5 m tall) and sapling (<10 cm dbh and >0.5 m tall) ground cover using 8 m line transects at three locations: 2 m east, 8.6 m north, and 8.6 m south of the center tree. We estimated tree canopy closure using digital hemispherical photos taken 1 m above the ground surface at points 2 m north and south of the base of the center tree (Jennings et al., 1999). We used Gap Light Analyzer v 2.0 (Frazer et al., 1999) to estimate canopy closure from the photos.

Canopy closure is the proportion of the sky hemisphere obscured by vegetation when viewed from a single point, usually on the ground (Jennings et al., 1999). Closure is affected by tree heights and canopy widths and takes into account light interception and other factors that influence microhabitat. Canopy cover is a measure of the percent of ground covered by a vertical projection of the tree canopy (Jennings et al., 1999). Cover can be measured from multiple points on the ground or estimated from aerial photographs. We used remotely sensed canopy cover estimates to focus our survey efforts and used canopy closure estimates in the model estimations. We felt canopy closure was the best metric to use to measure the canopy for a particular nest or roost site in recent or current use by an owl.

2.3. Data analysis

We quantified fire severity for each of the 16 burned owl survey areas using the Relative differenced Normalized Burn Ratio (RdNBR) developed by Miller and Thode (2006). They used differential remote sensing imagery from before and after fire to create a map of polygons representing four levels of fire severity for all of the fires in Yosemite since 1973. Miller and Thode (2006) classified areas as unchanged if the severity was so low that a change could not be detected in the images one year post-fire. Low severity stands were generally lightly burned with only the fine fuels removed and some scorching of the understory trees. Moderate severity stands retained some fuels on the forest floor, but created some small tree mortality and scorching of the crowns of medium and large sized trees. High severity areas had near complete combustion of all of the litter, duff, and small logs, higher mortality of small to medium sized trees, and consumption of the crowns of large trees. Fire severity levels ranged from "1" (an unchanged area within the fire perimeter) to "4" (burned completely at high severity). We used ArcMap 9.1 (ESRI, Redlands, CA) to calculate the proportional area of each fire severity class within each of the 3.75 km^2 polygons that we surveyed for owls. If a survey area contained multiple fires with spatial overlap, we used the most recent fire for the overlapping areas. We then calculated the fire severity index for each survey polygon as the sum of the proportional area of each fire severity level within that survey polygon multiplied by the fire severity level (1–4) for that proportional area.

We calculated the total basal area ($\mathrm{m}^2\,\mathrm{ha}^{-1}$) of live trees ⩾10 cm dbh (BAt), live trees ⩾50 cm dbh (BAt50 cm), and dead trees (snags)⩾80 cm dbh (BAs). We estimated CWD cover (%) based on the percent of the 35.6 m line transect that was covered by CWD. We estimated shrub cover (%) in each plot as the mean across the three 8 m line transects.

In our analyses of owl pair site occupancy, we used nest sites when possible ($n = 15$), roost sites ($n = 3$) when we did not observe nesting at a particular owl site, and night response sites ($n = 1$) when we were unable to locate nests or roosts. We calculated the mean of each habitat variable (canopy closure, BAt, BAt50 cm, BAs, shrub cover, CWD cover, and site elevation) within each owl activity type for sites where there was more than one nest ($n = 2$) or roost ($n = 2$) location for a territorial owl pair. In all analyses, we used only one site per owl pair to ensure independence among sites and followed established protocols when determining owl social status (G. Miller, Forest Service, unpublished paper).

We examined the correlation matrix for all of the habitat data to determine if any habitat variables were highly intercorrelated. To avoid collinearity in our models, we did not develop models that included highly correlated variables (e.g., correlation coefficient ⩾0.70; Burnham and Anderson, 2002). Canopy closure and basal tree area tend to be highly correlated. To avoid including these two intercorrelated variables as separate variables in the same model (Burnham and Anderson, 2002), we standardized them using z-scores and summed them into a single derived variable (BAtCan), which we believe provided an ecologically based (e.g., "owl-centric") perception of forest density.

We defined spotted owl pair occupancy as the probability that a pair of territorial spotted owls will occupy a particular patch of habitat. Before conducting owl surveys, we developed a list of candidate models for predicting pair occupancy as a function of site burn history, all seven habitat variables, and survey year. We standardized habitat variables using z-scores because they were measured at different scales. We determined the model that best predicted spotted owl occupancy with program PRESENCE v 2.1 (Hines, 2006), which estimates site occupancy (Ψ) as a function of the probability of detection (ρ); therefore, ρ was included in each candidate model. By including habitat characteristics in the candidate models, we tested if Ψ varied as a function of habitat while also investigating if ρ varied as a function of survey time or fire history (burned vs. unburned). To include survey-specific detection rates, we employed the full identity function in PRESENCE and followed the procedures for singles species, single season surveys detailed by MacKenzie et al. (2002). We considered only models with two to five parameters (including the intercept and probability of detection) to avoid the occurrence of spurious results by maintaining an approximate ratio of data to parameters >10 ($n = 32$ sites; maximum # parameters = $n/10$; Burnham and Anderson, 2002). We used Akaike's Information Criteria (AIC) corrected for low sample size ($\mathrm{AIC_c}$; Akaike, 1973; Hurvich and Tsai, 1989) to quantifiably and simultaneously compare candidate models (Burnham and Anderson, 2002).

We selected the "best" model on the basis of $\mathrm{AIC_c}$ values, Akaike weights (w_i), and evidence ratios as defined by Burnham and Anderson (2002). The Akaike weight (w_i) represents the probability that a particular model provides the best explanation of the data given the tested set of models. The difference in $\mathrm{AIC_c}$ values of alternative models relative to the model with the lowest $\mathrm{AIC_c}$ ($\Delta\mathrm{AIC_c}$) reflects the level of support for the alternative models. Models with $\Delta\mathrm{AIC_c} \leqslant 2$ have "substantial" support, whereas models with $\Delta\mathrm{AIC_c}$ of 4–7 have "considerably less" support, and models with $\Delta\mathrm{AIC_c} > 10$ have essentially no support. To compare an alternative model to the best model, we calculated evidence ratios as w_1/w_2, where w_1 and w_2 refer to Akaike weights for the two models being compared, with our best model always being the numerator.

Evidence ratios $\leqslant 2.7$ are equivalent to a $\Delta \text{AIC}_c \leqslant 2$ and indicate substantial support for the model being compared to the best model, whereas evidence ratios $\geqslant 3$ provide "little evidence" in favor of the alternative model (Burnham and Anderson, p. 79).

We applied the logistic model in program PRESENCE to incorporate habitat variables in our candidate models and to calculate the maximum likelihood estimates required for AIC calculations (Donovan and Hines, 2007). The logistic model employed by PRESENCE is

$$\log e[\Psi/(1-\Psi)] = X\beta, \tag{1}$$

where Ψ refers to the probability of owl pair occupancy, X is the row vector of the habitat variables, and β is the column vector of model coefficients.

We applied a closed population model because of the short survey period (2 years) relative to the life span of adult California spotted owls (14 years; Steger et al., 2002) and their high adult annual survival rates (83%; Blakesley et al., 2001). We estimated the total population size (N) of California spotted owls in Yosemite, as well as the population size within areas characterized by different burn histories (burned and unburned) following Lancia et al. (1996):

$$\hat{N} = O_{park}/(a\hat{\rho}) \text{ with}$$
$$\text{var}(\hat{N}) = \hat{N}^2 \times [(\text{var}O_{park}/O^2_{park}) \times (1-a) + (\text{var}\rho/\rho^2)] \tag{2}$$

where O_{park} is the total number of owl pairs observed in the field from the surveys from both years, a is the proportion of the total area surveyed, and ρ is the probability of detecting a spotted owl pair from the surveys. We calculated the density of owl pairs at each survey area as

$$\hat{D}_{site} = O_{site}/A \tag{3}$$

where O_{site} is the number of owl pairs observed from the surveys for that survey site, and A is the area of the survey site (3.75 km^2). To estimate owl density for the entire park ($\hat{D}_{park}$), we determined the grand mean and variance across all survey sites (n = 32)

$$\hat{D}_{park} = \left(\sum \hat{D}_{site}\right)/n \text{ with var}\hat{D}_{park} = (\text{SD}_{site})^2 \tag{4}$$

where SD is the standard deviation of owl pair density across all survey sites. For our population estimation, we only included individuals that we detected during the nocturnal surveys and if their nest or roost was inside the 3.75-km^2 survey area. We doubled our spotted owl density estimate to represent individual owls and compare it to other estimates in the Sierra Nevada, although owl pairs represent a more informative measure of owl density because pairs are the reproductive unit (Olson et al., 2005).

3. Results

3.1. Fire severity and habitat variability

The fire severity index of burned survey areas ranged from 0.4 to 3.1, with an overall mean (SE) of 2.0 (0.2). Across all burned survey areas, the mean (SE) proportion of area burned at unchanged, low, moderate, and high fire severity was 8% (2), 25% (4), 29% (4), and 14% (4), respectively. The maximum proportion of any given survey area that burned at high fire severity was 46%. Generally, survey areas burned at a low to moderate fire severity.

Canopy closure ranged from 28% to 94% ($\bar{x} = 77\%$) for burned sites and 63% to 96% ($\bar{x} = 87\%$) for unburned sites. The mean (SE) basal area of all trees ($\geqslant$10 cm; BAt) was 42.8 (6.5) m^2 ha^{-1} at burned sites and 56.3 (5.6) m^2 ha^{-1} at unburned sites. In burned and unburned sites, the mean basal area for large snags ($\geqslant$80 cm dbh) was 10.3 (2.0) m^2 ha^{-1} and 9.0 (2.0) m^2 ha^{-1}, mean coarse woody debris cover was 4.3% (1.2) and 6.6% (1.3), and mean shrub cover was 7.6% (2.2) and 12.9% (3.8), respectively.

The correlation matrix showed that BAt was highly correlated with BAt50 cm (r = 0.89) and canopy closure (r = 0.70). Consequently, neither of these appears as a separate variable together with BAt in the same model. The high correlation between BAt and BAt50 cm shows the BAt at our sites was driven by large trees and, on average, 74% of the BAt for any particular site comprised trees >50 cm dbh.

3.2. Spotted owl site occupancy

We detected 19 owl pairs and 2 single males (we did not include single owls in any analyses) after 116 h of nocturnal surveys confirmed by diurnal observations. Through the diurnal observations, we located 19 nests (9 in burned survey areas, 10 in unburned). We fitted 30 adults and 5 subadults with unique number and color leg bands. The unmodeled (naïve) site occupancy (Ψ) for owl pairs was 0.59 (SE = 0.09) across all site types and 0.50 (SE = 0.13) and 0.69 (SE = 0.12) for burned and unburned sites, respectively (Table 1). Detection rates at survey sites did not vary based on fire history.

The mean annual detection rates for spotted owl pairs (ρ) were consistently high, with ρ = 0.47 for 2004 and ρ = 0.59 for 2005 with the particular year in which we surveyed an area bearing no influence on site occupancy (Table 2). Within a year, owl pair detection rates (ρ) were similar across all sites within survey periods, but varied temporally, with ρ = 0.52 (SE = 0.11) in the first survey and 0.89 (SE = 0.05) thereafter. Because all pairs detected in the first survey were also detected in $\geqslant$1 subsequent survey within that survey year, we used only the second and third surveys in subsequent analyses (Table 1). We ran this same candidate model set using all three surveys and the results are exactly the same. Therefore, for brevity, we only present the most parsimonious model set (Table 2).

The best model for predicting the presence of owl pairs included basal area of trees >10 cm dbh and the ground cover of coarse woody debris in a model structured as:

$$\text{Logit}\hat{\Psi} = (3.92) + [41.81 \times Zscore(BAt)] - [10.52 \times Zscore(CWD)] + (2.13 \times \rho), \tag{5}$$

with an Akaike weight (w_i) of 0.40 (Table 2). The standard error of the parameter estimate for BAt was 84.29 and 24.94 for CWD. The second best model included the derived variable BAtCan (Table 2), with structure as follows:

$$\text{Logit}\hat{\Psi} = (0.24) + 4.56 \times [Zscore(BAt) + Zscore(canopyclosure)] + (2.12 \times \rho). \tag{6}$$

This model also had substantial support with w_i of 0.15 and an evidence ratio of 2.6 and ΔAIC_c of 1.90. The standard error (2.18) for the parameter estimate in this alternative model was much smaller than for either of the standard errors for the parameters in the "best" model. There was no support for a model that distinguished between burned and unburned sites (w_i = 0.00, ΔAIC_c = 35.09) indicating that indirect complexities of post-fire effects on forest structure (e.g., changes in canopy closure) influence owl site occupancy rather than the direct effect of fire on the owls. Applying the best model, the mean and standard error (SE) of estimated occupancy rate was 0.46 (0.12) for burned sites 0.72 (0.11) for unburned sites, and 0.59 (0.08) across all sites. Total basal tree area (BAt) was higher both at burned and unburned sites with owls than at no-response sites (Fig. 2).

Table 1
Total counts[a] and unmodeled mean (SE) occupancy and detection rate[b], population size[c], and density estimates of California spotted owls from random, systematic, nocturnal surveys in burned and unburned areas (April–July 2004–2005) in Yosemite National Park, California.

Burn treatment	Count of owl pairs[a]	Occupancy probability[b]	Detection probability[b]	Population size (pair)[c]	Density (owl pair km^{-2})
Burned	8	0.50 (0.13)	0.89 (0.05)	123 (10)	0.15 (0.04)
Unburned	11	0.69 (0.12)	0.89 (0.05)	156 (13)	0.21 (0.04)
ALL	19	0.59 (0.09)	0.89 (0.05)	356 (20)	0.18 (0.03)

[a] Count of owl pairs refers to the total number of pairs of owls observed in all survey areas within the burn treatment.

[b] Occupancy and detection rates refer to the mean and standard error (SE) of the occupancy and detection rates for each owl survey areas calculated from program PRESENCE (Hines, 2006).

[c] Population size refers to the total number of owl pairs calculated for each burn treatment with standard error representing the error rate in the estimate.

Table 2
Summary of model selection statistics[a] from logistic model[b] analysis of nesting and roosting habitat variables[c] predicting the site occupancy of California spotted owl (*Strix occidentalis occidentalis*) pairs in Yosemite National Park, California, 2004 and 2005 ($n = 32$; 16 burned sites, 16 unburned sites).

Model description[d]	K	log (L)[a]	AIC$_c$	ΔAIC$_c$	w_i
Occupancy{BAt}{CWD}	5	−15.03	40.07	0.00	0.40
Occupancy{BAtCan}	4	−16.99	41.97	1.90	0.15
Occupancy{BAtCan}{Shrub}	5	−16.71	43.42	3.35	0.07
Occupancy{BAt}{Elevation}	5	−16.72	43.44	3.37	0.07
Occupancy{BAtCan}{CWD}	5	−16.76	43.52	3.45	0.07
Occupancy{BAt}	4	−17.91	43.82	3.75	0.06
Occupancy{BAtCan}{BAs}	5	−16.91	43.82	3.75	0.06
Occupancy{BAtCan}{Elev}	5	−16.94	43.88	3.81	0.06
Occupancy{BAt} {Shrub}	5	−17.78	45.56	5.49	0.03
Occupancy{Canopy}{BAt50 cm}	5	−18.13	46.26	6.19	0.02
Occupancy{Canopy}	4	−22.63	53.26	13.19	0.00
Occupancy{Canopy}{Elevation}	5	−22.21	54.42	14.35	0.00
Occupancy{Canopy}{CWD}	5	−22.32	54.64	14.57	0.00
Occupancy{Canopy}{Shrub}	5	−22.47	54.93	14.86	0.00
Occupancy{Canopy}{BAs}	5	−22.59	55.18	15.11	0.00
Occupancy{BAt50 cm}	4	−24.52	57.04	16.97	0.00
Occupancy{Elevation}	4	−30.47	68.94	28.87	0.00
Occupancy{constant} (null model)	3	−34.17	74.33	34.26	0.00
Occupancy{Burned}	4	−33.58	75.16	35.09	0.00
Occupancy{Shrub}	4	−33.77	75.54	35.47	0.00
Occupancy{BAs}	4	−34.05	76.11	36.04	0.00
Occupancy{SurveyYear}	4	−34.10	76.20	36.13	0.00
Occupancy{CWD}	4	−34.15	76.30	36.23	0.00
Occupancy{constant}, detection rate{Burned}	2	−38.85	81.70	41.63	0.00

[a] Statistics include: log$_e$ likelihood (log(L)), Akaike's Information Criterion corrected for small sample size (AIC$_c$), relative AIC$_c$ (ΔAIC$_c$), Akaike weights (w_i), and the number of parameters (K) in the model.

[b] Logistic model used: $\log_e(\Psi/(1-\Psi)) = X\beta$, where Ψ refers to the probability of owl pair occupancy, X is the row vector of habitat variables, and β is the column vector of coefficient values.

[c] 'BAt' refers to basal area of all live trees >10 cm diameter at breast height (dbh), 'BAs' refers to basal area of snags ⩾80 cm, 'BAt50 cm' refers to basal area of all live trees >49 cm, 'canopy' refers to canopy closure estimated from digital hemispherical photos, 'BAtCan' refers to the sum of BAt and canopy closure at the owl site, shrub refers to mean shrub cover, and 'CWD' is the cover of coarse woody debris.

[d] Detection rate was survey-specific ("full identity") in every model except the last one, in which it varied by burn treatment.

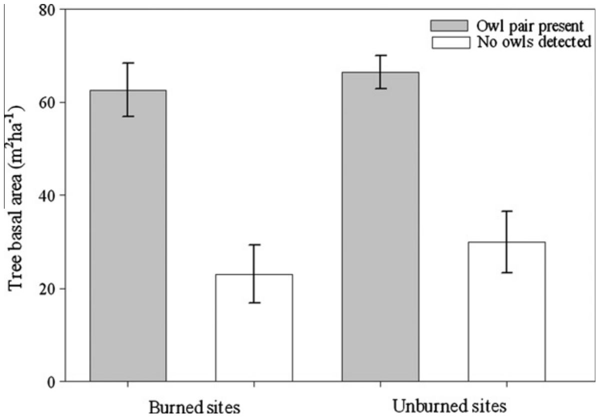

Fig. 2. Comparing the mean ± SE basal area of all live trees (⩾10 cm) at burned and unburned sites with owls (nest and roost sites) and without (random points) between April–July, 2004–2006 at Yosemite National Park, California.

3.3. Population estimation

Eighty-four percent of all of the nests or roosts we located were within the boundary of our 3.75 km^2 survey areas. Using the detection rate (ρ) estimated by PRESENCE and extrapolating across all potential habitat, we estimated the population size (SE) for Yosemite as 280 (16) pairs of California spotted owls, with 70 (6) pairs in the burned montane forest and 228 (18) pairs in the unburned forest (Table 1). The mean (SE) density of owl pairs was 0.15 (0.04) pairs km^{-2} in the burned forest and 0.21 (0.04) pairs km^{-2} in the unburned for an overall average of 0.18 (0.03) pairs km^{-2} across the entire park (Table 1), or 1 pair 6.25 km^{-2}. This is a conservative estimate because there were three pairs of owls we did not include in the estimate because their nests were 0.2 km, 0.7 km, and 1.3 km outside of the survey areas. We also omitted an additional pair that we detected only during the diurnal follow-up surveys (while looking for another pair) and not during our nocturnal surveys. The roost for this "consequential" pair were within the same survey area as the nest of another pair (<1.5 km apart).

4. Discussion

The relatively low mean fire severity index documented for our burned forests (2.0) suggests a fire history similar to what existed before Euro-American settlement (Skinner and Chang, 1996). Although we characterized individual survey areas with a single fire severity index value, burned areas contained a mosaic of different fire severities. This mosaic reflects heterogeneity among burned forest patches and creates a complex matrix of habitat characteristics at multiple scales (e.g., microhabitat, stand, and landscape). This post-fire heterogeneity may be one of the most important aspects of the burned landscape to spotted owls. Franklin et al. (2000) showed that owls with territories that contained a mosaic of vegetation types infused within old-growth conifer forest had higher fitness. Bond et al. (2009) found that California spotted owls use this mosaic for a variety of different activities such as low severity for nesting and roosting and higher severities for foraging.

4.1. Spotted owl occupancy

Based on our modeling results, California spotted owl nest and roost site occupancy in montane forests of Yosemite National Park was best predicted by combining the positive effect of total basal area (BAt), and the negative effect of coarse woody debris (CWD). However, there was substantial support for the alternative model that used the derived variable combined canopy closure and tree basal area (BAtCan). The abundance of large trees has a clear association with spotted owl nest and roost sties (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). These results also indicate that fire does not reduce the probability of spotted owl occupancy, especially if numerous large trees remain after a fire. Clark (2007) showed northern spotted owl occupancy declined and local extinction increased immediately following fire. However, his results are confounded by post-fire salvage logging and large areas of early-seral forests in his study area. Also, the fire age of our study is variable (2–14 years) while his was only 1–2 years. However, it is important to note the disparity of these results with ours suggests that salvage logging may have detrimental effects on spotted owl occupancy. Jenness et al. (2002) found a weak negative association of fire to Mexican spotted owl occupancy. However, they collected no data on the habitat characteristics to allow investigation into the post-fire forest structure that potentially drove that association.

We included detection rates in our models because the California spotted owl home range is potentially larger than our survey area (MacKenzie, 2005). According to MacKenzie et al. (2002), however, high detection rates (e.g., >0.5), such as what we estimated from our nocturnal surveys ($\rho = 0.89$; Table 1), produce accurate and unbiased predictive models for occupancy.

In an earlier study on habitat associations of California spotted owls in northeastern California, site occupancy was positively associated with large trees (>61 cm dbh) and high canopy cover (>70%; Blakesley et al., 2005). However, the proportion of smaller trees (<60 cm dbh) around the nest, even with high canopy cover (>70%), was negatively associated with occupancy (Blakesley et al., 2005). By contrast, models incorporating only large trees (>50 cm dbh; BAt50 cm) were not supported in our analyses (Table 2), indicating that a range of tree sizes influence site occupancy by spotted owls. Trees between 10 cm and 50 cm dbh contribute to a multilayered understory that presumably allows for efficient thermoregulation by owls (Barrows, 1981; Weathers et al., 2001). Large trees are important as nest sites for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel, 1995; Meyer et al., 2007), an important prey species for spotted owls in the Sierra Nevada (Williams et al., 1992).

The disparity between our results and those of Blakesley et al. (2005) could reflect several key differences between our studies. Blakesley et al. (2005) measured their vegetation at a larger spatial scale than our study and consequently used categorical canopy cover data. At our smaller spatial scale, we were able to use continuous canopy closure data. Additionally, their study was conducted in the northern Sierra Nevada which has a more recent history of logging, and thus large trees may be more limited there than in the more pristine forests in Yosemite. Their study site also suffered from decades of fire suppression, which resulted in a dense understory of regenerating white fir. These thickets of young trees could interfere with owl foraging which could explain the negative association of small trees to owl occupancy. Furthermore, Blakesley et al. (2005) quantified habitat only at nest sites, whereas we included roost sites (when nests were unknown). The presence of large trees may be less important in the selection of owl roosts versus nest sites (Verner et al., 1992b). Including roost sites in spotted owl occupancy models provides a more robust model than those excluding such features because the owls may not nest every year (Blakesley et al., 2001, 2005; Steger et al., 2002).

The spatially invariant detection rates reported here compared to the highly variable rates reported for northern spotted owls in Oregon (Olson et al., 2005) could be explained by the disparity in forest management practices. For example, forest managers favored clearcutting in the Pacific northwest over much of the range of the northern spotted owl, while much of the range of the California spotted owl predominantly experienced selective logging. Only a small portion (18%) of our study area was logged during the 1930s (National Park Service, 1930), and none of the study area contained co-habitating, invasive barred owls (*S. varia*), a species that typically has negative effects on detection rates and site occupancy of spotted owls (Kelly et al., 2003; Olson et al., 2005). Consequently, the mean per visit detection rate for spotted owl pairs in our study (0.89 ± 0.1) was higher than in Oregon (0.51) where barred owls and logging were more common (Olson et al., 2005, p. 930). The main factors influencing habitat structure in the montane forests of Yosemite are natural processes, predominately fire. Our results evaluated the role of fire unconfounded by large-scale logging, development, or competition with an aggressive congener.

In a study in the Sierra Nevada, Gutiérrez et al. (1992) found that California spotted owl nest and roost sites had higher snag basal area than random sites. However, study areas of these authors were predominantly in forests with a history of consistent logging, such that large snags likely were limited in availability. In the predominantly unlogged forests of Yosemite, large snags are relatively common and burned and unburned forests had similar basal areas of large snags.

The lower AIC_c value for the BAt-CWD model indicates that this model has the best fit to the data and, therefore, should reflect the best balance of precision (as measured by standard error) and bias (as measured by log-likelihood). In our candidate model set (Table 2), we hypothesized that CWD would be a positive influence on spotted owl site occupancy due its positive association with food for the northern flying squirrel in forests of the Pacific northwest (Amaranthus et al., 1994; Lehmkuhl et al., 2004). However, studies in the forests of the Sierra Nevada with typically lower fire return intervals have shown no relationship between CWD and northern flying squirrels (Pyare and Longland, 2002; Meyer et al., 2007). Fire transforms CWD into nutrient-loaded ash, resulting in less CWD in burned forests than unburned forests (Shaffer and Laudenslayer, 2006). It is possible that CWD interferes with owl foraging when attempting to extract prey from the ground.

Potentially unpredictable ephemeral effects (e.g., CWD or shrub cover) can be avoided by introducing variable(s) that measure more temporally stable effects. Our derived variable, BAtCan; is based on live trees that typically remain alive and upright for decades after the fire. Summing standardized total tree basal area ($m^2\ ha^{-1}$) and canopy closure (%) at a site creates a single variable that depicts forest density in the overstory as well as the understory. The model comparisons showed BAtCan was an acceptable alternative with greater precision for predicting spotted owl site occupancy in montane forest than the BA_t–CWD model. The consistent positive association of BAtCan with site occupancy in our study is in agreement with the consensus that dense forest with large trees are important nesting and roosting habitat for spotted owls in the Sierra Nevada bioregion (Bias and Gutiérrez, 1992; Call et al., 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997; Zabel et al., 1992). An important benefit to managers in using the BAtCan variable is the reduction in field data collection, as canopy closure is quickly and easily measured and requires little field or analysis training and minimal equipment. However, we caution the use of BAtCan in models for forests where >70% of the total basal area of a stand is dominated by smaller trees (<50 cm dbh) because in that situation, increases in stand basal area typically indicate increases in tree density rather than tree size. This leads back to the idea that too many small trees negatively affect spotted owl occupancy (Blakesley et al., 2005).

4.2. Population estimate

Similar density estimates of spotted owl pairs in burned and unburned forests (95% confidence intervals, CI: 0.07–0.22 and 0.14–0.28 owl pairs km^{-2}, respectively) of the type that we examined (predominately low to moderate severity burns of a relatively small percent of the landscape) suggest that fire did not affect owl densities in Yosemite. Consequently, detection and occupancy rates were similar in burned and unburned forests. Based on density estimates in Noon et al. (1992, p. 175), we calculated the 95% CI individual owl density for the area surrounding Yosemite including two national forests and a national park. This estimate (0.10–0.21 owls km^{-2}) was markedly lower than our estimate of total individual owl density in Yosemite (95% CI = 0.25–0.46 owls km^{-2}) and suggests that Yosemite has a higher density of spotted owls than the surrounding national forests and nearby parks. However, this comparison is tentative because Noon et al. (1992) presented only 'crude densities' and did not correct for unsuitable areas within their total available habitat. Consequently, if the amount of suitable habitat was substantially lower than the total area they used in their calculations, their spotted owl density estimates could be lower than reported.

For our population size estimate for the park, we caution that these could be biased slightly high because we treated both forest types (lower montane and upper montane) equally in terms of occupancy and detection rates and this may not be true. It is for this reason that we discuss our results in terms of density rather than the overall population estimation for the park.

5. Conclusions

Our data suggest that the landscape-level prescribed burning and wildland fire use programs of Yosemite National Park may benefit California spotted owls by protecting their nesting and roosting habitat from catastrophic fires while simultaneously creating a large, contiguous, and diverse landscape conducive to population persistence for spotted owls. This is especially evident in Sierra Nevada montane forests that historically burned at low to moderate intensity and usually resulted in a mosaic of burn severity, with minimal mortality of medium and large trees (van Wagtendonk and Fites-Kaufman, 2006). Our results are particularly relevant to forests where large aggregations of residual downed coarse woody debris create spatially continuous fuel loads and extremely flammable environments. Our results suggest that fire, particularly fire resulting in low to moderate tree mortality, can retain residual habitat features that are important for roosting and reproducing California spotted owls.

California spotted owl site occupancy rates and densities were similar in recently burned (<15 years) and unburned montane forests of Yosemite National Park. Our predictive model for site occupancy can assist managers in developing fire management plans with minimal impact and potential benefit to California spotted owls. Currently, the application of our site occupancy model relies heavily on local and site-specific data. A landscape scaled remote sensing and GIS model could assist in the evaluation of fire and land management plans both for Yosemite and more generally for the Sierra Nevada. Integrating remote sensing data with our derived variable, BAtCan, would create a reliable and simple model that would allow managers to move beyond the limitations (in both money and time) of having to collect ground based data.

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Natural Range of Variation for Yellow Pine and Mixed-Conifer Forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA

Hugh D. Safford and Jens T. Stevens

Forest Service

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Authors

Hugh D. Safford is the regional ecologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592, hughsafford@fs.fed.us; **Jens T. Stevens** is a postdoctoral researcher, University of California–Davis, John Muir Institute for the Environment, 1 Shields Ave, Davis, CA 95616, jtstevens@ucdavis.edu.

Cover photos: Top left—Mixed-conifer stand in the Sierra de San Pedro Mártir (SSPM), Baja California, Mexico, elevation 2600 m. Tree species are Jeffrey pine, sugar pine, white fir, and canyon live oak. The SSPM National Park is an important reference site for eastern Sierra Nevada yellow pine and mixed-conifer restoration, as it was never logged and has only experienced a few decades of fire suppression.

Top right—Jeffrey pine-white fir stand on the Humboldt-Toiyabe National Forest, Walker River Canyon, elevation 1850 m. This site was burned 2 years previous to the photo by the Larson Fire.

Bottom—Moist mixed-conifer forest on the Tahoe National Forest, above the Middle Fork of the Yuba River, elevation 1000 m. Forest is dominated by Douglas-fir, with some incense cedar and ponderosa pine, and black oak. This area was logged multiple times between the mid-1800s and 1970s. The black oak patch in the middle of the photo occupies the site of an earlier clearcut.

Abstract

Safford, Hugh D.; Stevens, Jens T. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. Gen. Tech. Rep. PSW-GTR-256. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 229 p.

Yellow pine and mixed-conifer (YPMC) forests are the predominant montane forest type in the Sierra Nevada, southern Cascade Range, and neighboring forested areas on the Modoc and Inyo National Forests (the "assessment area"). YPMC forests occur above the oak woodland belt and below red fir forests, and are dominated by the yellow pines (ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson] and Jeffrey pine [*Pinus jeffreyi* Balf.]); white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.); sugar pine (*P. lambertiana* Douglas); incense cedar (*Calocedrus decurrens* (Torr.) Florin); and black oak (*Quercus kelloggii* Newberry), along with a number of other hardwood and conifer species. We conducted an indepth assessment of the natural range of variation (NRV) of YPMC forests for the assessment area, focusing on ecosystem processes and forest structure from historical data sources from pre-Euro-American settlement times (16th through mid-19th centuries) and current reference forests (YPMC forests that have retained frequent fire and have suffered little human degradation), and comparing current conditions to the NRV. The Mediterranean climate of the assessment area, modified by strong latitudinal, topographic, and elevational gradients, plays an important role in shaping the structure and composition of YPMC forests. Fire was an historically important ecosystem process that occurred frequently, generally burned at low to moderate severity, created a heterogeneous forest structure at a fine spatial scale, and maintained pine dominance in many stands that would otherwise undergo succession to more shade-tolerant fir and cedar species. Forest structure at larger spatial scales was highly variable but was characterized mostly by relatively low tree densities, large tree sizes, high seedling mortality as a result of recurrent fire, and highly heterogeneous understory structure that could include locally abundant fire-stimulated shrub species. Following Euro-American settlement, wholesale changes occurred in YPMC forests in the assessment area, principally because of extensive logging followed by a century of highly effective fire suppression. Modern YPMC forests have departed from NRV conditions for a wide range of ecosystem processes and structural attributes. There is strong consensus among published studies that, on average, modern YPMC stands have much higher densities dominated by smaller trees (often of shade-tolerant species), much longer fire-return intervals, and less area burned across the landscape compared to reference YPMC forests. In addition, fires that escape initial attack are much larger and higher severity on average than the average pre-Euro-American settlement fire. There is more moderate consensus among published studies that the average modern YPMC stand in the assessment supports greater fuels and deeper forest litter, higher canopy cover and fewer canopy gaps, more coarse woody debris, a higher density of snags, and experiences a longer fire season compared to reference YPMC forests. Among the variables assessed, only basal area, overall plant species richness, and percentage cover of grass/forbs and shrubs appear to be within or near the NRV.

Keywords: Yellow pine forests, mixed-conifer forest, ecosystem function, fire regime, forest structure, historical range of variation, HRV, natural range of variation, NRV, species diversity and composition, succession.

Preface

In 1976, President Gerald Ford signed the National Forest Management Act (NFMA), which—together with the Forest and Rangeland Renewable Resources Planning Act of 1974 (FRRPPA)—committed the Forest Service to developing and periodically updating land and resource management plans (LRMPs) at the national forest or national grassland level. The principal purpose of the LRMPs is to provide for "multiple use" and "sustained yield" of natural resources in the National Forest System.

The NFMA and FRRPPA required the development of regulations by the Forest Service to guide the LRMP revision process. These guidelines came to be known as the "Planning Rule," and were first published in 1982. Various inadequacies of the original rule became apparent over time, and multiple abortive efforts were made to modify or "modernize" it. In 2012, a new rule was finally adopted (36 CFR 219) (USDA FS 2012), and new forest plans are following the revised process as of 2013.

According to 36 CFR 219.1(c), the purpose of the 2012 Planning Rule is "to guide the collaborative and science-based development, amendment, and revision of land management plans that promote the ecological integrity of national forests and grasslands..." The rule is focused on maintaining biological diversity on Forest Service units, and ensuring the "integrity of the compositional, structural, and functional components comprising… ecosystems."

The 2012 Planning Rule places heavy emphasis on the concepts of "sustainability" and "ecological integrity." In the rule, sustainability is defined as "the capability of ecosystems to maintain ecological integrity" (36 CFR 219.19 p 21272), and ecological integrity is defined as:

> The quality or condition of an ecosystem when its dominant ecological characteristics (for example, composition, structure, function, connectivity, and species composition and diversity) occur within the natural range of variation and can withstand and recover from most perturbations imposed by natural environmental dynamics or human influence (36 CFR 219.19 p 21271).

The definition of ecological integrity in the 2012 Planning Rule thus inherently requires the determination of the "natural range of variation" (NRV) for a suite of important ecosystem variables, organized by their composition, structure, and function (connectivity belongs to structure, and species composition and diversity are nested in composition). Natural range of variation is defined by Forest Service Handbook 1909-12 Chapter 10 as:

> Spatial and temporal variation in ecosystem characteristics under historic disturbance regimes during a reference period… The NRV can help identify key structural, functional, compositional, and connectivity characteristics, for which plan components may be important for either maintenance or restoration of such ecological conditions.

As mandated by NFMA, national forests in the "Sierra Nevada bioregional assessment area" will revise and update their forest plans over the course of the next 6 to 10 years. The assessment area (see the outline map in fig. 1) includes the Sierra Nevada proper, the southern Cascade Range in California, the Modoc Plateau, the Warner Mountains, and the White and Inyo Mountains, among other areas. It is essentially the same area that was analyzed by the Sierra Nevada Ecosystem Project (Erman and SNEP Team 1996) and the Sierra Nevada Forest Plan Amendments of 2001 and 2004 (USDA FS 2001, 2004). Between October 2012 and May 2013, the Ecology Program of the Forest Service's Pacific Southwest Region carried out assessments of NRV for 11 major vegetation types across the Sierra Nevada bioregional assessment area. These NRV assessments fed the development of a more wide-ranging bioregional assessment that treats ecological, economic, social components and provides a broad-scale framework for the forest-level assessments that began in late 2013.

The intent is to publish the Ecology Program's NRV assessments as Forest Service general technical reports over the course of the next few years. This document, the NRV assessment for yellow pine and mixed-conifer forests, is the first installment of these publications. An earlier draft of this document was available online between February 15, 2015, and June 6, 2016, at http://www.fs.usda.gov/detail/r5/plants-animals/?cid=stelprdb5434436.

Summary

Yellow pine and mixed-conifer (YPMC) forests are among the most widely distributed forest types in California. Within the assessment area, these forests are primarily mid-elevation montane forests, with the distributions of the dominant canopy species limited by cold conditions at upper elevations and by dry conditions at lower elevations. YPMC forests occupy a Mediterranean climate zone with prolonged summer drought and sufficient winter precipitation to support tree growth, with greater precipitation and productivity on the western slopes of the Sierra Nevada and southern Cascade Range. The yellow pines, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Jeffrey pine (*P. jeffreyi* Balf.) are important canopy species within these forests, predominating at drier and frequently burned sites while mixing with other more shade-tolerant conifer species (white fir [*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.], incense cedar [*Calocedrus decurrens* (Torr.) Florin], and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]) at sites with less moisture stress or less frequent fire; sugar pine (*P. lambertiana* Douglas) and black oak (*Quercus kelloggii* Newberry) are other important tree species in YPMC forests. Important ecological differences among these canopy species (e.g., tolerance of shade, fire, and drought) have influenced their distribution and abundance across climatic and topographic gradients, which in concert with frequent fires have led to high levels of heterogeneity within this general forest type. Despite climatic fluctuations during the Holocene Epoch, the assessment area has been at least partially forested for 10,000 years, with an increase in the mixed-conifer component over the past 4,000 years when fire also has been very frequent, at least partially because of burning by American Indians. The past 150 years have seen extensive changes to assessment area YPMC forests, which experienced large-scale logging and subsequent, nearly ubiquitous fire exclusion that have dramatically altered contemporary forest structure and ecological processes.

Fire has been a major force in YPMC forests for millennia owing to the productive yet seasonally dry climate of the assessment area. Prior to Euro-American settlement in the mid-1800s ("presettlement"), fires were generally frequent, with a mean fire-return interval of 11 to 16 years. Fire occurrence during the summer dry season was often fuel limited, but also increased during periods of drought. These frequent fires kept fuel loads low and heterogeneously distributed across the landscape, and therefore fire severity under presettlement conditions tended to be low to moderate. Most estimates of presettlement high-severity proportions ranged from 5 to 15 percent, based on historical observations and surveys, studies of contemporary reference forests, and landscape-scale modeling. Mean fire size (of all fires >10 ha) was relatively small (c. 200 to 400 ha), while the mean annual area burned was about 5 percent of total YPMC forest area.

Forest structure in presettlement YPMC forests was generally characterized by fine-grained (within-stand) heterogeneity controlled by fire interacting with geologic, topographic, and climatic features that influenced vegetation productivity and structure primarily via their effects on growing-season water availability (the primary limiting resource in YPMC forests). Models and present-day reference landscapes suggest that roughly 50 percent of the presettlement landscape would have been in an old-growth condition, but this old-growth condition included both open stands of yellow pine and dry mixed conifer, and more closed-canopy stands of moist mixed conifer. Thus, stand structure within YPMC stands was likely highly variable, but in general, stands were characterized by relatively low

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tree densities and large tree sizes. Reconstructed tree densities from presettlement conditions range from 60 to 328 trees/ha, with an average of 159 trees/ha. Basal area estimates generally ranged from 21 to 54 m^2/ha depending on site productivity, with a mean of 35 m^2/ha. Some portions of the presettlement landscape were characterized by coarse-grained gaps occupied by montane chaparral, often in more productive areas that burned one or more times at high severity.

The heterogeneity of presettlement landscapes in YPMC forests has been simplified over the past 150 years, primarily by logging and fire exclusion, which have led to an increase in small-tree density and a decrease in large-tree density relative to the natural range of variation.

The heterogeneity of presettlement landscapes in YPMC forests has been simplified over the past 150 years, primarily by logging and fire exclusion, which have led to an increase in small-tree density and a decrease in large-tree density relative to the natural range of variation (NRV). Contemporary mean tree density of YPMC forests is 397 trees/ha, with densities ranging from 238 to 755 trees/ha in stands for which presettlement reconstructions exist. Most of this increase is in trees <60 cm diameter at breast height (d.b.h.). Corresponding changes in forest and understory structure from the presettlement era include a decrease in the average tree size (d.b.h.) by 25 to 40 percent; an increase in canopy cover by ~25 percent; a near-complete loss of fine-scale canopy gaps; increases in snag density, coarse woody debris, litter, and duff depth; and surface fuel volume and continuity. These changes in stand structure have caused changes in other ecosystem processes. For instance, insect and pathogen activity has probably increased with stand density (although presettlement information on this is sparse), while litter and duff accumulation can increase nutrients leaching to surface and ground water, and, combined with increased small-tree density, increase vulnerability to high-severity fire.

Modern fire suppression practices have caused a strong departure from presettlement fire-return intervals in YPMC forests, with an average of 80 to 85 percent fewer fires per 100 years than during the presettlement era. Although the frequency of fires has been greatly reduced, the characteristics of fires that do burn have also changed. The mean proportion of high-severity fire in YPMC forests has increased to between 30 and 35 percent in the past 30 years, while the size of high-severity patches also has increased. The mean fire size (of all fires >10 ha) over the past 30 years was ~1400 ha. As future climates continue to warm, future fire size, severity, and frequency are likely to increase.

Regeneration and understory dynamics in YPMC forests are complex. Regeneration dynamics historically were greatly influenced by fire (along with other gap-forming processes and precipitation patterns), with pine regeneration particularly enhanced by low- and moderate-severity fires, which maintained low canopy cover and exposed bare microsites for improved germination success. Presettlement regeneration was patchy and likely determined by interactions between fire, climate, topography, surface litter depth, and canopy cover. Modern tree regeneration is still highly variable, but survival of seedlings is promoted by fire exclusion, and the seedling class is more dominated by shade-tolerant fir, Douglas-fir, and incense cedar. Presettlement shrub cover was also quite variable. Areas of continuous shrubfields may have dominated after one or more severe fires, as is the case with modern severe fires, but shrubs could also be quite abundant in the understory of open stands that experienced frequent lower severity fires, as is the case in many modern reference stands. Contemporary YPMC forests may be within the NRV of shrub cover at a landscape scale, but many stands have likely experienced increases in shrub cover within large contiguous patches of high-severity fire, while others have seen reductions in shrub cover in fire-suppressed stands owing to increased shading. Presettlement herbaceous cover was likely low but diverse, and modern forests may be within the NRV in terms of herbaceous cover, but contemporary herbaceous diversity increases in stands that experience fire.

Contents

Chapter 1: Introduction

Natural range of variation (NRV) assessments (essentially, equivalent to historical range of variation [HRV] assessments) provide baseline information on ecosystem conditions (composition, structure, and function) that can be compared to current conditions to develop an idea of trend over time and an idea of the level of departure of altered ecosystems from their "natural" state (Landres et al. 1999, Manley et al. 1995, Morgan et al. 1994, Wiens et al. 2012) (see chapter 2). These trend assessments form part of the basis for the assessment of ecological integrity that is required in the 2012 Forest Service Planning Rule. Natural range of variation assessments were carried out for 11 terrestrial ecosystems by the USDA Forest Service Pacific Southwest Region (Region 5) Ecology Program between October 2012 and May 2013 using historical information (primarily from the pre-Euro-American period, 16th century to the mid-19th century) as well as information from modern-day reference ecosystems and other sources (see "Methods" and the appendix). The assessments were later updated for more recent scientific findings, and can be considered generally current as of late 2015, with some sections updated to 2016 or even early 2017.

In Region 5, forest planning under the 2012 Planning Rule is moving forward in geographically contiguous groups of national forests. Each forest will carry out its own set of assessments, but Region 5 also elected to carry out a bioregional assessment covering the same area as the 1996 Sierra Nevada Ecosystem Project (SNEP) to update trends and conditions described in the SNEP report and the Sierra Nevada Forest Plan Amendment (USDA FS 2004), and to better provide consistency among national forest plans with respect to conditions and trends at spatial scales greater than the size of a single national forest (400 000 to 800 000 ha), and temporal scales greater than the typical lifespan of a forest plan (15 to 20 years). In this report, we provide (1) an estimate of the NRV for key elements of yellow pine and mixed-conifer forest ecosystems, including quantitative ranges for specific variables whenever possible; and (2) a comparison of our NRV analysis with current conditions in the bioregional assessment area. Our NRV assessments also go farther in time, and summarize the current science concerning projected future conditions for key ecosystem elements.

Physical Setting and Geographic Distribution

Yellow pine and mixed-conifer forests are found throughout the assessment area (fig. 1). In this contribution, we jointly consider the two forest types and refer to them collectively as “YPMC” forests (the reasoning behind this combination is given in “Ecological Setting” below). YPMC forests are the most widely distributed vegetation type in the assessment area. Based on the California Wildlife Habitat Relations vegetation types (Mayer and Laudenslayer 1988), forest types corresponding to YPMC forest cover about 3 million ha (7.5 million ac) of the assessment area (fig. 1).

YPMC forests are found on a variety of soils and bedrocks, and there is little evidence of strong soil chemistry-driven differences in plant species composition or forest structure in the assessment area, except in the case of ultramafic (“serpentine”) soils, which are extremely nutrient deficient but relatively rare in the YPMC forest belt, aside from parts of the northern Sierra Nevada (Alexander et al. 2007). On the other hand, variations in soil depth and texture, which are strongly related to topography (slope, aspect, elevation, slope shape, etc.) in the assessment area’s Mediterranean climate, are major drivers of variation in forest species composition, density, cover, and other related variables. A major role of soils in YMPC forests in the assessment area is their contribution to water availability (O’Geen et al. 2007).

Most of California, including the assessment area, falls within the North American Mediterranean climate zone. Five geographic areas on Earth share the unique Mediterranean climatic characteristics, which are typically expressed on the western boundaries of continents between about 30° and 45° north latitude. Under the Köppen (1931) classification, the Mediterranean climate (“Cs” in the Köppen classification) is described as a temperate rainy climate with warm to hot, dry summers. YPMC forests in the assessment area fall primarily within the Köppen subcategory “Csb,” in which the average temperature of the warmest month is <22 °C and at least 2 months average above 10 °C (oak woodland, foothill pine, and chaparral vegetation types fall mostly in the warmer “Csa” type). As Bailey (2009) noted, the combination of wet winters with dry summers is rare along world climate types and leads to a distinctive vegetation dominated by evergreen trees and shrubs. The major environmental stress is the severe summer drought, which can last from 3 to 6 months, and leads to high evaporative demand during much of the growing season. In a Mediterranean climate, the demand for water and its supply are exactly out of phase (Major 1988). Within the Cs climate zone, there is a gradient in intensity of the dry summer season from areas with relatively mild summer temperatures (northern assessment area and higher elevations) to areas with hot summer temperatures (lower elevations, especially in the southern and eastern assessment areas) (SSP 2010).

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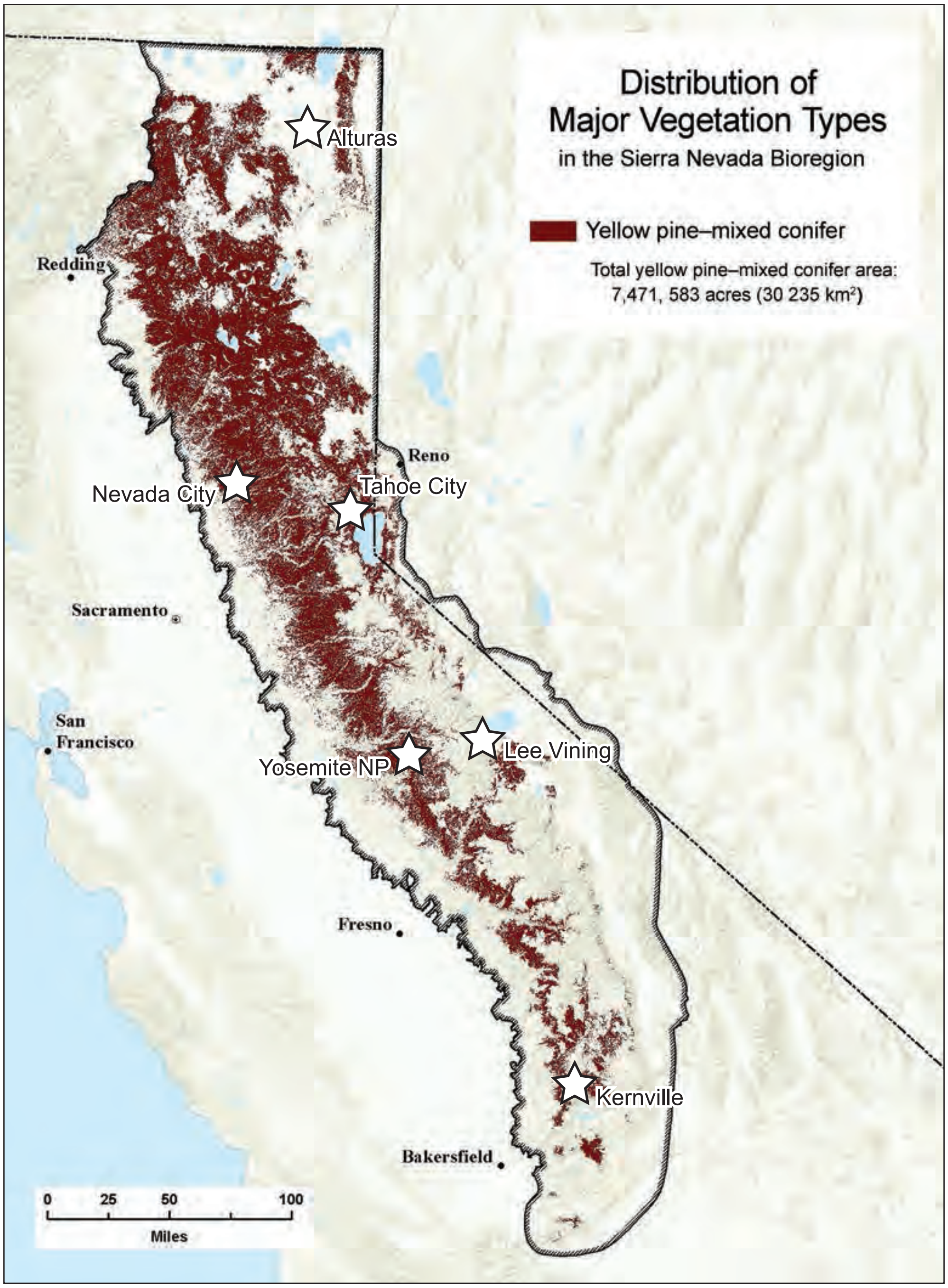

Figure 1—Distribution of yellow pine and mixed-conifer forests in the assessment area, with climate station locations indicated.

Figure 2 shows Walther-type climate diagrams for six National Weather Service weather stations in or near YPMC forests in the assessment area; data are from the Western Regional Climate Center (2013). The diagrams are organized to approximately match their locations in figure 1. As per Walter and Lieth (1967), the temperature and precipitation axes are scaled such that 20 mm precipitation = 10 °C temperature. The dry season is found approximately where the precipitation line undercuts the temperature line; the wet season occurs where precipitation supersedes temperature. We say approximately because moisture stored in the soil and snowpack is available for plant use after the end of the wet season and can reduce true dry season length by a month or more depending on annual precipitation (see Major 1988).

The climate diagrams underline the major climatic gradients in the assessment area (fig. 2). Dry season length is shortest along the west slope, especially in the north (3 to 4 months), and longest in the extreme south and on the east slope (5 to 6 months). Precipitation is higher in the northwest than the rest of the assessment area. Stations east of the hydrologic divide (which is either the Sierra Nevada or Cascade Range crest in most of the assessment area) are subject to a rain shadow effect, as is the Modoc Plateau, represented by Alturas. All stations receive some monsoon-derived precipitation in the summer months, with the magnitude and importance of that precipitation increasing to the east and southeast in concert with the influence of the Great Basin climate. Of the stations shown, Alturas and Lee Vining are the most influenced by periodic summer precipitation. Temperatures are warmest in the south, and coolest in the north and at higher elevations (fig. 2).

Topography drives major differences in ecosystem distribution across the assessment area. Elevation increases from north to south, and local relief is generally much higher in the central and southern Sierra Nevada than the rest of the assessment area. The Sierra Nevada is also narrower in the south, and the combination of less land area, higher mountains, and steeper slopes means that the YPMC forest belt is much more compressed south of the latitude of Sacramento (fig. 1). The southern Sierra Nevada also rises to a high plateau relatively quickly from the floor of the Central Valley. As a result, the area on the west slope dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) in the southern Sierra Nevada is relatively narrow, and higher elevation mixed-conifer forests with an important white fir (*Abies concolor* Gord. & Glend.) component are more widespread. Steeper terrain, a drier climate, and the predominance of granitic bedrock in the central and south Sierra Nevada also lead to much greater prevalence of bare rock substrates and cliffs. Overall, the natural lay of the land means that physical barriers to ecological processes like animal migration, plant seed dispersal, and fire spread are greater in the southern and central Sierra Nevada than elsewhere, but land ownership and land use follow the opposite pattern, with much more fragmentation of habitat in the northern subregion.

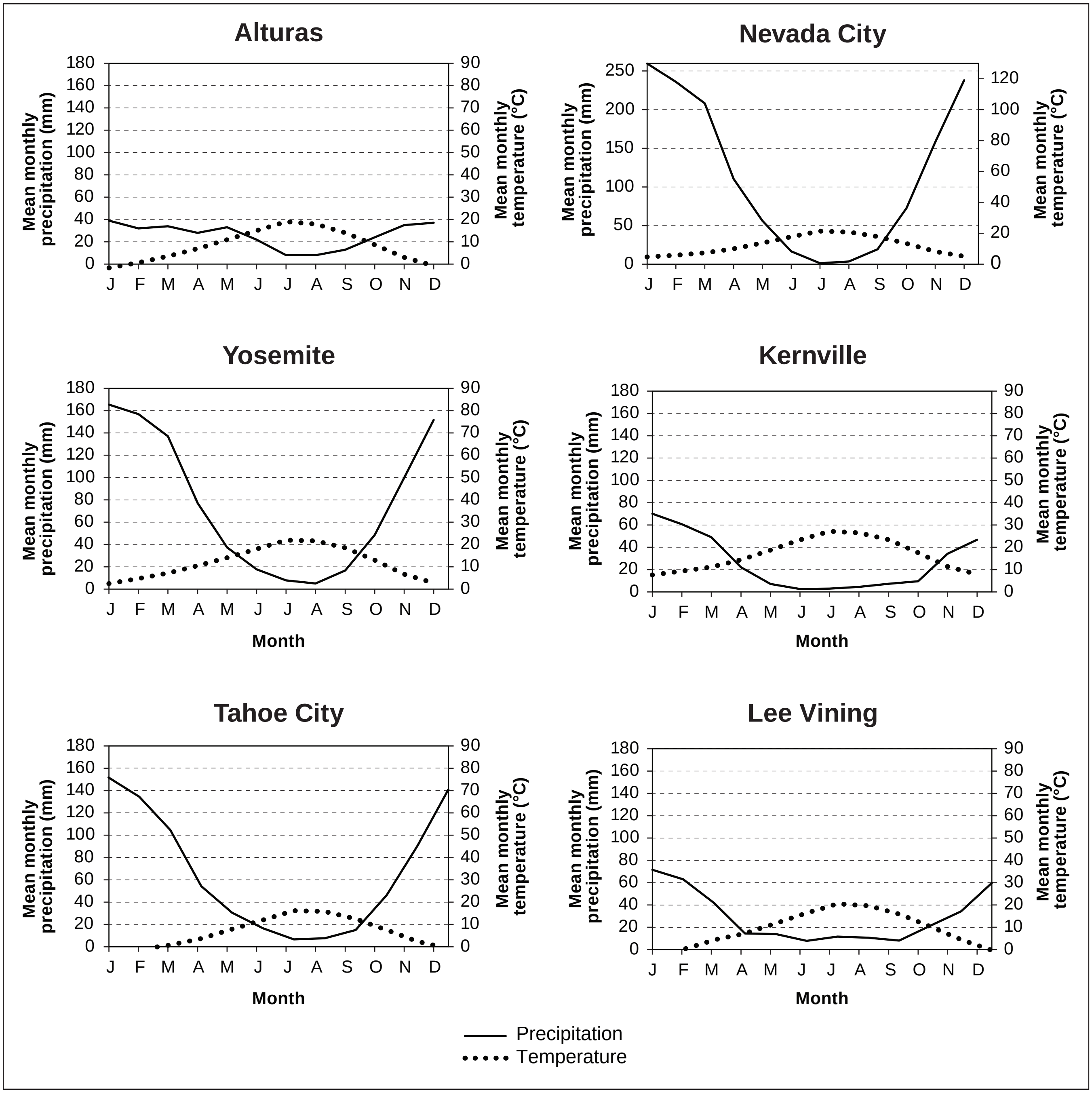

Figure 2—Walther-type climate diagrams for six weather stations in or near yellow pine and mixed-conifer forest in the assessment area; elevations are provided. Locations shown in figure 1. Dry season length is approximately the period during which the precipitation curve undercuts the temperature curve.

Because of dry growing season conditions in the assessment area, water availability is a major driver of ecosystem distribution and condition (Barbour et al. 2007, Loik et al. 2004, Major 1988). Topography exerts strong influence on water availability, both directly through its influence on temperature, solar insolation, and evaporation, and indirectly through its influence on soil depth and texture. Forest conditions in the YPMC forest belt differ substantially along topographic gradients (Barbour et al. 2007, North et al. 2012b, Sugihara et al. 2006). It can be generalized that, all other environmental factors being equal, YPMC forest cover and density tend to be higher on north-facing ("cool") aspects (where water availability is higher), and more open and less dense on south- and west-facing ("warm") aspects. Because higher elevations receive more precipitation because of orographic effects and also lose less water to heat evaporation, they also tend to support denser stands of forest than lower elevations. The upper portions of mountain or canyon slopes lose substantial water to gravity-driven flow and tend to support more open forest conditions, whereas lower slopes are net importers of water from higher slopes, and they support denser forest conditions. The most open forest conditions tend to be on south- or west-facing, upper, convex canyon slopes at lower elevations; the densest forest conditions tend to be on north-facing, concave, lower slopes. Overlain on these topographic effects are precipitation and temperature gradients across the broader assessment area. In general, forests are more open (and more composed of drought-tolerant species) in the southern and eastern portions of the assessment area than in the western and, especially, the northern portions.

Ecological Setting

Yellow pine forests in the assessment area are those that are dominated by one or both of the "yellow pine" species present in California: ponderosa pine and Jeffrey pine (*P. jeffreyi* Balf.); Washoe pine is now considered a variety of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *washoensis* (H. Mason & Stockw.) J.R. Haller & Vivrette) (Baldwin et al. 2012). Ponderosa and Jeffrey pine are closely related (they are both in the subgenus *Pinus,* section *Pinus*, subsection *Ponderosae*), and they occasionally hybridize. Ponderosa pine, the most widely distributed pine species in North America, is found throughout the mountainous regions of California, whereas Jeffrey pine is primarily a California tree, with some occurrences in westernmost Nevada, southwestern Oregon, and northern Baja California. Of the two species, Jeffrey pine is more stress tolerant, and replaces ponderosa pine at higher elevations, on poorer soils, and in colder or drier climates (Barbour and Minnich 2000, Haller 1959). Ponderosa pine-dominant forests can occur from about 300 m elevation to about 1800 m in the northern subregion of the assessment area, and from about 1200 to 2100 m in the southern subregion (Fites-Kaufman et al. 2007). Jeffrey pine-dominant forests occur mostly between 1500 and 2400 m in the northern subregion and from 1700 to 2800 m in the southern subregion, with the highest elevations usually being on the east side of the Sierra Nevada (Barbour and Minnich 2000, Fites-Kaufman et al. 2007). Both yellow pine species can also occur in other forest types. A large area of the Lassen, Plumas, and Tahoe National Forests east of the Sierra Nevada crest supports a mixed-yellow pine forest with codominance by ponderosa and Jeffrey pine; this forest type is often called "eastside pine."

Many conifer species with overlapping geographic distributions are found in the assessment area, and difficulties in differentiating obvious forest types have led to the general recognition of a "mixed-conifer" belt in the lower montane zone, usually intermixed with yellow pine-dominant stands at its lower edge and up to 2000 to 2200 m elevation at its highest, depending on latitude. Major tree species include the yellow pine species, sugar pine (*Pinus lambertiana* Douglas), white fir, incense cedar (*Calocedrus decurrens* (Torr.) Florin), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and black oak (*Quercus kelloggii* Newberry). Red fir (*Abies magnifica* A. Murray bis), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and western white pine (*Pinus monticola* Douglas ex D. Don) are upper montane species that also make appearances in higher mixed-conifer stands; a variety of hardwood species also occur in lower elevation stands, including canyon live oak (*Quercus chrysolepis* Liebm.), interior live oak (*Q. wislizenii* A. DC.), and tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh). As Barbour and Minnich (2000) noted, the yellow pine species (especially ponderosa pine) are "the biological thread that holds the [mixed-conifer] forest together," but the very fine-grained pattern of local dominance makes it difficult to clearly discriminate the various "phases" for classification or mapping purposes. It should be noted that the topography of the southern Sierra Nevada (see "Physical Setting") leads to a relatively narrow belt of ponderosa pine-dominant forest, and many YPMC stands in this part of the assessment area support a notable component of white fir.

Although Sawyer et al. (2009) described nearly 20 different forest alliances that make up the montane mixed-conifer forest, we stick with common practice and treat the mixed-conifer forest as a single, if geographically mutable, entity. In some cases in this assessment we refer to "dry mixed-conifer" or "moist mixed-conifer" forests. These terms are used only in a general sense, and differentiate mixed conifer based on the yellow pine and fir components (yellow pine dominance in dry mixed conifer; greater fir presence in moist mixed conifer) and the annual precipitation (mostly <1000 mm in dry mixed conifer, mostly >1000 mm in moist mixed conifer); moist mixed-conifer stands are also more common at higher elevations. We also follow Barbour and Minnich (2000) in combining yellow pine forest and mixed conifer in this chapter. This is because yellow pine forests have become rare on the west side of the Sierra Nevada, owing to logging of the ponderosa pine or fire-exclusion-driven succession to mixed stands dominated by more shade-tolerant and fire-intolerant species like white fir and incense cedar (the same can be said of sugar pine, which was even more targeted by logging). Indeed, in drier sites throughout, and up to 2000–2500 m elevation at its highest Yellow pine-dominant forests remain common on the east side of the Sierra Nevada, however.

We do not explicitly treat giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) in this NRV assessment. Giant sequoia occurs in scattered groves in the southern assessment area, with a few occurrences in the central assessment area. Giant sequoia is a locally dominant member of moist mixed-conifer stands with particular topographic and soils conditions (Barbour et al. 2007, Sugihara et al. 2006). Our treatment of moist mixed-conifer forest, which is otherwise dominated by species like white fir and sugar pine, is generally applicable to giant sequoia stands, but we direct the reader to the forest-level assessments for more detail. Stephenson (1999) is an excellent treatment of ecological, management, and restoration issues in giant sequoia-dominant mixed-conifer forest.

An understanding of past, current, and possible future conditions in YPMC forests in the assessment area requires consideration of the ecological differences between the major tree species. Forestry experience and scientific investigation have provided us with a wealth of information vis-à-vis the relative ecological tolerances of major tree species in the YPMC forests of the assessment area. Table 1 offers some summary information about geographical and elevational distributions of the seven major tree species in assessment area YPMC forests. Four of the seven species are broadly restricted to the North American Mediterranean zone (Jeffrey pine, sugar pine, incense cedar, black oak), and three are more widely distributed (ponderosa pine, Douglas-fir, white fir), with the two former species among the most widely distributed tree taxa in North America. Species restricted primarily to the YPMC forest zone include ponderosa pine, sugar pine, white fir, incense cedar, and black oak. Douglas-fir is also found at lower elevations in the northern and central parts of the assessment area, usually in moist, mixed-evergreen forests with a number of hardwood/broadleaf associates. Jeffrey pine ranges into higher elevation forests and is a common member of red fir forests and even some warm sites in the subalpine zone (table 1).

Table 1—Dominant tree species of yellow pine and mixed-conifer forests in the assessment area, their geographic distribution, approximate elevational range within the assessment area, and comparisons of leaf flammability and seed weight

Species	Scientific name	Geographic distribution	Elevation[a]	Leaf flammability[b]	Seed weight[c]
			Meters		*Grams*
Ponderosa pine	*Pinus ponderosa*	Western United States; southwest Canada; northern Mexico	300–1800 N; 1200–2100 S	Very high	0.02–0.07
Jeffrey pine	*Pinus jeffreyi*	Eastern edge of North American Mediterranean zone; southern Oregon to Baja California	1500–2400 N; 1700–2800 S	Very high	0.08–0.2
Sugar pine	*Pinus lambertiana*	Oregon to Baja California	1000–2000 N; 1400–2700 S	High	0.15–0.3
Incense cedar	*Calocedrus decurrens*	Oregon to Baja California	600–2100	Moderate	0.015–0.07
Douglas-fir	*Pseudotsuga menziesii*	Western United States; southwest Canada; northern Mexico	300–2100 N; 600–2100 S	Low	0.01–0.02
White fir	*Abies concolor*	Southern Rockies; Southwest United States; southern Oregon to Baja California	800–2300 N; 1500–2500 S	Moderate	0.015–0.055
Black oak	*Quercus kelloggii*	Southern Oregon to Baja California	900–1500 N; 1400–2100 S	Very high	3–9

Note: elevations are rounded to the nearest 100 m; N = north, S = south.

[a] Sources: Lanner 1999, Storer and Usinger 1963, van Wagtendonk and Fites-Kaufman 2006.

[b] Sources: de Magalhães and Schwilk 2012, Engber and Varner 2012, Fonda et al. 1998.

[c] Sources: Bonner and Karrfalt 2008, Burns and Honkala 1990, Fowells and Schubert 1956.

We have compiled and condensed important information related to comparative ecological traits and tolerances for the important tree species in assessment area YPMC forests. Table 1 provides information on seed weights, which are inversely related to dispersal distances (and therefore scale with the relative rapidity by which these species can recolonize or migrate to distant habitat), and leaf flammability, which is a trait strongly associated with the importance of fire to species ecology (Fonda et al. 1998, Keeley and Zedler 1998, Keeley et al. 2012, Schwilk and Caprio 2011). Table 2 ranks tree species in assessment area YPMC forests by their relative tolerances to shade, frost, temperature, drought, and fire. Figure 3 compares growth rates of young shade-tolerant and -intolerant tree species, and figure 4 compares bark thickness of young trees of the six major conifer species from table 1.

Table 2—Comparative ecological tolerances of common tree species in assessment area yellow pine and mixed-conifer forests[a].

Shade	Frost	Temperature[b]	Drought	Fire[c]
Black oak/western juniper	Madrone	Lodgepole pine	Red fir	Lodgepole pine
Ponderosa pine	Douglas-fir	Red fir	White fir	Sugar pine/white fir
Lodgepole pine	White fir	Jeffrey pine	Western white pine	Incense cedar
Sugar pine	Sugar pine	White fir	Sugar pine	Jeffrey pine/ponderosa pine/Douglas-fir
Incense cedar/western white pine	Incense cedar	Douglas-fir/sugar pine/ incense cedar	Douglas-fir	
Douglas-fir	Ponderosa pine/Jeffrey pine/red fir	Ponderosa pine/black oak/madrone	Lodgepole pine/incense cedar/madrone	
Red fir	Lodgepole pine, western white pine		Ponderosa pine	
White fir			Jeffrey pine	
			Black oak	

[a] Species arranged from low tolerance (top) to high tolerance (bottom).

[b] Least heat tolerant/most cold tolerant on top.

[c] Fire tolerance of mature trees. Fir and Douglas-fir seedlings and saplings are less tolerant of fire than yellow pine and sugar pine.

Source: Burns and Honkala 1990, Minore 1979, USDA FS 2013b.

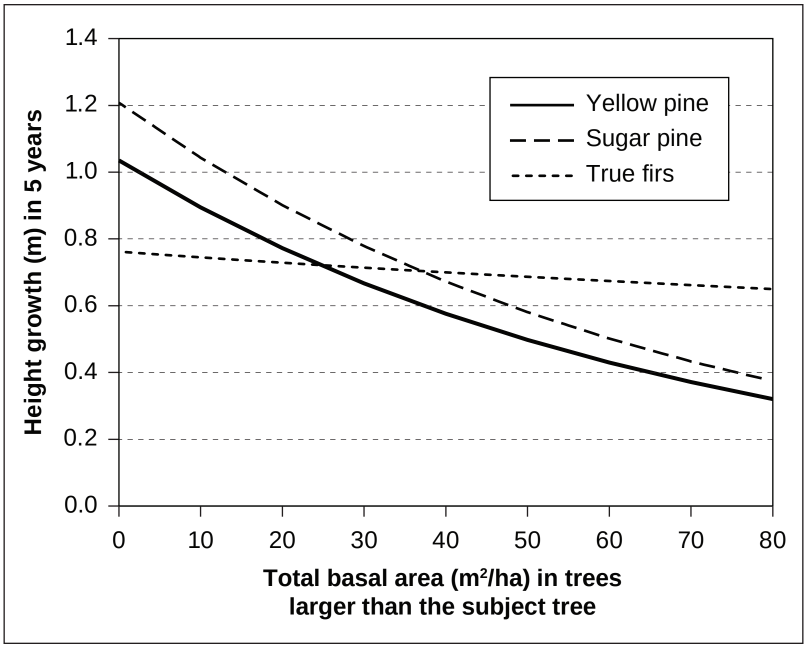

Figure 3—Comparison of predicted small tree (between 3.8 and 7.6 cm diameter at breast height) growth rates of yellow pines, sugar pine, and true firs as a function of the basal area of trees larger than the subject tree. Curves shown are for a site of moderate productivity (site index of 80) and crown ratio of 50 percent.

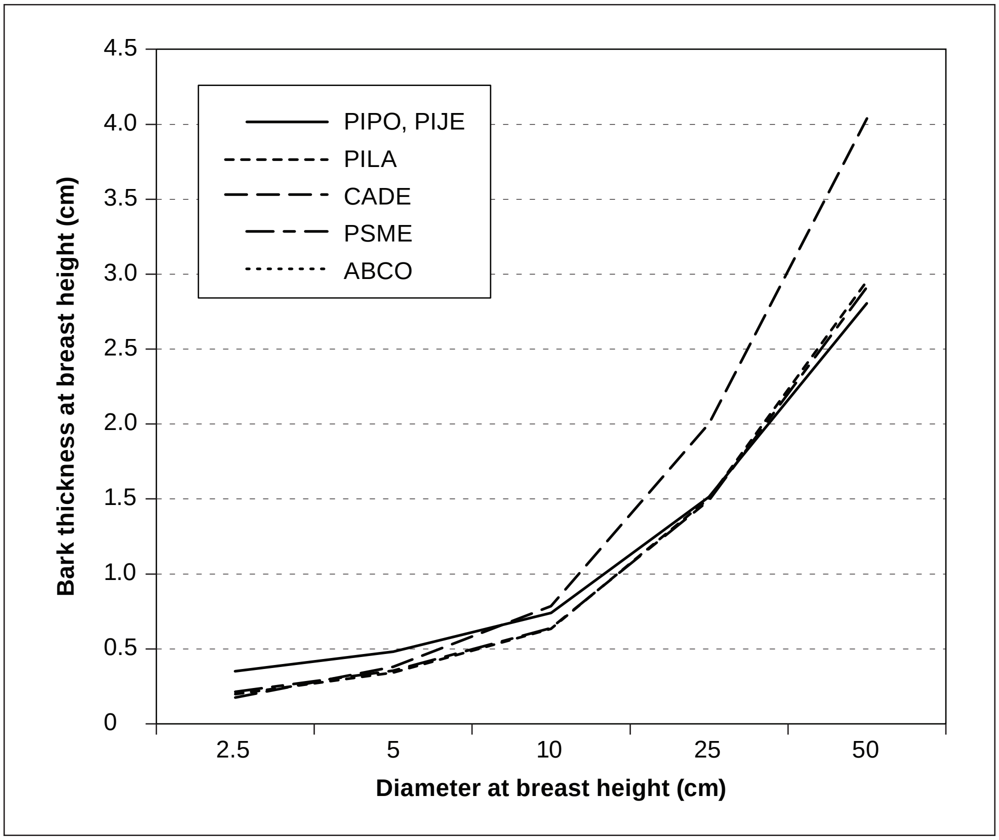

Figure 4—Bark thickness of six tree species in the assessment area, as a function of diameter at breast height. Thickness is calculated based on formulas in Dolph (1984). ABCO = *Abies concolor* (white fir); CADE = *Calocedrus decurrens* (incense cedar); PIJE = *Pinus jeffreyi* (Jeffrey pine); PILA = *P. lambertiana* (sugar pine); PIPO = *P. ponderosa* (ponderosa pine); PSME = *Pseudotsuga menziesii* (Douglas-fir).

McCune (1988) defined groups of North American pines that could be reliably differentiated based on their ecological characteristics. Ponderosa, Jeffrey, and sugar pine all formed part of his “fire resisters” species group, which was characterized by traits and tolerances that promoted the ability to survive low- to moderate-intensity surface fire. This group was generally marked by long needles, thick twigs (which protect growing tissues), thick bark, thick cone scales (which may protect seeds from heat), relatively slow growth, and an extended adolescent period (the mean time to seed-producing age was 16.3 years). McCune (1988) noted that this group of pines was tolerant of frequent surface fire “and reacts to fire more as a stress than as a disturbance.”

Bark thickness of young YPMC tree species as a function of tree diameter is shown in figure 4. Among YPMC tree species, the two yellow pine species have the thickest bark at young ages, but are equaled and even passed by incense cedar at about 10 cm diameter at breast height (d.b.h.) and other species between 25 and

50 cm d.b.h. (Dolph 1984, also see van Mantgem and Schwartz 2003). Note that its thick bark notwithstanding, mature incense cedar is somewhat more susceptible to cambial injury than its bark thickness might indicate owing to the bark's dry, stringy, and highly furrowed nature (Lachmund 1923). Yellow pines are thus well protected from fire during the sapling stage, which is critical in an ecosystem characterized by fires every 5 to 20 years on average (Van de Water and Safford 2011). Other fire-related traits of ponderosa, Jeffrey, and sugar pine include self-pruning of lower branches (Keeley and Zedler 1998) and highly flammable needles and cones, which promote fires that kill competitors that are less fire tolerant (Fonda and Varner 2004, Fonda et al. 1998, van Wagtendonk et al. 1998). Black oak, which is a common member of drier YPMC forests in the assessment area, also produces extremely flammable litter (it is the most flammable Western U.S. oak) (Engber and Varner 2012). Douglas-fir is an interesting case. Young Douglas-firs are quite susceptible to fire mortality, but mature individuals can be extremely fire resistant (Agee 1993, Skinner et al. 2006). The species develops very thick bark when mature, and the bark is less prone to sloughing and collecting at the base of the tree than pine bark. Douglas-fir needles are also short and relatively inflammable (Fonda et al. 1998; see below). It has been hypothesized that Douglas-fir's presence in frequent-fire forests was favored by a variable fire frequency over time, one that periodically included fire-free intervals sufficiently long to allow recruitment of Douglas-fir seedlings into age classes that are more fire resistant (Agee 1993).

Fonda et al. (1998) tested flammability and burning characteristics of the needles of 13 common conifer species from the Western United States. Based on six burning characteristics, ponderosa and Jeffrey pine were ranked first and second, and sugar pine was seventh (giant sequoia was sixth). Douglas-fir and the two tested fir (*Abies*) species were three of the four lowest ranked species (Fonda et al. 1998). Fonda et al. (1998) noted that the highest ranked species were characterized by fire regimes supported by nonwoody fuels (e.g., needle litter, herbaceous fuels), whereas the lower ranked species typically required woody fuel accumulation over decades to support fires. In another flammability study, de Magalhaes and Schwilk (2012) found that black oak, ponderosa pine, and Jeffrey pine had the highest flammability across most parameters tested. White fir and red fir were less flammable, but they were both more flammable than the fir species tested by Fonda et al. (1998), which is not surprising given their presence in the highly fire-prone Sierra Nevada. Also, de Magalhães and Schwilk (2012) found that flammability of species mixtures of needles was mostly driven by the most flammable species in the mixture, which were Jeffrey pine, ponderosa pine, sugar pine, and black oak. See table 2 for a fire tolerance ranking of assessment area species.

Major tree species in YPMC forests differ notably with respect to the size of their seeds (table 1), the distances these seeds are dispersed, and the number of seeds they produce. In general, heavier seeded species disperse shorter distances, although animal vectors play an important role in the dispersal of some species. Fowells and Schubert (1956) measured seed rain in a YPMC forest during a 9-year period and found that, on average, white fir produced about 2.5 times as much seed as either ponderosa or sugar pine, and incense cedar produced about four times as much seed. Fowells and Schubert (1956) found very high interannual variability, and in some years the pines outseeded the two shade-tolerant species. Working in Yosemite and Sequoia & Kings Canyon National Parks, van Mantgem et al. (2006) concluded from a 5-year study that, standardized by basal area, fir species produced between seven and eight times as much seed as pines (yellow and sugar), and incense cedar produced about three times as much seed. Zald et al. (2008) found the seed rain of shade-tolerant white fir and incense cedar to be 5 to 26 times greater than Jeffrey and sugar pine in southern Sierra Nevada mixed conifer. Stark (1965), in a study of natural tree regeneration after logging, reported that, over a 13-year period, more than 80 percent of surviving seedlings were incense cedar or white fir, 10 percent were sugar pine, and 4.3 percent were yellow pine. Fowells and Schubert (1956) found that white fir and ponderosa pine had similar dispersal distances, which were 50 to 75 percent farther than sugar pine. Vander Wall (2003) found that rodents and birds were important dispersers of pine seeds in YPMC forests. Rodents moved seeds of ponderosa, Jeffrey, and sugar pine about 25 m on average from the parent plants, which approximately doubled the dispersal distances for the latter two species.

Growth rates of YPMC forest trees differ by species and environmental conditions. Yeh and Wensel (2000) found that diameter growth of assessment area YPMC species typically occurs between late March/early April and mid-September, but growth ends earlier at lower elevations (owing to summer drought) and starts later at high elevations (e.g., growth at Blacks Mountain Experimental Forest in the northern assessment area, which ranges from 1700 to 2100 m elevation, generally begins in May).[1] Yeh and Wensel (2000) found that the pines were less disadvantaged by water stress than other tree species. Overall, the most important factors to growth were tied to water availability and included the previous winter's precipitation (related to water storage) and the current summer temperature (related to water loss).

Light availability is an important environmental driver of growth for plants, and YPMC tree species differ notably in the effects that canopy shading has on

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[1] Taylor, A.H. 2013. Personal communication. Professor, Department of Geography, Pennsylvania State University, University Park, PA 16802.

their growth rates (table 2). Keyser (2010) provided equations for growth of major tree species in the assessment area. Small tree (d.b.h. between 3.8 and 7.6 cm [1.5 and 3 in]) growth is modeled as a function of site productivity (site index, or the mean potential height in feet of a free-grown tree at 100 years); crown ratio (ratio of crown length to tree height); and competition/shading by larger trees (basal area of trees larger than the subject tree) (Keyser 2010). Figure 3 shows how both the yellow pine species and sugar pine grow more rapidly than white fir and red fir in open stands but are outgrown by the fir species once the basal area of larger trees exceed about 30 m^2/ha (130 ft^2/ac). Bigelow et al. (2011) examined the crossover-point irradiance (CPI), the light at which the height-growth rank of pairs of species changes, and found that an understory light environment with 41 percent or more of full sunlight favored ponderosa pine regeneration over white fir. Moghaddas et al. (2008) showed that black oak and ponderosa pine seedling survival was strongly connected to high light environments. Oliver and Dolph (1992) found that ponderosa pine grew more slowly than the other YPMC tree species at even moderate shade levels, while sugar pine showed quite strong growth at 50 to 60 percent of full sunlight. They noted that sugar pine appeared to be adapted to exploit small forest gaps and showed some characteristics of the more shade-tolerant species (e.g., fir).

YPMC tree species also differ with respect to their tolerances to frost, heat and cold, and drought. In general, shade-tolerant species from low- and middle-elevation forests (e.g., Douglas-fir and white fir) are more susceptible to frost damage than the pine species and red fir (table 2). Not surprisingly, the most cold-tolerant species are those from higher elevations, and the most heat tolerant are those from lower elevations and warmer microsites (table 2). Drought tolerance is a very important trait, as precipitation in the assessment area is highly variable between years, and models of future climate in the assessment area project increased occurrence of drought (Dettinger 2011, Liu et al. 2010). The true fir species are the least drought-tolerant members of YPMC forests in the assessment area, whereas sugar pine, Douglas-fir, and incense cedar are intermediate. The yellow pines and black oak are the most drought-tolerant species in YPMC forests (table 2).

In summary, the major YPMC tree species are differentially adapted to the physical and biotic environment in the assessment area, and the different tolerances of these tree species play a major role in determining forest composition, structure, and function. Considering the overwhelming importance of fire and water availability to YPMC forest ecology and management in the assessment area, perhaps the most important distinction to be made is between those species that are highly tolerant of fire and drought but intolerant of shade (black oak and the yellow pines), versus those that are less tolerant of fire and drought but grow relatively well in

The major YPMC tree species are differentially adapted to the physical and biotic environment in the assessment area, and the different tolerances of these tree species play a major role in determining forest composition, structure, and function.

low-light conditions (white fir, incense cedar, and Douglas-fir; recall, however, the high-fire tolerance of mature individuals of the latter species). These ecological differences are at the root of general topographic tendencies in forest composition across the assessment area. Locations with higher water availability (north aspects, lower slopes, concave topography, higher elevations) tend to support higher densities of the shade-tolerant, fire-intolerant species, whereas sites with lower water availability (south aspects, upper slopes and ridgetops, convex topography, lower elevations) are more likely to be dominated by shade-intolerant, fire-tolerant species.

These ecological differences among species translate into successional differences as well. In regions that can support forest cover, trees that specialize in high-light environments will be generally restricted to early-successional stages, and locations where ecological factors slow successional processes. The very high frequency of fire before Euro-American settlement (see below) played such a role, and essentially kept YPMC forest in the assessment area in a state of arrested development; where early-successional species such as the yellow pines and black oak were able to maintain canopy dominance, even in places of relatively high water availability. In the general absence of fire disturbance over the past century, successional processes have become "unblocked" and more competitive; later-successional species like the firs and incense cedar have come to dominate most of the YPMC belt in the assessment area. Early-successional species continue to dominate where fire regimes have not been much perturbed, and where local soil productivity acts to slow succession. We will make reference to these differences in fire, shade, and drought tolerance and successional relationships throughout this report.

Temporal Variability in the Ecological Setting

The mutable nature of the climate has never been more apparent than today, with human inputs to the atmosphere rapidly increasing greenhouse gas levels and global temperatures. Although the concept of "climate" is one that suggests long-term stability, climates are constantly changing, and climatic variability throughout the Holocene Epoch has had major effects on YPMC forests in the assessment area. It is also important to note that temporal changes in climate have not been uniform across the assessment-area landscape, and the timing of changes in temperature and precipitation, as well as biotic responses, differ from one area to another. Nonetheless, some useful generalizations can be made.

The Holocene Epoch is now considered to have begun about 12,000 YBP (years before present). The entire epoch falls within a broadly defined "interglacial" period. The Earth's climate has been in "glacial" periods for about 90 percent of the past 850,000 years, and interglacial periods as warm as the Holocene are relatively rare (Tausch et al. 2004). Overall, mean annual temperatures have fluctuated by 3 to 6 °C through the Holocene, and precipitation has also risen and fallen. Researchers generally divide the Holocene into three periods that are defined by broad (and somewhat ill-defined) changes in temperature and precipitation. The Early Holocene stretches from the beginning of the epoch to 8,000 or 7,000 YBP, and was characterized by post-glacial warming, but generally cool and moist conditions compared to today; however, data from the northern Great Basin portion of the assessment area (e.g., Warner Mountains) suggest that post-glacial conditions were somewhat warmer and drier than today (Minckley et al. 2007). Many closed basins east of the Sierra Nevada crest supported large rain- and snowmelt-fed lakes at the beginning of the Holocene, but most of these dried or decreased greatly in size over the ensuing couple of millennia (Minnich 2007). At the beginning of the Holocene, elevations that currently support YPMC forests were largely vegetated by high-elevation sagebrush and grass species, with a minor presence of pine and juniper (Anderson 1990, Woolfenden 1996). By 9,000 to 10,000 YBP, however, conifer forests had established themselves in most of these areas (Minnich 2007), except in the Great Basin portions of the assessment area (Minckley et al. 2007).

The Middle Holocene, about 8,000 to 4,000 YBP, is also often referred to as the “Xerothermic,” “Hypsithermal,” or “Altithermal” Period. Climates became much warmer and drier, with the driest and warmest conditions occurring around 6,000 YBP. Glaciers completely disappeared from the Sierra Nevada (Clark and Gillespie 1997), and lake levels dropped precipitously. For example, Lake Tahoe was apparently permanently below the Truckee River outlet elevation during the period between about 6,300 and 4,800 YBP (Lindström 1990). Fire frequency also increased during the Middle Holocene, at least in places that were able to maintain plant cover (Beaty and Taylor 2009, Woolfenden 1996). Paleoecological data suggest that forests of fir and pine were replaced by oak, sagebrush, and juniper in many areas, and forest structure was likely very open, with abundant understory shrubs. Conifers invaded formerly moist areas of meadow, and desert plant and animal taxa migrated upslope (Anderson 1990, Minnich 2007).

The Late Holocene (4,000 YBP to present) has been generally characterized by cooling, with some warmer periods. Precipitation increased, and small glaciers began to form again in the Sierra Nevada. Millar and Woolfenden (1999) suggested that the basic spatial and compositional outlines of modern Sierra Nevada ecosystems developed by the beginning of the Late Holocene (note that Minckley et al. [2007] suggested that ecological conditions similar to today were already in place in the northwestern Great Basin by the Middle Holocene). As temperatures cooled, available moisture rose, and fir and incense cedar abundance increased relative to pine and oak; giant sequoias began to colonize their current groves (Millar and Woolfenden 1999).

White fir was a mostly minor component of assessment area YPMC forests before the general cooling and increase in precipitation seen over the past 4,000 years. Oaks have declined in importance since the end of the Middle Holocene. Earlier in the Holocene, sagebrush was a major component of low-elevation west-side landscapes, but now it is primarily restricted to higher elevations on the east side of the assessment area (Anderson 1990). Fire has been present as an important ecosystem process ever since deglaciation at the beginning of the epoch, but the presettlement period, characterized by frequent fire and large areas of fire-adapted vegetation, began during the Late Holocene for most of the assessment area (Millar and Woolfenden 1999).

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The past 1,000 years of the Holocene have been marked by short-term changes in temperature and precipitation that have had major impacts on assessment-area ecosystems (Millar and Woolfenden 1999, Minnich 2007, Woolfenden 1996). Between about 900 and 1100 CE, and from 1200 to 1350, two long drought periods (the "medieval droughts," or collectively, the Medieval Warm Period) led to very low levels in lakes and streams (Stine 1994) and increased fire frequencies. This was followed by a shift to cooler temperatures known as the Little Ice Age, initiated apparently by a series of massive volcanic eruptions that caused atmospheric reflection of solar radiation (Miller et al. 2012a). The Little Ice Age lasted from about 1400 to 1880, and the period between 1650 and 1850 was the coolest since the Early Holocene (Stine 1996). Glaciers expanded in the Sierra Nevada, tree line dropped, and fire frequencies moderated. Minnich (2007) noted, however, that there is little evidence for major changes in vegetation composition during the Little Ice Age. It is important to underline that the period of the Little Ice Age is also the period most commonly used as an historical reference period for restoration planning in the Western United States.

Most recently, human emissions to the atmosphere have resulted in renewed warming, even though Earth orbital cycles should be resulting in a cooling trend (Ruddiman 2005). Current temperature trends include increased temperatures especially at nighttime, a decrease in the number of days with below-freezing temperatures, and an increase in the number of extreme-heat days. The 20th century was one of the wettest centuries in the Late Holocene (Stine 1996), and recent precipitation trends in most of the assessment area have been steady or positive (Safford et al. 2012b). Interannual variability in precipitation is up at many stations in the assessment area, and the proportion of precipitation falling as rain versus snow is increasing; as a result, the depth of the winter snowpack is decreasing, except in the southern assessment area, where mountain elevations are very high (Safford et al. 2012b). Recent trends in fire activity are positive, with burned area, fire size, and fire frequency all rising in assessment area YPMC forests, accompanied by an increase in fire severity on lands where fuels have accumulated as a result of long-term fire exclusion policies (Mallek et al. 2013, Miller and Safford 2012, Miller et al. 2009b, Steel et al. 2015).

Cultural Setting

Humans have actively managed yellow pine and mixed-conifer forests for resource benefits for thousands of years. YPMC forests are generally productive and accessible to denser human settlements at lower elevations, which has made them attractive to humans for a variety of uses. The period of human settlement and forest management in California may be divided into four time periods—the American Indian era, the Euro-American settlement era, the fire-exclusion era, and the ecosystem management era (Sugihara and Barbour 2006). Each of these periods was characterized by distinct cultural values and practices that shaped the management of YPMC forests. Of particular importance to the management of YMPC forests throughout these eras are the role of fire and use of timber resources. The suite of human uses in YPMC forests has been fairly consistent among the different parts of the assessment area. The southern Cascade Range and Modoc Plateau have generally had lower human population densities than the Sierra Nevada region and may have been less affected by some human activities (e.g., urbanization, agriculture, mining), but the high accessibility of much of the forest land in the southern Cascades and Modoc Plateau led to high levels of logging and grazing use (Dasmann 1965, Riegel et al. 2006, Skinner and Taylor 2006, van Wagtendonk and Fites-Kaufman 2006).

American Indians have lived in present-day California for at least 11,000 years (Anderson 2005, Sugihara and Barbour 2006). During this period, human use of YPMC forests was common, although permanent settlements were often located at lower elevations (Anderson 2006). Forest uses were generally related to providing food and materials for building, and often incorporated fire. American Indians set fires in YPMC forests to promote oak growth for acorn harvesting, encourage sprouting of hardwoods for basketry materials, increase understory vegetation for wildlife forage and hunting purposes, and reduce woody fuels that could otherwise lead to severe fires (Anderson 1993). Impacts to YPMC forests were likely not uniform, but rather targeted at specific areas, including those near water sources, hunting grounds, and settlements (Vale 1998). This variable pattern of management likely led to increased heterogeneity of forest structure across the landscape (Anderson 2006, Vale 2002).

European settlement in California began with settlement by Spanish explorers and missionaries during the late 1700s, but impacts in YPMC forests were minimal until settlement by Euro-Americans from the Eastern United States, beginning with the 1850s gold rush that initiated a period of intense resource use and extraction (Beesley 1996, Stephens and Sugihara 2006). The primary impacts of this wave of settlement were felt in the Sierra Nevada portion of the YPMC forest belt, where mining operations were established, and extensive logging was conducted to support these mining operations (Stephens and Sugihara 2006, van Wagtendonk and Fites-Kaufman 2006). Initial logging operations were conducted with animal teams, while railroad logging opened previously inaccessible areas to extraction after the 1890s (Beesley 1996, Conners 1997, McKelvey and Johnston 1992, TCHS 2016). Yellow pine and mixed-conifer forests were the most intensively logged of all forest types in California, and logging often focused on removing the largest trees from a stand (Leiberg 1902, Stephens and Sugihara 2006). In some more accessible locations, such as the Lake Tahoe basin, entire watersheds were clearcut during this period. In addition to direct impacts to YPMC forests from mining and logging, grazing from domesticated livestock increased dramatically during this period (Sugihara and Barbour 2006), although there is uncertainty about the extent to which grazing reduced grass cover in YPMC forests, which is presently quite low (North et al. 2015).

During the early 20th century, with the professionalization of America's forestry industry and the creation of protected forest reserves for conservation, resource managers began to argue that YPMC forests were understocked because of wildfires and excessive historical use of fire (Show and Kotok 1924, Stephens and Sugihara 2006). This perspective became more widespread after 1910 when large fires burned through the northern Rocky Mountains, and extensive resources for managing federal lands were dedicated to fire suppression, including within the YPMC belt (Sugihara and Barbour 2006). This fire-suppression era coincided with a large increase in logging demand following World War II, when timber yields in Sierra Nevada YPMC forests increased tenfold (Beesley 1996). Much of this demand was met by high-grade logging on national forest lands, as most of the private land in the YPMC belt had already been harvested (Ruth 1996). The combination of timber harvesting and fire suppression led to structural changes throughout YPMC forests, with losses in the large tree component, general increases in stand density, shifts toward even-aged structure, loss of structural heterogeneity, and increases in fir dominance within areas that had previously been primarily yellow pine stands (Benedict 1930, McKelvey et al. 1996, North et al. 2015, Skinner and Taylor 2006, Thorne et al. 2008).

The 1960s marked the beginning of the transition to the ecosystem management era, although fire suppression and timber harvesting remained dominant practices through much of this era (Sugihara and Barbour 2006). With much of the YPMC belt situated on Forest Service land, the multiple-use mandate of that agency began to be cited in legal challenges to the large-scale timber harvesting operations. Other cultural values placed on YPMC forests began to gain traction among the public, including ecosystem services such as water and carbon storage, wildlife habitat, and recreation (Ruth 1996). The Wilderness Act of 1964 and subsequent wilderness designations protected many alpine and subalpine regions from extractive activities, but most designated wilderness in California did not cover YPMC forests, with the exception of some national parks. Most YPMC forests on federal lands therefore fall under the purview of both the National Environmental Policy Act of 1969 and the National Forest Management Act of 1976. Environmental organizations have used these pieces of legislation to prevent timber harvests in YPMC forests on the grounds of their negative impacts to habitat for wildlife species including the California fisher and the California spotted owl (Ruth 1996, Truex and Zielinski 2013). During the 1970s and early 1980s, approximately 69 percent of growth on timbered national forest lands in the Sierra Nevada (primarily from YPMC forests) was harvested; however, recent rates of harvesting have slowed dramatically (Ruth 1996). Associated with this downward trend in timber harvesting has been a decline in the processing capacity for timber and other wood products in the bioregion: California-wide, the number of forest product mills dropped by approximately 85 percent between 1968 and 2000, and the number has declined further since then (Laaksonen-Craig et al. 2003). Today, many communities that were once supported by the timber industry have suffered economic downturns or have turned to other sources of jobs such as tourism and forest recreation.

Despite growing awareness of the importance of frequent fire to YPMC forest health, fire suppression remains the dominant federal policy in these forests.

Despite growing awareness of the importance of frequent fire to YPMC forest health, fire suppression remains the dominant federal policy in these forests (Stephens and Ruth 2005). A number of obstacles prevent the increased use of fire as a tool for ecosystem management in these forests. Foremost among these are the public health consequences of smoke in communities, the rapidly increasing extent of wildland-urban interface within YPMC forests, and opposition to landscape-level fuel-reduction treatments the Forest Service asserts are needed to safely reintroduce low- to moderate-severity fire (North et al. 2012a, North et al. 2015). Human population densities in some areas are greater than 100 times what they were prior to Euro-American settlement, leading to considerable restrictions on fire use (Sugihara and Barbour 2006). The Sierra Nevada foothills region is one of the most rapidly growing areas of California, with much of the development occurring directly below the YPMC forest belt and susceptible to risks associated with fire spread and smoke production (Bryant and Westerling 2014).

Chapter 2: Methods

The natural range of variability (NRV), or "range of natural variation," was defined by Landres et al. (1999) as:

> …the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal.
>
> "Historical range of variation" (HRV) is a related concept, and was defined by Wiens et al. (2012) as:
>
> …the variation of ecological characteristics and processes over scales of time and space that are appropriate for a given management application.

HRV was developed to allow the explicit incorporation of human influences on ecosystems into the analysis, because in most places on Earth humans have been major ecological players for millennia. We evaluate human influences on assessment area ecosystems in our analyses, thus they may have been more properly called HRV assessments than NRV assessments, but Forest Service guidance for implementation of the 2012 Planning Rule adopts the term "natural range of variability," so we have stuck with this term.

The Forest Service Handbook 1909-12 chapter 10 (USDA FS 2013c), which guides the development of the resource assessments that must precede forest plan development, defines NRV as:

> Spatial and temporal variation in ecosystem characteristics under historic disturbance regimes during a reference period. The reference period considered should be sufficiently long to include the full range of variation produced by dominant natural disturbance regimes, often several centuries, for such disturbances as fire and flooding and should also include short-term variation and cycles in climate. "Natural range of variation" (NRV) is a term used synonymously with historic range of variation or range of natural variation. The NRV is a tool for assessing ecological integrity, and does not necessarily constitute a management target or desired condition. The NRV can help identify key structural, functional, compositional, and connectivity characteristics, for which plan components may be important for either maintenance or restoration of such ecological conditions.

NRV/HRV assessments are tools used by managers to bring insights from historical ecology to resource management (Hayward et al. 2012). NRV/HRV characterizes variations in ecosystem function, structure, and composition over scales of time and space. The basic purpose of NRV/HRV is to define the bounds of ecosystem behavior or trends in those bounds. As Morgan et al. (1994) put it:

"The concept of HRV (NRV) provides a window for understanding the set of conditions and processes that sustained ecosystems prior to their recent alterations by humans." Morgan et al. (1994), Manley et al. (1995), Landres et al. (1999), and Wiens et al. (2012) all listed the purposes of conducting HRV/NRV assessments and the issues that must be considered in the assessment. These include the ecosystems of interest, the spatial and temporal scales of analysis, the ecological indicators to be assessed, whether to include human influences, whether to use only historical information or to use contemporary reference conditions and modeling as well, and so on.

According to Manley et al. (1995), HRV/NRV assessments should include the following steps:

1. Determine key ecosystem elements (e.g., functions/processes; structures/patterns; composition),
2. Identify measurable indicators for those ecosystem elements (e.g., fire frequency, tree density, species diversity), and
3. Estimate values for the indicators over the selected HRV reference period.

The appendix contains details, in outline form, of the process by which the Forest Service Pacific Southwest Region Ecology Program carried out these steps for the 11 ecosystem types assessed.

We are greatly indebted to the thorough HRV assessments funded by the Forest Service's Rocky Mountain Region (Region 2) in the early 2000s (e.g., Dillon et al. 2005, Meyer et al. 2005, Veblen and Donnegan 2005). These valuable documents provided a sort of template for our efforts and set a high bar against which to gauge our own efforts.

Historical Reference Period

Morgan et al. (1994) and Wiens et al. (2012) noted that the temporal scale of analysis will always be constrained by our ability to look clearly back through time. Certain data types permit insight into ecological patterns and processes thousands or millions of years in the past, but most reasonably decipherable data sources extend back only decades and, in some cases, a few centuries. In addition, climate and other environmental conditions tend to diverge more from current conditions the farther one goes back into the past. As a result, most NRV/HRV assessments use the past 100 to 400 years as their baseline or "reference" period. In this NRV assessment, our principal reference period was the three to four centuries before significant Euro-American settlement of the assessment area, i.e., the 16th century to the late 19th century. It is important to underline that this reference period is coincident with the Little Ice Age, and current warming trends are making future use of NRV/HRV reference conditions as management targets gradually more tenuous (this, however, does not diminish the value of NRV/HRV assessments, just the ways in which they are used) (Millar et al. 2007; Safford et al. 2012a, 2012c). Therefore, as recommended by Manley et al. (1995) and Jackson (2012), we also collected and interpreted information as far back as the beginning of the Holocene Epoch (12,000 years before present [YBP]) when it was available. We were especially interested in patterns and processes from warmer, drier periods in the past (Xerothermic Period, medieval droughts), because most future climate projections for the assessment area project much warmer and somewhat drier conditions (at least during the growing season) by the end of the current century.

Spatial Scale

NRV/HRV analyses are focused on change over time, but variation in space must also be considered. Our historical and contemporary reference data sources are more often than not derived from specific locations or landscapes in the assessment area, but our analysis is intended to apply to the bioregion as a whole. Wherever possible, we sought data that represented the variety of different geographic regions and environmental situations that are found in the assessment area. Usually, though, we simply had to accept the limitations of those data we could find, and use inference and our understanding of environmental variation across the bioregion to extend those data points to the larger assessment area. We report the geographic locations of our data sources throughout the report.

Information Sources

Since the Sierra Nevada Ecosystem Project report was published in 1996, there has been a veritable explosion of scientific information on the ecology and current and past status of yellow pine mixed-conifer forests in the assessment area. Although we would like more data on every indicator we assessed, our principal problem was trying to assemble and filter all of this information into a coherent whole.

This NRV assessment is based on both historical and contemporary reference sites and information sources. Historical data are especially useful when they precede the onset of major anthropogenic disturbances and alterations that have degraded assessment area ecosystems. These sorts of data are few, however, and, in most cases, we were forced to resort to evaluation of information sources that postdated the settlement of Euro-Americans in the assessment area. We used modern-day data from reference ecosystems whenever possible. By “contemporary reference ecosystems,” we mean current-day ecosystems that have suffered relatively little degradation and may serve as a more natural reference against which degraded ecosystems may be compared. There are many advantages to using contemporary reference sites in NRV/HRV analyses, including the availability of modern data on ecosystem condition, and the fact that climatic and atmospheric conditions in current reference sites and current degraded sites are more or less equivalent. Safford et al. (2012a: 57) noted that:

> We use historical data principally to understand ecological events and processes that we cannot observe firsthand, but directional changes in the baseline state (climate, air, water, soil, etc.) mean that historical conditions may make poor templates for the future. To compensate, contemporary reference ecosystems that are functioning as we desire should form part of the package of information that underlies restoration and resource management.

The problem is that human alteration and degradation of assessment area ecosystems is so pervasive that identification of appropriate reference ecosystems is difficult in all instances, and impossible in some.

In our assessment, we used direct data analysis and interpretation whenever possible, and we resorted to inference where necessary and justifiable. This NRV assessment includes comparisons to current conditions, as well as a summary of the literature regarding possible future trends, whenever that literature existed. Our focus was on peer-reviewed publications, including papers in press or soon to be in press; government publications; Forest Service and other federal and state agency data; and, in some cases, academic theses or dissertations. Because information on the historical state of some ecosystems and ecological processes and patterns is scarce, we also refer to published anecdotal information from the mid-19th to early 20th centuries in some cases. We do not refer to anecdotal information from more recent times.

The Forest Service's Forest Inventory and Analysis (FIA) program is the U.S. national forest inventory. Plots are found across the United States and are located randomly within a grid defined by latitude and longitude. We used a compilation of the most recent FIA data in the assessment area provided by the Pacific Southwest Region Remote Sensing Laboratory to provide current-day data on many forest structure and composition variables. It is important to stress that FIA is a statistically robust sample of all stand conditions across the assessment area, including areas with reduced tree density and cover owing to natural disturbances or harvest.

Determination of Deviation From NRV

Our NRV assessments are based primarily on a "range of means" approach.

Like the Rocky Mountain Region HRV analyses (e.g., Meyer et al. 2005), our NRV assessments are based primarily on a "range of means" approach. Variation in data can be characterized in a number of ways. For example, the entire range of variation in a dataset is captured by reporting the extremes (minimum and maximum), but these extreme values more often than not represent rare cases that do not provide a clear picture of central tendencies. Use of extreme values to bound ecosystem variation makes NRV/HRV assessment more or less impossible, as nearly all values for a variable are theoretically possible at some time and at some place on the landscape. Generation of a standard deviation or standard error (the latter is standard deviation scaled to the sample size) is the usual statistical method for reporting variation, but in NRV/HRV analyses, the availability of data and sample sizes are often inadequate. A middle path is to base the assessment on an estimate of the range of means from multiple sources for a given variable. This produces a narrower, more discernible, and probably more meaningful range of variation that can be quantitatively or qualitatively compared to modern data. See figure 1 in Meyer et al. (2005) for an excellent depiction of how NRV/HRV varies with the type of variation used and the spatial scale of analysis.

Determination of deviation from NRV was accomplished by comparing the modern range of variation for some indicator variable (ideally represented by a mean, median, and standard deviation) with the range of means for the same variable from the NRV period or contemporary reference sites. In practice, direct statistical comparison was rarely possible, owing to small sample sizes in the reference sources, the lack of measures of statistical variation, orders-of-magnitude differences in sample sizes between current and historical data when multiple historical data points did exist, or not uncommonly, the lack of concrete quantitative measures in the historical dataset. Our assessment of current deviations from NRV was necessarily deductive in nature, and we came to conclusions about the status of specific variables based to a great extent on our general knowledge about the ecosystems in question. Table 11 on page 178 summarizes our conclusions about current deviation (or "departure") from the NRV for key ecosystem elements in YPMC forests in the assessment area.

Note that measuring departure from historic or reference conditions and incentivizing and operationalizing realistic action are not the same thing, and this NRV assessment attempts only to measure departure. See Moritz et al. (2013), Thompson et al. (2009), and Wiens et al. (2012) for discussions on how socioeconomic considerations are really at the heart of the matter, and how they might be integrated with NRV/HRV types of information.

Chapter 3: Natural Range of Variability Descriptions

Function (Including Disturbance)

Extreme Climatic Events

Drought—

***NRV*—**California's Mediterranean climate is characterized by an annual drought of 3 to 6 months at most weather stations in the assessment area (Major 1988). This is a longer drought than most stations in the northern Rocky Mountains experience in a 50-year period. Aside from the predictable annual warm season drought, California is also characterized by extremely wide variation in annual precipitation and a high dependence of annual precipitation on a small number of very wet winter storms (note that this variability in precipitation decreases with latitude) (Dettinger et al. 2011). Most California plant taxa are therefore adapted to significant periods of time without access to atmospheric water. Nonetheless, periods of multiple, consecutive dry years can have major impacts on yellow pine and mixed-conifer (YPMC) forests (e.g., Guarín and Taylor 2005), as evidenced by the massive die-off of conifer trees in the San Bernardino Mountains after the drought of the late 1990s and early 2000s, and the even more massive tree mortality event that was beginning in the southern Sierra Nevada as we completed this assessment. Drought itself is usually not the proximal cause of tree mortality, however, as drought-induced stress also leads to greater susceptibility to insects and disease, and dry years tend to support more fire as well (Allen et al. 2010, Fettig et al. 2007, Logan et al. 2003, Savage 1994). Forest density can also intensify the effects of drought on tree mortality, through stress brought about by increased competition for water (Dolph et al. 1995, Innes 1992 , Young et al. 2017).

Most California plant taxa are therefore adapted to significant periods of time without access to atmospheric water. Nonetheless, periods of multiple, consecutive dry years can have major impacts on yellow pine and mixed-conifer forests.

The Holocene Epoch, which began about 12,000 years ago, has been characterized by a fairly stable climate, but that is only in geological terms. Over the past 7,000 to 8,000 years, dry climatic periods have occurred on average every 80 to 260 years, with durations of droughts lasting 20 to 100 years on many occasions. Between 8,000 and 6,300 years before present (YBP), drought conditions dominated in the northern and eastern assessment area (during the Xerothermic Period), and many large lakes in and near the assessment area either dried completely (e.g., Owens Lake) or dropped significantly in depth (e.g., Lake Tahoe). Aridity is thought to have been less pronounced in the southwestern assessment area (Yosemite National Park and points south) and to have eased earlier, perhaps as early as ±7,500 to 7,000 YBP. Over the ensuing 2,000 to 3,000 years, aridity lessened and distinct wet and dry climatic phases occurred. During the past 2,500 years, decades-long droughts have occurred on multiple occasions, with especially severe events occurring around 800 and 650 YBP (Benson et al. 2002, Mensing et al. 2004, Minnich 2007, Stine 1994).

Biogeographically, forest vegetation in the assessment area responds to warmer and drier climatic periods by retreating to moister, cooler locations. For example, the alpine tree line rises during warmer periods and retreats with cooling; under extended drought, trees become more restricted to areas with permanent water. Lake Tahoe dropped below its sill during a number of Holocene droughts, and tree stumps can now be found under the surface of the lake. The Walker River between Bridgeport and Topaz Valleys was dry during these droughts, and trees grew directly in the current river channel (Stine 1994). Species composition also changes in response to drought. During dry periods in the Holocene, pollen data show that oaks, pines, junipers (*Juniperus*), and dryland shrubs (e.g., *Artemisia, Atriplex*) dominated much of the assessment area; less drought-tolerant species like the firs and incense cedar were reduced, but then increased when conditions became cooler or wetter (Minnich 2007).

One of the main drivers of vegetation structure and composition is fire, and long-term shifts to drier conditions can greatly enhance fire activity (frequency). Note, however, that climatic drying can also act to decrease the size of fires, as such conditions may lead to less accumulation of live fuel (Swetnam 1993). Beaty and Taylor (2009) studied Holocene fire in the Lake Tahoe basin and showed that maximum fire activity occurred at around 6,500 YBP, at the height of the Xerothermic Period. Fire became gradually less prevalent thereafter, with notable peaks occurring in later drought periods at about 3,000 and 1,000 to 800 YBP (Beaty and Taylor 2009). Other authors have shown similar drought-fire interactions in and around the assessment area (e.g., Enfield et al. 2001, Swetnam and Baisan 2003, Trouet et al. 2010, Whitlock et al. 2003). Because the yellow pine species and black oak are more fire and drought tolerant (table 2), drying climates and increasing fire frequency would be expected to benefit them over less tolerant tree species like the firs.

Comparison to current—By many accounts, the late 19th and 20th centuries were anomalously wet and have experienced few drought events compared to earlier periods of the Holocene (Haston and Michaelsen 1997, Hughes and Brown 1992). Numerous authors have argued that the climate of the recent past is likely not a reliable roadmap for the future of the Western United States (Millar et al. 2007, Saxon et al. 2005, Williams and Jackson 2007). Nonetheless, Allen et al. (2010) noted that scientific documentation of climate-related forest mortality has been rising over the past few decades, and some recent drought episodes have been among the most severe of the past few centuries (e.g., the recent 4-year drought in California may have been the worst in 1,200 years or more) (Griffin and Anchukaitis 2014). The increasing abundance of drought-intolerant species, and the very high stem densities and structural homogeneity that characterize much of the contemporary YPMC forest in the assessment area, have primed these forests for more severe impacts of drought and related disturbance factors than would have likely been the case under reference conditions. A major concern is that larger and older trees are often more prone to drought-induced mortality (Allen et al. 2010). In many places, this may be exacerbated by higher densities of younger trees in the surrounding forest (Dolph et al. 1995, Ritchie et al. 2008). Higher levels of drought stress have recently been linked to higher probabilities of mortality resulting from fire (van Mantgem et al. 2013).

***Future*—**Forest-landscape change driven by drought tends not to be gradual, but rather episodic and rapid, because trees grow relatively slowly but die quickly (Franklin et al. 1987). Increased drought and heat have been amply documented to increase tree mortality around the globe, principally owing to secondary factors like insects, disease, and fire (Adams et al. 2009, Allen et al. 2010, van Mantgem et al. 2013). McDowell et al. (2008) outlined three interacting mechanisms by which drought can lead to broad-scale forest mortality:

1. Extreme drought and heat kill trees through cavitation of the xylem water column.
2. Long-term water stress results in carbon deficits and metabolic limitations that result in carbon starvation and reduced capacity to defend against attack by biotic agents like insects and disease.
3. Extended warm spells during droughts can facilitate rapid population growth in these biotic agents, which then overwhelm the already stressed tree hosts.

Under warmer future climates, both drought-avoiding and drought-tolerating tree species may thus be negatively affected; the former by carbon starvation, the latter by hydraulic failure (McDowell et al. 2008).

Bachelet et al. (2001) modeled future vegetation cover and biomass under a number of different global circulation models (GCMs). One of their modeled response variables was a drought area index related to the Palmer Drought Severity Index. The authors found that the area of the United States subjected to drought stress rose approximately linearly with increasing temperatures. The assessment area was not identified as especially sensitive to increasing drought under their scenarios, but most of their scenarios assumed increasing precipitation in California during the 21st century, which runs counter to most of the more recent GCMs (Dettinger 2005).

Liu et al. (2010) modeled the Keetch-Byram Drought Index for the 2070 to 2100 period under different GCMs. They projected increasing drought potential across most of the contiguous United States, including eastern and southern California and the assessment area. In the Western United States, most of the summer drying trend was predicted to depend on warming temperatures more than reductions in precipitation. They concluded that much of their study area will experience greatly increased fire potential during the course of the coming century.

Extreme precipitation events—

NRV and comparison to current**—**On a year-to-year basis, California experiences the most variable precipitation regime in the United States. In addition, no other state depends as much on a few large storms to generate precipitation: in the Mediterranean-climate part of California, a third to half of annual precipitation falls in only 5 to 10 wet days per year. So-called atmospheric rivers (ARs) generate 20 to 50 percent of the state's precipitation totals (Dettinger et al. 2011). Such ARs are narrow bands (less than 200 km wide typically) of concentrated water vapor that develop over the oceans and direct large amounts of moisture toward continental areas. Owing to the influence of periodic ARs developing over the tropical Pacific, California experiences more extreme precipitation events than any other part of the United States, including the hurricane-affected Gulf Coast (Dettinger et al. 2011).

The dependence of annual precipitation totals on extreme precipitation events leads to highly variable streamflows, as well as the propensity for landslides and other earth movement on unstable geologic substrates (Kerr 2006). Because they are more maritime, more tectonically active, and constituted of less consolidated bedrock, the California Coast Ranges are more heavily affected by flooding and earth movement associated with ARs, but the Sierra Nevada also experiences massive precipitation events that cause widespread flooding and landsliding. An example is the New Year's storm of January 1997, which forced evacuations of 120,000 people, flooded Yosemite Valley, and closed Highways 140, 50, and 395 for months. Dettinger (2011) noted that ARs accounted for all major historical floods in some California river systems.

There is little direct evidence to compare the occurrence of ARs and other extreme precipitation events in the assessment area between current and past time periods. Paleoecological studies have documented the enhanced occurrence of extended droughts at different times of the Holocene Epoch (see "Drought" above), and because a large proportion of California precipitation stems from AR events, we can hazard the inference that major changes in precipitation must involve changes in the frequency of ARs.

Future**—**Dettinger (2011) modeled the occurrence and intensity of ARs under a variety of future climate change scenarios. He found that, under the most realistic emissions scenarios, average AR statistics did not change much, but the extremes changed markedly. For example, the frequency of larger than average ARs increased, the number of years with many AR episodes rose, and the temperatures of AR storms rose, which could feed into greater occurrence and magnitude of winter flooding and associated earth movement (Dettinger 2011).

Fire

Background: fire regime—

Ecological disturbances can be classified according to their characteristics, including frequency, size, season, intensity, severity, pattern, and so on. A "fire regime" describes the manner in which fires tend to occur in a given ecosystem, in a generalized sense and averaged over many fires over a long period of time. Fire regimes necessarily simplify a very complex phenomenon, but they offer a convenient and useful way to better understand and manage wildland fire (Sugihara et al. 2006). Under presettlement conditions, yellow pine and mixed-conifer forests in the Sierra Nevada supported fire regimes characterized by frequent, low- to moderate-severity fires (Agee 1993; Arno 2000; Barbour et al. 1993, 2007; Skinner and Taylor 2006; van Wagtendonk and Fites-Kaufman 2006). These characteristics placed presettlement YPMC forests in Fire Regime I (fire-return intervals [FRI] 0 to 35 years, low to moderate severity), using the Schmidt et al. (2002) classification, which, although it uses only two fire regime attributes, has become somewhat of a national standard. The YPMC forests in the assessment area supported fire regimes limited principally by the amount of available fuels (rather than by fuel moisture), because a 3- to 6-month drought is typical in California's Mediterranean climate, and temperatures at low and moderate elevations are very warm in the summer (Steel et al. 2015). As elevation increases, the role of fuel moisture becomes gradually more important, until it becomes a more important driver of fire regime than fuel load (Agee 1993, Miller and Urban 1999b). Various authors have identified the boundary between high-elevation mixed-conifer and red fir forests (2000 to 2300 m or more, depending on latitude), which is the elevation of the average freezing limit in winter storms and the zone of maximum snowfall, as a zone of major transition in fire regimes (Mallek et al. 2013, Miller and Urban 1999b, Safford and Van de Water 2014, Sugihara et al. 2006). Temporal and spatial variability in regional climate also plays a major role in driving fire regimes, and ocean-atmosphere phenomena like ENSO (El Niño-Southern Oscillation), the PDO (Pacific Decadal Oscillation), and the PNA (Pacific-North America Pattern) are important determinants of burning patterns across the Western United States (Taylor and Scholl 2012; Trouet et al. 2006, 2010).

Under presettlement conditions, yellow pine and mixed-conifer forests in the Sierra Nevada supported fire regimes characterized by frequent, low- to moderate-severity fires.

Today, because of human influences since Euro-American settlement, including timber harvest, grazing, and fire suppression, many YPMC forests in the assessment area now support conditions that are more characteristic of Fire Regimes III (FRIs of 35 to 200 years, moderate severity) and IV (FRIs of 35 to 200 years, high severity) (Schmidt et al. 2002). These are often referred to as "climate-limited" fire regimes, as fuel moisture, rather than fuel load, tends to drive fire occurrence and behavior (Agee 1993, Schoennagel et al. 2004, Steel et al. 2015). Evidence for this shift can be seen in the growing importance of climate in driving fire characteristics in the assessment area over the past century (Heyerdahl et al. 2008, Miller and Urban 1999a, Miller et al. 2009b, Running 2006).

In this section, we summarize information available on the different components of the fire regime for YPMC forests before Euro-American settlement and compare this to current conditions. At the end of the section, we summarize the results of studies that have generated qualitative or quantitative projections for future fire conditions in YPMC forests in the assessment area.

Background: the role of ignitions by humans prior to the 20th century—The presettlement fire record is mostly derived from fire-caused injury lesions in tree stems or charcoal in layers of sediment or peat, and we are mostly unable to discern lightning-ignited fires from anthropogenic fires. Although lightning occurrence varies temporally (van Wagtendonk and Cayan 2008), lightning strike densities (LSDs) may provide a rough idea as to how the ratio of lightning to anthropogenic ignitions might have varied across the landscape (with the important caveat that LSDs will only correlate reasonably well with lightning ignition densities if fuels are in sufficient quantity and sufficiently dry). California is one of the least lightning-prone states in the United States, with most of the Mediterranean part of the state averaging 0 to 0.25 strikes/km^2/yr (compare to the Gulf Coast, with more than 6 strikes/km^2/yr, or the southeastern and Midwestern United States, with more than 3 strikes/km^2/yr) (Orville 2008). The highest LSDs in California are in the deserts of southeastern California and the eastern and higher western slopes of the Sierra Nevada, where average annual LSDs range from 0.3 to 0.55 strikes/km^2/yr.

Given very low lightning-strike densities in westernmost California, pre-Euro-American settlement fire frequencies in the California Coast Ranges clearly resulted primarily from human use of fire. The relative magnitude of human inputs to the fire regime in the Sierra Nevada before Euro-American settlement is much less certain, although anthropogenic fire was certainly a significant factor within some radius of many American Indian cultural sites (Anderson 2005, Kilgore and Taylor 1979, Sugihara et al. 2006, Vale 2002). Rightly or wrongly, some observers in the late 19th century were convinced that much of the very frequent fire that characterized presettlement YPMC forests had been set by American Indians (e.g., Greeley 1907, Manson 1906). Pyne (1982) opined that American Indian management of vegetation through fire was widespread in the Western United States for thousands of years before Euro-American arrival. Kilgore and Taylor (1979 (see also Taylor et al. 2016)) noted a sharp decline in fire frequency after the 1870s in their southern Sierra Nevada study area, and correlated this with the replacement of American Indian populations by Euro-American settlers.

Fire frequencies did not follow the same late 19th century pattern everywhere, and some researchers have come to different conclusions. For example, Burcham (1960) suggested that fires set by Euro-Americans between 1850 and 1900 created an artificially high frequency of fire that observers mistook as representative of American Indian influences (but Burcham came from a school that discounted natural fire ignitions and did not base his opinion on actual data).[2] Wagener (1961) summarized fire scar sites in the central and northern Sierra Nevada and determined that fire frequencies did not change until after 1900, when the national forests were established. Because the arrival of Euro-Americans after 1850 did not change fire frequencies in the records he studied, Wagener (1961) concluded that most presettlement fires were probably caused by lightning, not humans. Swetnam and Baisan (2003) noted that recent data on lightning-strike densities had documented much higher lightning incidence than assumed by earlier researchers. Based on their research in the Southwestern United States and the Sierra Nevada, they concluded that, "fire regimes in large portions of these regions would probably have had similar characteristics… if people had never entered the Americas." Parker (2002) maintained that vegetation patterns in assessment area forests when Euro-Americans arrived were largely explainable based on topography, lightning ignitions, and climate. Probably the truth lies somewhere between the extreme views. Lewis (1973) noted that, "Despite a precontact population that is estimated to be among the highest in North America, (Indians) probably lacked sufficient numbers to burn all or even most of the vegetation on any regular and consistent basis, even had they so wanted."

In the last decades of the 1800s, there was a general decrease in overall fire frequency, but an increase in large destructive fires in many parts of the Sierra Nevada, ignited by shepherds, miners, loggers, and other forest users (Barbour et al. 1993, Cermak 2005, Erman and SNEP Team 1996, Jackson et al. 1982, Kilgore and Taylor 1979, Leiberg 1902, Miller and Safford 2017, Sudworth 1900, Vankat and Major 1978). Shepherds were especially singled out for blame in the literature (although some authors contend that burning by shepherds was simply an extension of American Indian practices in their absence) (Vankat 1977). Forest managers decried the loss of forest cover and timber that was accompanying Euro-American settlement and the role that indiscriminate fire was playing (Greeley 1907, Jackson et al. 1982, Show and Kotok 1924). Cermak (2005) noted the plethora of photos from the period between 1880 and 1910 showing huge brush fields in and around

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[2] Skinner, C.N. 2012. Personal communication. Research fire geographer, USDA Forest Service, Pacific Southwest Research Station, Redding Silviculture Laboratory, 3644 Avtech Parkway, Redding, CA 96002.

settled or logged watersheds in the Sierra Nevada, areas that are now forest. By the end of the 19th century, much of the Sierra Nevada was being policed for fire, and by the second or third decade of the 20th century (and in some places earlier), fire frequencies began to noticeably drop as federal and state fire suppression policies and tactics were successfully implemented.

Components of the fire regime: fire frequency—

***NRV*—**Fire frequencies are usually measured as FRIs, which measure the number of years between fire events. The most commonly referenced measures of FRIs in conifer-dominant vegetation are derived from small-scale (<4 ha) "composite" dendrochronological fire histories (which measure fire scars in the annual growth rings of trees), which include records from multiple trees in a defined area. Composite FRIs tend to represent the fire history of a given area better than point FRIs (derived from a single tree) because some fire events fail to scar every recording tree within the fire perimeter, and most trees are not recording trees, especially in regimes characterized by frequent low-intensity fire (Collins and Stephens 2007, Falk et al. 2011, Stephens et al. 2010). Composite FRIs are also more sensitive and better suited to analyzing changes in fire occurrence than point FRIs (Dieterich 1980, Swetnam and Baisan 2003). Although there is some variability introduced by using composite FRIs from different size areas, they are less likely to underestimate presettlement FRI values than point (single tree) FRIs (Farris et al. 2010, van Horne and Fulé 2006).

Van de Water and Safford (2011) conducted an exhaustive review of the published and unpublished literature pertaining to mean, median, minimum, and maximum FRIs observed prior to significant Euro-American settlement (i.e., the middle of the 19th century). Sources included fire histories derived from dendrochronological and charcoal deposition records, modeling studies, and expert quantitative estimates; a total of 298 sources were accessed. Van de Water and Safford's (2011) results for yellow pine and mixed-conifer forests are given in table 3. These values represent the NRV reference period, i.e., the 16th century to about 1850. Averaged across the state, they found that mean FRIs ranged from 11 to 16 years in YPMC forests, and median FRIs ranged from 7 to 12 years. Mean minimum FRIs were around 5 years for both forest types, and mean maximum FRIs ranged from 40 to 80 years (table 3) (Van de Water and Safford 2011).

As table 3 makes clear, presettlement fire frequencies were highest in the drier, lower elevation forest types (YPMC) and lower in moister and higher elevation stands (Caprio and Swetnam 1995, Fites-Kaufman et al. 2007, Gill and Taylor

Table 3—Reference fire-return intervals in years) from the centuries preceding Euro-American settlement for yellow pine and mixed-conifer forests in California, derived from literature review[a]

Forest type	Mean	Median	Mean minimum	Mean maximum	Number of sources
			Years		
Yellow pine	11	7	5	40	24
Dry mixed conifer	11	9	5	50	37
Moist mixed conifer	16	12	5	80	53

[a] Mean minimum and mean maximum are rounded to the nearest multiple of 5

Source: Van de Water and Safford 2011.

2009, Sugihara et al. 2006, Taylor 2000). Fire frequencies are also driven directly and indirectly by local topographic variables, and various researchers have documented differences in FRIs between cool (mostly north-facing) and warm (mostly south-facing) slopes, and lower and higher slope positions and elevations. Overall, fire frequencies tended to be higher on warm slopes and upper slope positions, and lower on cool slopes and lower slope positions (Beaty and Taylor 2001, Fites-Kaufman 1997, Kilgore and Taylor 1979, Taylor 2000), but some site-to-site variability occurred, and obvious topographic patterns in fire frequencies were not always apparent (Beaty and Taylor 2007, Scholl and Taylor 2010).

Through the Holocene, fire activity has changed significantly with major changes in climate (Millar and Woolfenden 1999). Working at Lake Tahoe, Beaty and Taylor (2009) found that fire frequencies were low in the Early Holocene, but then reached their highpoint at the height of the Middle Holocene (Xerothermic Period). Frequencies dropped gradually through the Late Holocene, with upward trends during the Medieval Warm Period. Beaty and Taylor (2009) noted that current fire frequencies (under fire suppression) are at their lowest in probably the last 14,000 years. Other researchers have found similar broad patterns (see citations in Beaty and Taylor 2009).

***Comparison to current*—**Safford and Van de Water (2014) compared pre-Euro-American settlement FRIs to FRIs from the last century of fire records in California, using a set of fire return interval departure (FRID) metrics. Figure 5 shows one of these metrics, mean PFRID, generalized to the ecological subregions of California mapped by Miles and Goudey (1997), using only the Forest Service and National Park Service lands within each subregion. "Mean PFRID" represents the current percentage departure from the mean presettlement fire return interval (see Safford and Van de Water [2013] for details). Clearly most of the assessment area is highly positively departed, which means that FRIs are much longer than under

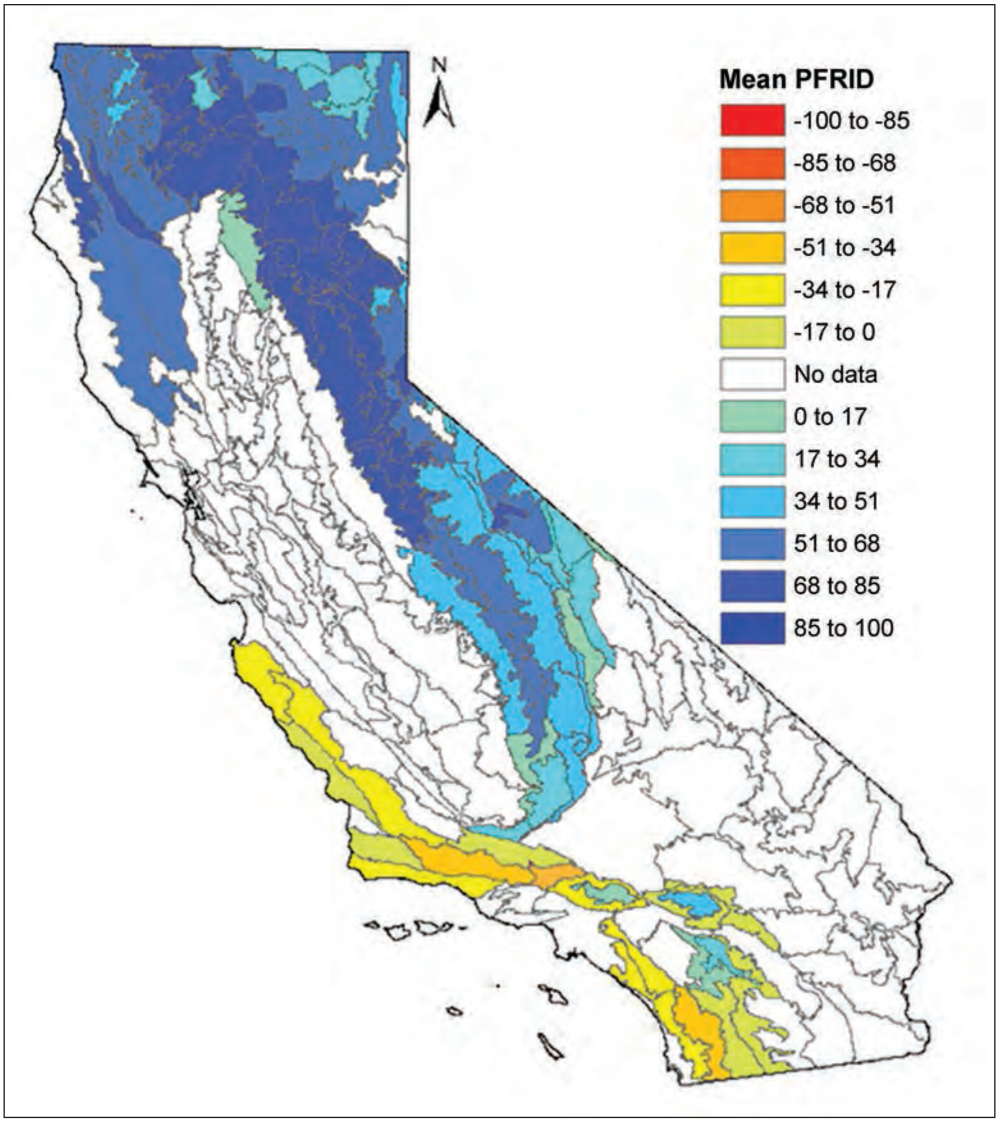

Figure 5—Mean percentage of fire return interval departure (PFRID), generalized to the ecological subregion (Miles and Goudey 1997) from U.S. Forest Service and National Park Service lands found within each subregion. Warm colors are experiencing more fire than under pre-Euro-American conditions; cool colors are experiencing less fire. Illustration from Safford and Van de Water (2014).

presettlement conditions. Areas in figure 5 that are greater than +33 percent departed have current FRIs that are at least 1.5 times longer than under presettlement conditions; areas greater than +67 percent departed have current FRIs that are at least 3 times longer than in presettlement times. To put this into perspective, yellow pine and dry mixed-conifer forests supported mean presettlement FRIs of about 11 years according to Van de Water and Safford (2011), which means that an average of 9.1 fires would occur over any given period of 100 years. Areas in figure

5 that are greater than 67 percent departed from this presettlement FRI have experienced three fires or fewer over the past century. The map shows that the southern and eastern regions of the assessment area are less departed than the central and northern regions. Most YPMC forest types in the latter two regions are more than 85 percent departed; i.e., most of the landscape has seen zero to one fire over the past century. Safford and Van de Water (2014) also calculated mean PFRID by vegetation type (see their table 4). They found that yellow pine and dry mixed-conifer were the most departed of 28 vegetation types analyzed (averaging 84 percent and 85 percent departure across California); moist mixed-conifer was tied with aspen for third (average of 80 percent departure). Steel et al. (2015) showed that about three-fourths of YPMC forest in California had not experienced a fire since 1908, after experiencing an average of 5 to 10 fires per century for many centuries before 1908.

Table 4—Reference fire rotations (in years) from the centuries preceding Euro-American settlement for yellow pine and mixed-conifer forests in California[a].

Forest type	Mean	Low	High	Number of sources
		Years		
Yellow pine	22	11	34	9
Dry mixed conifer	23	11	34	8
Moist mixed conifer	31	15	70	12

[a] Reference area is the assessment area
Source: Mallek et al. 2013.

Components of the fire regime: fire rotation—

NRV—Fire rotation is the time in years required for fire to burn an area that is equivalent to the study area's total extent (Agee 1993, Heinselman 1973). Fire rotation can be thought of as a landscape-level FRI, and avoids the difficulties of extrapolating point or composite FRI data to landscapes (indeed, it is roughly equivalent to the grand mean of all point FRIs) (Mallek et al. 2013). Mallek et al. (2013) summarized information from the published literature on presettlement fire rotations for seven major forest types in the bioregional assessment area. Results for YPMC are given in table 4. Mean fire rotations in YPMC forests in the assessment area ranged from 22 to 31 years. As with the FRIs, presettlement fire rotations were longer in the higher and moister mixed-conifer forests.

Comparison to current—Miller et al. (2012b) calculated fire rotations for the period 1984-2009 for YPMC forests in the assessment area, and compared rotations between Yosemite National Park, where fire during the study period was mostly managed rather than suppressed, and Forest Service lands in the assessment area, where most fires are suppressed. From their table 3, the area-weighted average fire rotation for Forest Service-managed mixed-conifer forest over the study period was about 258 years (range 95 to 355), for Forest Service-managed yellow pine forest, it was about 280 years (range 115 to 516); the longest rotations were in the southern Cascades and Modoc Plateau, the shortest in the eastern Sierra Nevada. This compared to about 55-years fire rotation for both forest types in Yosemite National Park. In summary, YPMC fire rotations were about 10 times longer than presettlement on Forest Service lands in the assessment area, but only about 2 times longer in Yosemite (Miller et al. 2012b).

Components of the fire regime: fire severity—

Fire severity is a measure of the magnitude of the effect that fire has on an ecosystem (Sugihara et al. 2006). The severity of fire can be assessed from the standpoint of any ecosystem characteristic; here we focus on the severity of fire on the vegetation. Fire "severity" is not synonymous with fire "intensity," although it is usually correlated. Fire intensity is a measure of the rate of energy released by fire, whereas severity results from the interactions among intensity, fire residence time, fuel and air moistures, the plant species involved, other sources of plant stress, and other factors that cause change in ecosystem condition (Keeley 2009, Sugihara et al. 2006).

In yellow pine mixed-conifer and related forest types, fires in the presettlement period were dominated by areas of low- and moderate-severity effects in which low flame lengths consumed shrubs, herbs, and tree regeneration but only infrequently killed large groups of adult trees.

***NRV*—**In YPMC and related forest types, fires in the presettlement period were dominated by areas of low- and moderate-severity effects in which low flame lengths consumed shrubs, herbs, and tree regeneration but only infrequently killed large groups of adult trees (Cooper 1906; Fitch 1900; Greeley 1907; Hodge 1906; Larsen and Woodbury 1916; Leiberg 1902; Muir 1894; Show and Kotok 1924, 1925, 1929; Sudworth 1900). Large, severe fires could occur, but before Euro-American settlement they were comparatively rare. Show and Kotok (1925: 2–3) concisely summarized the observations of many authors:

> Fires run through these pine forests, but comparatively lightly. Only occasionally and in the younger stands do they flare up into the tops of trees and become crown fires. For the most part the fires are confined to the underbrush and forest litter, burning fallen dead trees, and killing by heat rather by actual flame the crowns of live, full grown trees.

In another report, the same authors (Show and Kotok 1924) wrote:

> The virgin forest is uneven-aged, or at best even-aged by small groups, and is patchy and broken; hence it is fairly immune from extensive, devastating crown fires. Extensive crown fires, though common in the forests of the western white pine region, are almost unknown in the California pine region.

Even today, with a greatly increased component of high-severity fire in YPMC forests, the proportion of fire area experiencing low- and moderate-severity effects is still generally larger than the proportion experiencing high-severity fire (Miller and Safford 2008, 2012; Miller et al. 2009b), however, the proportional balance between the three fire severity classes has changed considerably (fig. 6).

Aside from historical accounts, estimates of past fire severity patterns in

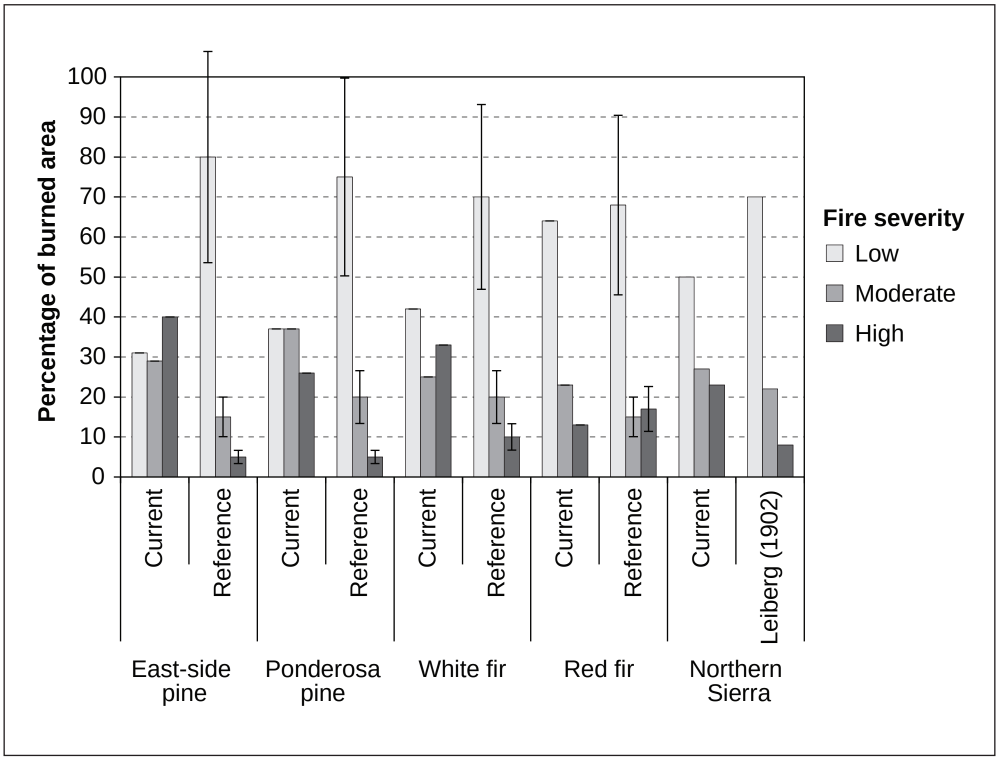

Figure 6—Comparison of average fire severity proportions measured in fires from 1984 to 2004 in the assessment area versus reference (presettlement) estimates for four major forest types and a composite for the northern half of the assessment area. Reference/presettlement estimates from LANDFIRE BpS modeling (Rollins 2009, Rollins and Frame 2006), except for northern Sierra, which are empirical estimates from Leiberg (1902) (see text). Forest types organized from driest and lowest on the left to highest and wettest on the right. East-side pine and ponderosa pine are both types of yellow pine forest; white fir belongs primarily within moist mixed conifer. Red fir pictured to show how higher elevation forests are not strongly departed from presettlement severity patterns. Illustration adapted from Miller and Safford (2008); see this source for severity class definitions.

conifer forests are usually developed from studies of forest stand structure. "High-severity" fires kill most trees on the landscape and leave their footprint through the mostly single-aged stands of regeneration that replace the original forest. Classic examples of vegetation types characterized by high-severity fires include lodgepole pine (*Pinus contorta* Douglas ex Loudon) in the northern Rocky Mountains, chaparral in southern California, and closed cone conifers like knobcone pine (*Pinus attenuata* Lemmon), whose reproduction is closely linked to the passage of stand-replacing fires.

The problem with estimating presettlement fire severity patterns in YPMC forests in the assessment area is that stand structures are and were extremely diverse, with stands typically composed of a mixture of young and old trees, often from a number of different species. Even where groups of even-aged trees are found, other factors than fire could be the cause (windfall, insect outbreak, disease, auspicious climatic conditions, etc.). Very few studies have found evidence of abundant large canopy gaps (>100 ha) in presettlement YPMC forests that after fire were repopulated by single-aged stands of trees (such large gaps, although still comparatively rare, are more commonly found in northern assessment area YPMC forests that supported higher densities of fir species). The prevalence of large canopy gaps caused by high-severity fire is partly related to precipitation and forest productivity, as—assuming everything else equal—wetter forest types grow fuels more rapidly and support denser forest stands, and moister fuels require more heat input to combust, which results in longer fire-free intervals but higher severity fires when fire does occur. These moister forests also tend to support higher densities of shade-tolerant, relatively fire-intolerant tree species like fir, whose canopy structure is much more conducive to rapid movement of surface flames into the forest canopy. Higher elevation forests in the Sierra Nevada generally receive more precipitation and support more fir and other relatively fire-intolerant species. A similar gradient occurs from south to north, with precipitation and the importance of fire-intolerant species increasing with latitude (along the west side of the assessment area; the eastern regions are drier in general and more dominated by drought-tolerant species of pine, etc.) The elevation- and precipitation-driven increase in the proportion of high-severity fire moving from lower and drier vegetation types to higher and wetter vegetation types can be seen in the reference conditions in figure 6, moving from left to right.

The prevalence of large canopy gaps caused by high-severity fire is partly related to precipitation and forest productivity, as—assuming everything else equal—wetter forest types grow fuels more rapidly and support denser forest stands, and moister fuels require more heat input to combust, which results in longer fire-free intervals but higher severity fires when fire does occur.

The relatively fine-grained heterogeneity that characterized forest structure in YPMC forests (see "Structure" on page 87) was the product of a largely low- and moderate-severity fire regime (Fire Regime I), with occasional occurrences of high-severity fire in larger patches under the right weather and fuels conditions

It is important to remember that "low-severity" fire does not imply the absence of tree mortality.

(Agee 1993, Arno 2000, Stephenson et al. 1991, Sugihara et al. 2006, Weatherspoon et al. 1992). It is important to remember that "low-severity" fire does not imply the absence of tree mortality. Most classification systems define low severity as occurring below 25 to 30 percent canopy mortality. Taking the midpoint of that class, an average of around 12.5 to 15 percent of canopy trees in low-severity areas would be expected to be killed by fire. "High-severity" fire is usually defined as encompassing those areas where fire-caused mortality exceeds 75 to 80 percent, although recent satellite-imagery derived severity assessments (relative differenced Normalized Burn Ratio [RdNBR] assessments) usually map high-severity areas in polygons where mortality is more than 90 or 95 percent (Miller et al. 2009a, 2009b, 2012b). Thus, these RdNBR-based studies are mapping "stand-replacing" fire, where tree mortality is almost complete. In this assessment, we use >95 percent mortality as our definition of high-severity fire. "Mixed-severity" or "moderate-severity" fire is simply the area between low and high (we use the term "moderate" in this assessment). Moderate-severity areas are really areas where the intermix of low- and high-severity effects is at a fine enough grain to not be discernible with the analysis tools at hand. For most classifications, the midpoint of the moderate-severity class falls between 50 and 60 percent mortality, so canopy tree loss in such areas may actually be substantial.

There are many ways to quantitatively estimate fire severity in presettlement YPMC forests. One is through direct evaluations of fire severity patterns in contemporary reference forests, in which fire suppression does not occur or has been relaxed, and where extensive logging did not occur. Such forests occur in Yosemite National Park and in the Sierra de San Pedro Mártir of northern Baja California, Mexico. Yosemite was mostly unlogged, but fire management in the park practiced strict fire suppression until 1972 (van Wagtendonk et al. 2002). Since then, extensive areas of the park have been managed under a policy allowing most naturally ignited fires to burn. As such, Yosemite is not a surrogate for presettlement conditions, but it is the closest large landscape we have today in the assessment area. Collins et al. (2009) used RdNBR data to study fire severity in Yosemite's Illilouette Valley, which was relaxed from strict fire suppression in the early 1970s. The watershed is dominated by moist mixed conifer, red fir, and lodgepole pine, so it is most useful as a reference for high-elevation mixed-conifer stands. Collins et al. (2009) did not differentiate their fire severity results by forest type, but overall they found that over a 31-year period, a total of 13 percent of the fire areas they assessed had burned at high (stand-replacing) severity. Van Wagtendonk et al. (2012) studied the same area and found that the proportion of first-entry fire area that burned at high severity was 1 percent in red fir, 3 percent in white fir, 8 percent in Jeffrey pine/western white pine, 12 percent in Jeffrey pine/shrub, 4 percent in lodgepole, and 19 percent in montane chaparral. Among subsequent fires that burned through the same vegetation types, the proportion of high severity was 13 percent in red fir, 16 percent in white fir, 13 percent in Jeffrey pine/western white pine, 14 percent in Jeffrey pine/shrub, 23 percent in lodgepole, and 59 percent in montane chaparral.

Miller et al. (2012b) analyzed RdNBR fire severity data from the entirety of Yosemite National Park, for the period 1984–2009. During their study period, about 72 percent of the fires they analyzed were managed for resource benefit (although five were later suppressed after they exceeded their prescriptions), while the remaining 28 percent were suppressed. They found that YPMC forests in the park burned at about 14 percent high severity (13.7 percent mixed conifer, 14.6 percent yellow pine).

Another contemporary source of reference fire regime information for YPMC forests in the assessment area is the Sierra de San Pedro Mártir National Park in northern Baja California, Mexico. This area is in the southernmost part of the North American Mediterranean climate zone and supports yellow pine (in this case Jeffrey pine) and dry mixed-conifer forests that are very similar to those of drier portions of the Sierra Nevada, for example, on the eastern slope (Dunbar-Irwin and Safford 2016, Stephens and Fulé 2005). Unlike the Sierra Nevada, most of the Sierra de San Pedro Mártir was not logged, and fire suppression has only been in effect for the past few decades, so the forests are much closer to pre-Euro-American settlement conditions. Minnich et al. (2000) reported results from aerial photointerpretation of two fires that burned in the Sierra San Pedro Mártir in 1989. Using photos from 1991, they estimated that 16 percent of the analyzed fire area had experienced >90 percent mortality, thus perhaps 8 percent or so experienced stand-replacing fire effects (>95 percent mortality). Aerial photo analysis is known to underestimate the area of low-severity fire, as fire extent is primarily mapped based on fire effects to canopy trees, so surface fires are difficult to pick out, especially when a number of years have passed since the fire event. Minnich's analysis also took place 2 years after fire, whereas most RdNBR assessments occur 1 year after fire. Consequently, we view Minnich et al.'s (2000) numbers as an upper estimate of fire severity. Stephens et al. (2008) used field plots to measure severity in a fire area in the Sierra San Pedro Mártir. Only 1 of their 27 plots (4 percent of their sample area) experienced high-severity effects (>95 percent mortality). Rivera-Huerta et al. (2016) carried out an RdNBR-based assessment of 25 years of fire severity patterns in the Sierra San Pedro Mártir, and found that the proportion of YPMC forests burning at high severity was about 3 percent, although most of the assessed fires had entered YPMC stands from chaparral under severe-fire weather conditions.

Sudworth (1900) inventoried forestlands in the central Sierra Nevada (Lake

Tahoe basin to the latitude of Yosemite National Park) at the end of the 19th century. Concerning the nature of fire in his study region, he wrote (Sudworth 1900: 557–558):

> The fires of the present time are peculiarly of a surface nature, and with rare exception there is no reason to believe that any other type of fire has occurred here… The instances in this region where large timber has been killed outright by surface fires are comparatively rare. Two cases only were found… One of these burns involved less than an acre, and the other included several hundred acres. They are exceptional cases, and the killing of the trees is accounted for by the fact that long protection from fire and from all but cattle grazing had resulted in the accumulation of much fallen timber, considerable humus in depressions and on benches, and a dense undergrowth of brush and seedlings. The fires burned deep enough to badly injure the surface roots, which resulted in the subsequent death of the timber.

Leiberg (1902) carried out a field inventory of forestlands in the northern Sierra Nevada (American River watersheds to the Feather River watersheds) at the beginning of the 20th century and made estimates of the amount and severity of burning that had occurred in the region over the previous century. Euro-American presence in the Sierra Nevada was minimal until after 1850, and exclusion of fire from most Sierra Nevada forests is not noticed in the fire scar record until at least the 1870s or 1880s (Sugihara et al. 2006), so Leiberg's (1902) results at least partly reflect presettlement conditions. That said, northern Sierra Nevada forests suffered heavier Euro-American degradation between 1850 and the early 20th century than the southern Sierra Nevada (Miller and Safford 2017). Leiberg tallied burned area by watershed for the northern Sierra Nevada and estimated that 8 percent of the 19th century fire area had experienced "total destruction," i.e., stand replacement. Leiberg's (1902) assessment did not quantitatively discern among forest types, although most of the fires he visited had taken place in upper elevation mixed-conifer and red fir forests.

Cooper (1906) noted: "Forest fires in California are usually ground fires, and as the mature trees of all species are more or less fire resisting, these fires seldom kill the timber outright, nor does a single fire greatly affect the virgin forest as a whole." In the same year, Hodge (1906) wrote: "In virgin timber ground fires are the rule, and it is seldom the flames reach up into the foliage of large trees, even in stands of fir."

Show and Kotok (1925) stated that fires in the "California pine region," which equates to YPMC forest, rarely burned the forest canopy, but killed canopy trees through heat from surface fires and successive scarring and hollowing out of the trunk, which resulted in typical fire-caused losses of about 5 percent of the "merchantable forest" (mature trees). In another publication, the same authors noted that the typical fire type for yellow pine and drier mixed-conifer forests was surface fire, while moister forests with a high sugar pine and white fir component would tend to experience creeping fires that also consumed the duff layer (Show and Kotok 1929).

Beaty and Taylor (2001) used tree-age data from forest plots and aerial photos from 1941 to reconstruct spatial variation in fire severity in the Cub Creek Research Natural Area on the Lassen National Forest. Vegetation in the area is dominated by moist mixed conifer. Severity classes were assigned based on a categorization of the numbers of emergent trees seen in the aerial photos. The authors found that forests in lower slope positions experienced mostly low-severity fire, middle slope positions experienced mostly moderate- and low-severity fire, and upper slope positions experienced mostly high-severity fire (Beaty and Taylor 2001). Assuming that the landscape was evenly divided among lower, middle, and higher slopes, the areal proportions amounted to about 32:30:38 (low:moderate:high). Also working on the Lassen National Forest and using the same methodology, Bekker and Taylor (2001) mapped fire severity using 1939 and 1943 aerial photos of the Thousand Lakes Wilderness on the Lassen National Forest. For mixed-conifer and white fir-Jeffrey pine stands, fire severity was calculated to have been "high" on 52 to 63 percent of the landscape. In both studies, the earliest fires assessed for severity occurred in the 1880s, so results may or may not be representative of pre-Euro-American conditions, as many destructive fires were set by settlers during the mining, logging, and grazing boom that occurred between 1850 and the early 1900s (Cermak 2005, Jackson et al. 1982, Leiberg 1902, Miller and Safford 2017, Sudworth 1900). Also, because severity classes were based on the numbers of emergent trees seen in aerial photos, they are not easily correlated with measures of biomass loss like RdNBR, and they could have just as easily resulted from a series of moderate/mixed-severity fires over time rather than from one fire event (see footnote 2). It would be useful to determine (1) how to translate the "number of emergent trees" measure to RdNBR, and (2) to what extent these late 19th and early 20th century fires were representative of the presettlement fire regime.

Stephens et al. (2015) used historical timber survey data from 1911 in the Greenhorn Mountains on the Sequoia National Forest to estimate the occurrence of high-severity fire across an 11 500-ha landscape. Forty-one percent of the landscape was dominated by ponderosa pine, while 59 percent was classified as mixed conifer. High-severity fire was estimated using surveyor notes as well as surveyed areas that were dominated by montane chaparral and stands of dense immature timber, which are common vegetation conditions following stand-replacing fire. The percentage of surveyor transects that included evidence of high-severity fire ranged from 2.5 to

7.7 percent in mixed-conifer forests and 7.1 to 13.5 percent in ponderosa pine forests (depending on whether the estimate was based strictly on surveyor notes or also included vegetation condition). Accounting for the fact that only a proportion of each surveyor transect usually included evidence of high-severity fire, Stephens et al. (2015) calculated that high-severity fire occurred across 1 to 3 percent of all mixed-conifer forests and 4 to 6 percent of all ponderosa pine forests in the study area.

Fire severity patterns in presettlement forests can also be modeled. The national, interagency LANDFIRE project collaborated with The Nature Conservancy to convene dozens of workshops nationwide, where state-and-transition models were built of hypothesized presettlement fire and forest successional dynamics by forest and fire ecology professionals (Long et al. 2006, Rollins and Frame 2006). Different models were developed for major vegetation types, which were known as biophysical settings (BpS) (http://www.landfire.gov/NationalProductDescriptions24.php). The models were peer reviewed and extensively refined and calibrated, and then delivered to the LANDFIRE modeling group, which used the BpS models to develop national fuels, vegetation, and Fire Regime Condition Class spatial data layers. In contrast to maps depicting current vegetation distributions, the LANDFIRE BpS layer is a modeled output of potential vegetation representing the distributions of vegetation types as they are hypothesized to have existed prior to Euro-American settlement, based on topography, climate, soils, and the presettlement disturbance regime (Rollins 2009). The advantage of the LANDFIRE BpS layer, as opposed to maps of current vegetation, is that fire regimes both influence and are influenced by vegetation, so maps representing current vegetation may confound the ability to detect shifts in fire regime over time. The disadvantages of the BpS layer include the fact that the models are hypotheses and are difficult to validate empirically. Local inaccuracies in the mapped product can also make it difficult to use the map at fine scales, but at regional and statewide scales, the BpS map conforms closely to the broad biophysical gradients (e.g., Miller and Safford 2012, Safford and Van de Water 2014). In addition, the LANDFIRE BpS output is the only map of potential vegetation in California that is based on a transparent and peer-reviewed modeling process, incorporates the effects of fire, includes lands of all management jurisdictions, and extends across the entire assessment area.

Each BpS model includes documentation that summarizes, among other things, the fire severity outputs from 100 runs of 500 simulation years under presumed presettlement conditions. Mallek et al. (2013) summarized the percentage of high-severity outputs from these models and computed area-weighted averages (since multiple BpS models correspond to each of the major vegetation types analyzed in the study) for the assessment area: the yellow pine models averaged 5.9 percent high severity; dry mixed conifer, 7.1 percent high severity; and moist mixed conifer, 11.6 percent high severity (see also fig. 6). Note that the LANDFIRE project based their severity categories on the Fire Regime Condition Class (FRCC), which defines high severity as >75 percent mortality. Using the 95-percent cutoff used by the RdNBR assessments and our assessment, the percentage of high-severity values from these BpS models would be somewhat lower than those reported.

Stephens et al. (2007) provided literature- and field observation-based estimates of pre-Euro-American fire severity in 12 forest types in California. Their measure of severity was "percent(age of) crown burned," which correlates closely with the RdNBR-derived severity measures, as RdNBR is driven primarily by canopy loss from fire (Miller et al. 2009a). Stephens et al. (2007) used vegetation types described by Barbour and Major (1988) and estimated that an average of 5 percent of the tree canopy suffered burning (torching) in mixed-conifer and ponderosa/shrub forest types, and 2.5 percent in Great Basin pine (Jeffrey pine) forests.

Quigley et al. (1996) summarized scientific work that was done to support forest planning in the interior Columbia River basin, just north of the assessment area. According to Quigley et al. (1996), presettlement burning in eastern Oregon and Washington, which support large areas of semiarid ponderosa pine-dominant forest averaged between 10 and 15 percent "lethal" (high-severity) fire, and 55 to 60 percent "nonlethal" (low-severity) fire. Contemporary fires were very different, with annual burning averaging 30 to 35 percent lethal fire and 25 to 30 percent nonlethal fire.

Comparison to current—Miller et al. (2009b, 2012b), Miller and Safford (2008, 2012), and Mallek et al. (2013) studied contemporary fire severity patterns on Forest Service lands in the assessment area, using RdNBR data. The time periods, the minimum sizes of fires considered, and the vegetation type classification used differed somewhat among the studies. Miller and Safford (2008) and Miller et al. (2009) based their analysis on the existing forest types used in the Sierra Nevada Forest Plan Amendment, and considered severity trends between 1984 and 2004. Based on an area-weighting of their severity results, fires in yellow pine forests (ponderosa pine plus east-side pine) burned about 33 percent of their total area at high (stand-replacing) severity, while mixed-conifer forests (mixed conifer plus white fir) burned at about 29 percent high severity. Miller et al. (2012b), Miller and Safford (2012), and Mallek et al. (2013) based their analyses on potential forest types (biophysical settings) from the LANDFIRE national mapping project, and considered severity trends between 1984 and 2009 (2010 in Miller and Safford 2012). After area-weighting their results, they found that yellow pine types burned at about 42 percent high severity during the study period, and mixed-conifer types at 23 to 30 percent, depending on whether mixed conifer was divided into dry mixed-conifer and moist mixed-conifer types (Mallek et al. 2013, Miller et al. 2012b). Miller and Safford (2012) joined yellow pine and mixed conifer, and found the combination burned at 33 percent high severity during the study period. By contrast, upper elevation mixed-conifer forests in Yosemite National Park during the same period burned at about 14 percent high severity (Miller et al. 2012b).

Using potential vegetation types (which are modeled from environmental and vegetation data) in comparisons between historical and current conditions avoids the complication introduced when vegetation type has changed over time, e.g., owing to human management. However, it is difficult to assess the accuracy of modeled vegetation typing. Miller and Safford (2012) combined yellow pine and mixed conifer precisely because of inaccuracies they found in the vegetation classification. When we consider the combined YPMC forest type, the results using the existing vegetation mapping (~30 percent high severity) (Miller and Safford 2008, Miller et al. 2009b) are very close to those derived using the potential vegetation mapping (33 to 35 percent) (Mallek et al. 2013, Miller and Safford 2012, Miller et al. 2012b). Either way, current fires in YPMC forests managed by the Forest Service in the assessment area are burning at much higher severity (30 to 35 percent high severity as an assessment area average) than was generally the case under presettlement conditions (long-term assessment area-wide average probably <10 percent, ranging from 3 to 15 percent; see fig. 6). Furthermore, since 1984, fire severity in Forest Service YPMC forests has risen substantially, from an average in the low 20 percent in the mid 1980s to more than 30 percent in 2010 (fig. 7). Severity in related forest types, such as black oak and white fir, has also risen over the past few decades (Miller et al. 2009b). In comparison, fire severity since the 1980s has not risen appreciably in upper elevation mixed-conifer forests in Yosemite National Park (Collins et al. 2009, van Wagtendonk and Lutz 2007), where five decades of wildland fire use (also referred to as "fires managed for resource benefit") have reduced fuels and restored forest structure.

Although we have generally been discussing proportional fire severity as applied across all YPMC forests in the assessment area, note that fire severity is not expected to be uniform within this forest type, either in presettlement or in modern times. Fire severity at multiple scales is known to be influenced by a range of factors, including gradients in precipitation, elevation, slope position, species composition, and previous fire history. Within the assessment area, fuel accumulation at the landscape scale is driven by both climate and land management practices (among other things); so higher proportions of high-severity fire

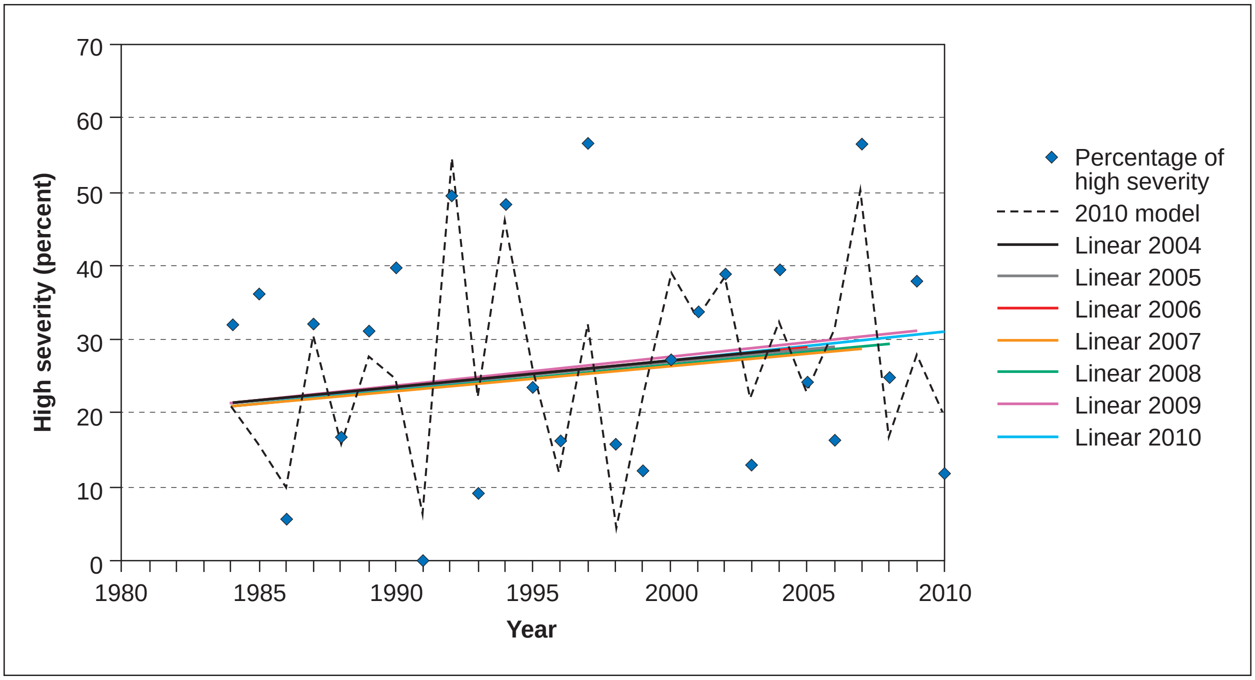

Figure 7—Temporal trends in the percentage of high-severity fire for yellow pine–mixed-conifer forests in the assessment area between 1984 and 2010. The figure shows annual percentages of high-severity fire, the time series (ARIMA) model for the 1984–2010 period, and linear trend lines for seven time series beginning in 1984 and ending in 2004 to 2010. Illustration adapted from Miller and Safford (2012); the definition of high severity is as described in this document.

would be expected in areas with higher precipitation, lower evapotranspiration, higher elevation, and/or a longer legacy of fire suppression (Agee 1993, Noss et al. 2006, Schoennagel et al. 2004, Sugihara et al. 2006). Severity also varies at the stand scale, with greater severity expected in stands on north-facing slopes, in riparian areas, and with higher concentrations of fir (North et al. 2012b, Perry et al. 2011). Geographically, the higher precipitation and higher fir component found in the northwestern assessment area probably led to somewhat more severe fires on average than in the rest of the area.

An Alternative Viewpoint of Fire Severity in YPMC Forests

A small school of researchers and environmentalists maintains that the standard model of mostly low and moderate severity in presettlement YPMC forests is mistaken, and that modern efforts to reduce fuels in such forests are misguided. It is important to acknowledge the existence of this school of thought, although the vast bulk of evidence (summarized throughout this assessment) suggests otherwise. Science produced by this group can be characterized fairly as controversial. For example, Odion and Hanson (2006) used soil-burn-severity mapping of three fires to generalize about fire effects on vegetation across the entire Sierra Nevada, suggesting that modern levels of fire severity and sizes of high-severity patches were within NRV. Safford et al. (2008) responded to Odion and Hanson, and showed that the soil-burn-severity mapping Odion and Hanson used had little correlation to vegetation-burn severity, and that their analyses of fire patchiness and relationship between fire-return interval and fire severity were flawed.

In another example, Williams and Baker (2012) and Baker (2012, 2014) used General Land Office (GLO) data from the mid- and late-1800s (see "Forest structure," "Tree size," and "TreeSize-Class Distribution" below) to generalize about tree densities in YPMC forests in a number of locations across the Western United States (Baker [2014] specifically refers to the Sierra Nevada), and the role of fire in driving these densities. These studies similarly claim that current fire patterns—i.e., high levels of high-severity fire—are within the NRV. Aside from the obviously tenuous use of GLO data to compute landscape tree densities, which involves extrapolating from ≤8 trees per square mile, Baker and colleagues' work also requires the belief that any area of denser-than-average small- to medium-size trees is necessarily the result of high-severity fire, even where there is no evidence of fire and even where the relationship between tree size and tree age is not known (Fulé et al. 2014). Furthermore, in the absence of fire, simple differences in site productivity and antecedent forest structure are sufficient to explain major variation in tree density in YPMC forests (Maxwell et al. 2014). Comparison of direct forest inventories from the early 20th century demonstrates that the Baker (2012, 2014) studies greatly overestimated forest stand density. Such inventories, which sampled orders of magnitude more trees than the GLO effort used by Baker, showed his stand density estimates to be from 2.1 to 5.9 times too high (Collins et al. 2011; Hagmann et al. 2013, 2014; Stephens et al. 2015). Similarly, Levine et al. (2017) used Baker's algorithm to predict tree densities on a series of 6-ha mapped forest plots in YPMB forests in the Sierra Nevada and NW Mexico and found that Baker methodology notably overpredicted densities in every case (1.2 to 4.8 times higher than the true density). Fulé et al. (2014), Stephens et al. (2015), and Collins et al. (2015) also showed that the Baker methods greatly overestimated historical fire severity.

Hanson and Odion (2013) claimed to refute the trends of increasing high-severity fire in the Sierra Nevada national forests found by Miller et al. (2009b) and Miller and Safford (2012). However, Safford et al. (2015) uncovered a high number of compounded errors in Hanson and Odion's analysis, including issues with their data layers, errors in cartographic analysis, unorthodox forest groupings that conjoined different fire regimes, and the inclusion in their analysis of prescribed fires. In their dataset, Hanson and Odion (2013) also included large areas of fire on private lands (where high-severity fire areas are generally salvage logged before the postfire imagery used to determine the level of severity is acquired, which makes a credible severity assessment on such lands impossible) and wildland fire use areas in the national parks, which have no place in a test of fire patterns on Forest Service lands.

Odion et al. (2014) suggested that Forest Inventory and Analysis (FIA) "stand-age" data proved that YPMC forests across the Western United States were largely younger forests that had arisen after high-severity fire events. Odion et al. (2014) used data only from wilderness areas and national parks, which are at higher elevations in the assessment area and are not very representative of typical YPMC forest. The major problem with Odion et al. (2014), however, is that FIA stand-age data, which are a very rough estimate of the canopy-area-weighted mean age in a plot, are uninterpretable and essentially meaningless in the highly heterogeneous age structure of YPMC forests.[3] Stevens et al. (2016) showed that most of the plots analyzed by Odion et al. (2014) included numerous trees that were older, in some cases hundreds of years older, than the "stand-age" computed in their study, which makes Odion et al.'s (2014) claim that high-severity fire had reset succession in all of these plots an impossibility, given that high-severity fires kill all or nearly all trees in the affected stand (Miller and Quayle 2015).

A standard claim made by this group is that their findings challenge the reigning model for presettlement YPMC forests, which they define as permitting only low-severity fire and open, park-like stands of large trees. This definition does not represent the scientific consensus. In 1996, the SNEP report (Erman and SNEP Team 1996) summarized the consensus regarding fire severity in the Sierra Nevada thusly: "In most lower-elevation oak woodland and conifer forest types of the Sierra Nevada, presettlement fires were frequent, collectively covered large areas, burned for months at a time, and, although primarily low to moderate in intensity, exhibited complex patterns of severity."

This was the consensus 20 years ago, and it remains the consensus today. As noted throughout this assessment, YPMC forests in their reference state were extremely heterogeneous, and were characterized by areas of low-, moderate-, and high-severity fire (but with the balance more shifted to low severity than is currently the case).

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[3] Fried, J. 2013. Personal communication. Research forester, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 620 SW Main St., Ste. 400, Portland, OR 97205.

Components of the fire regime: high-severity patch size—

***NRV and comparison to current*—**In low- and middle-elevation forests, high-severity patch size has also increased, with a dominance of small, scattered patches in presettlement and reference estimates, versus more contiguous coarser grained patchiness in modern fire-suppressed forests. High-severity patches more than a few hectares in size were relatively unusual (although not unknown) in fires in Sierra Nevada YPMC forests before Euro-American settlement (Agee 1993, Kilgore 1973a, Show and Kotok 1924, Skinner 1995, Skinner and Chang 1996, Stephenson 1990, Sudworth 1900, Weatherspoon and Skinner 1996), but in recent years high-severity patches >500 ha have become a regular occurrence (Miller and Safford 2008, Miller et al. 2012). Between 1984 and 2006, mean high-severity patch size in Forest Service fires in the assessment area almost doubled (Miller et al. 2009b). Comparisons between current reference YPMC forests (in which full fire suppression is not practiced) and Forest Service forests (managed primarily under full fire suppression) further reflect these changes. For example, Minnich et al. (2000) reported that patches of high-severity fire (>90 percent mortality in their study) in the Sierra de San Pedro Mártir were almost entirely <16 ha in size; mean patch size was 1.7 ha. Scholl and Taylor (2010) used a forest reconstruction of an 1899 mixed-conifer stand in Yosemite National Park to show that even-aged patches indicative of high-severity fire were generally <0.2 ha. In contrast, Miller et al. (2012b) found that the average size of high-severity patches in modern Forest Service-managed fires in the assessment area was 12.2 ha (1.6 SE); high-severity patches during the same time period in Yosemite, where many fires have not been suppressed for the past four decades, averaged 4.2 ha (0.6 SE). Van Wagtendonk and Lutz (2007) found that mean high-severity patch size for Yosemite from 1984 to 2005 was approximately 1.6 ha for prescribed fires, 2.5 ha for "fire-use" fires (natural ignitions that were not suppressed), and 6.7 ha for wildfires (any ignition that was managed for suppression). Collins and Stephens (2010) analyzed fire-severity patchiness in Yosemite's Illilouette watershed and found that 48 percent of the total high-severity area was in patches >60 ha, which comprised only about 5 percent of the total number of patches. Data from Miller and Safford (2008) showed that patches >60 ha comprise 70 percent of high-severity fire area in recent Forest Service fires.

To summarize, the NRV of high-severity fire patch size in assessment-area YPMC forests was strongly dominated by a "salt-and-pepper" pattern of small areas mostly (much) less than a few hectares in size. Patches larger than a few hectares did occur, but they were rarely more than 100 ha. Nonetheless, such larger patches comprised perhaps half of the total high-severity area.

The NRV of high-severity fire patch size in assessment-area YPMC forests was strongly dominated by a "salt-and-pepper" pattern of small areas mostly (much) less than a few hectares in size. Patches larger than a few hectares did occur, but they were rarely more than 100 ha. Nonetheless, such larger patches comprised perhaps half of the total high-severity area.

Components of the fire regime: fire size—

***NRV*—**When we consider only fires >4 ha (the minimum fire size recorded in the California Fire Perimeter Database),[4] mean fire size in California YPMC forests before Euro-American settlement was much smaller than under current conditions (fig. 8). We were able to find eight published estimates (Beaty and Taylor 2001, Bekker and Taylor 2001, Collins and Stephens 2007 [which contains estimates for two separate national park areas; raw data provided to authors], Scholl and Taylor 2010, Taylor 2000, Taylor and Skinner 1998, and Taylor and Solem 2001) and two unpublished estimates[5] of presettlement fire size statistics in YPMC-type forests in northern California. Restricting our consideration to fires ≥10 ha to facilitate comparison, mean

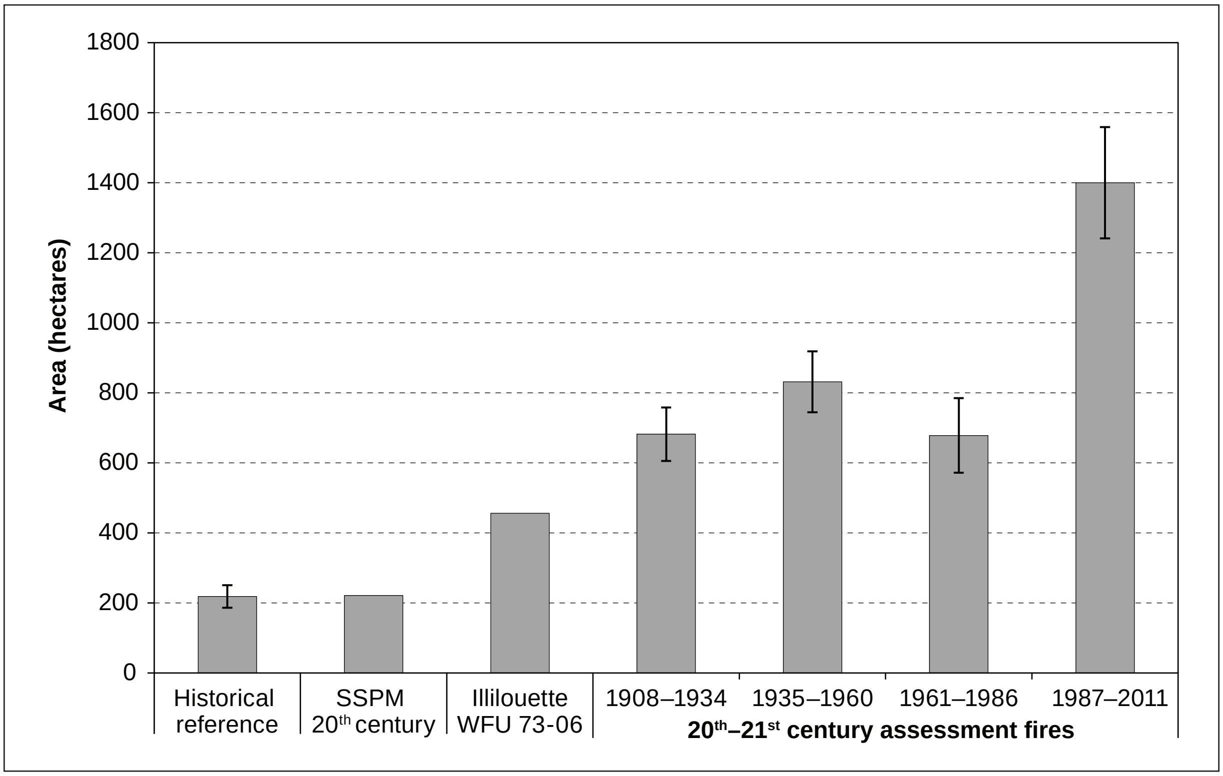

Figure 8—Comparison of mean fire sizes from yellow pine and mixed-conifer reference sites with intact fire regimes and the assessment area (forest fires only) since the institution of fire suppression in the early 20th century (the latter are divided into four equal time periods [1908–1934, 1935–1960, 1961–1986, 1987–2011] to show temporal trends). Only fires ≥10 ha are included. Ten sources were used for historical reference numbers; see text. SSPM = Sierra de San Pedro Mártir; data are from Minnich et al. (2000). Illilouette watershed wildland fire uses fires from B. Collins (see footnote 6); 20th- and 21st-century fires are from the California Fire Perimeter Database (see footnote 4).

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[4] California Department of Forestry and Fire Protection, Fire and Resource Assessment Program: http://frap.fire.ca.gov/index.

[5] Taylor, A.H. 2012. Personal communication. Professor, Department of Geography, Pennsylvania State University, University Park, PA 16802.

presettlement fire size averaged from these 10 sources is 210 ha (±33.6 SE, range of means = 85 ha to 457 ha). Finally, there are two published fire size estimates from contemporary reference areas (again, we only include fires ≥10 ha in size to permit comparison among studies): mean fire size in the SSPM, Baja California, Mexico was measured at 221 ha (167 ha if all measured fires are included) between 1925 and 1991 (Minnich et al. 2000); mean fire size in the Illilouette Creek watershed in Yosemite National Park, where most naturally ignited fires are allowed to burn, was 456 ha (61.4 ha if fires of all sizes are included) between 1973 and 2006[6] (see van Wagtendonk et al. (2012) for info on fires >40 ha in the same watershed). The overall average of these 12 sources is 296 ha. In addition, Show and Kotok (1923) reported fire sizes in the assessment area and northwestern California forests (then, as now, most fires occurred in the YPMC belt) for the 10-year period between 1911 and 1920, just as the federal government was beginning to engage in fire suppression. They found the average size of all recorded fires to be 48.3 ha (± 12.8 SE), and the average of all fires ≥4 ha was 177.8 ha (± 32.7 SE).

Another estimate of mean presettlement fire size in assessment-area YPMC can be made by dividing the total area extent of YPMC forest by the presettlement fire rotation (area-weighted mean for yellow pine, dry mixed conifer, and moist mixed conifer from Mallek et al. [2013] to generate an annual area burned, then dividing the area burned by the mean annual number of lightning ignitions in YPMC forests, also area-weighted by forest type), under the assumption that modern fire ignition data are representative of presettlement patterns (Short 2013). This approach yields a mean prehistorical fire size of 435 ha for YPMC forests (391 ha in yellow pine, 692 ha in dry mixed conifer, and 434 ha in moist mixed conifer),[7] but ignores ignitions by humans and therefore overestimates mean fire size, especially in the lower elevation forest types (yellow pine and dry mixed conifer).

Note that there is evidence that fires in areas of simple topography may have often burned areas in excess of this ±300- to 400-ha mean. Norman and Taylor (2003) reported evidence of recurrent landscape-scale fires in an area of subdued topography in the southern Cascade Range; data from other parts of the southern Cascades show similar patterns.[8] Their interpretation was that these larger fires

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[6] Collins, B.M. 2013. Personal communication. Fire ecologist, Center for Fire Research and Outreach, University of California, Berkeley, CA 94720.

[7] Miller, J.D. 2013. Personal communication. Remote sensing specialist, USDA, Forest Service, Pacific Southwest Region, 3237 Peacekeeper Way, Suite 101, McClellan, CA 95652.

[8] Skinner, C.N. 2012. Personal communication. Research fire geographer, USDA, Forest Service, Pacific Southwest Research Station, Redding Silviculture Laboratory, 3644 Avtech Parkway, Redding, CA 96002.

were driven by herbaceous fuels (mostly in and around meadow complexes, but not exclusively there), where fuel loadings increased in wet years and then burned in subsequent dry years (Norman and Taylor 2003). Clearly topography and landscape conditions (presence of previously burned areas, rock outcrops, large streams, etc.) played a significant role in limiting fire size in the assessment area.

***Comparison to current*—**Data from the California Fire Perimeter Database (see footnote 4) shows that average fire size (all fires >10 ha) over the 25-year period up to 2011 for fires in YPMC forests in the assessment area (all jurisdictions) was 1400 ha (±55 SE) (fig. 8), about five times larger than either the assessment area historical data sources or the modern SSPM data, and about three times larger than the average in the Illilouette Creek watershed in Yosemite National Park (not an entirely clean comparison, as Illilouette is included in the assessment area data). Note that modern YPMC fire areas (since 1908) in figure 8 were calculated by removing those portions of fires that burned in other vegetation types.

Figure 9 provides a graphic comparison of fire size frequency distributions in the assessment area (1910 to 2006) (see footnote 4) versus the SSPM (1925 to 1991) (data from Minnich et al. 2000). The climates and vegetation are similar in the two

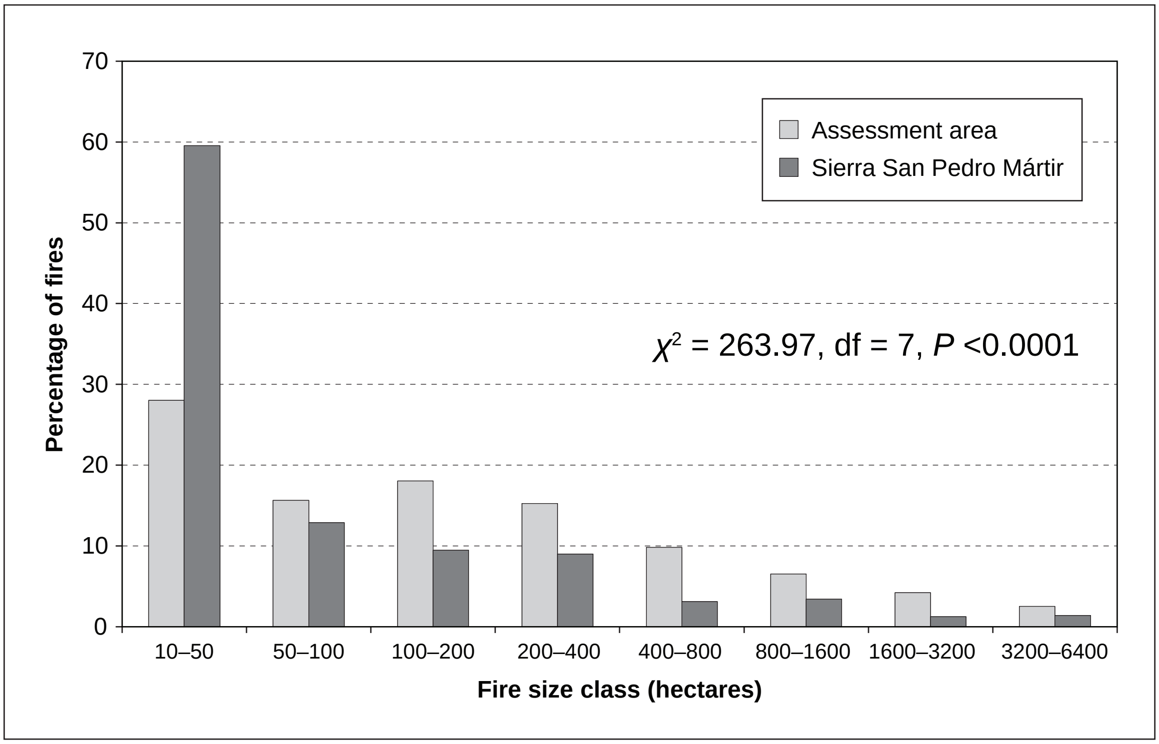

Figure 9—Comparison of 20th-century fire size frequency distributions, assessment area versus Sierra San Pedro Mártir. Proportionally speaking, the assessment area experiences many more large fires and many fewer small fires. Only fires >10 ha in size are included.

areas (the latter being drier than the western and northern portions of the former). The former has experienced significant timber harvest and a century of fire suppression; the latter was not logged, and at the time of the last fire had experienced fewer than 15 years of fire management. The assessment area has experienced proportionally more than twice as many large (>400 ha) fires and proportionally less than half as many small (<50 ha) fires compared to the SSPM over the study period (fig. 9).

Comparing the same two datasets, fires greater than and smaller than 1600 ha contributed equally to the total area burned in the Sierra de San Pedro Mártir, but large fires (>1600 ha) contributed 70 percent of all burned area in the assessment area.

It is important to finish with a caveat: we have focused our comparison on fires >4 ha, as there are no presettlement data on small fires, and the California Fire Perimeter Database includes only fires >4 ha. However, a recent unpublished analysis by Miller and Safford (manuscript in preparation) of all fire sizes compares a post-1992 dataset for the assessment area against a 1911–1920 dataset from Show and Kotok (1923) and a 1980–2012 dataset from managed lightning fires in Yosemite National Park. Miller and Safford (in prep) found that, because of fire suppression, the proportion of fires that remain below 4 ha in size is much higher in the general assessment area (mostly Forest Service and private lands under fire suppression policies) today than at the beginning of the 20th century or in managed fires in Yosemite National Park. In summary: when considering **all** fire sizes, the average fire size before fire suppression was actually larger than today, but when considering fires >4 ha, fires today are larger on average. This is due to the strong statistical "mass" provided by the growing set of very large modern fires.

Components of the fire regime: annual area burned—

***NRV*—**A number of published studies have estimated probable presettlement annual burned area, but only a few have split their estimates by vegetation type. Stephens et al. (2007) estimated burning rates for mixed-conifer and yellow pine forests across California, and found that 5 to 15 percent of the total area of YPMC forests burned per year before Euro-American settlement, depending on the fire frequency estimate used. Using the LANDFIRE BpS estimates of forest area before Euro-American settlement (3.65 million ha for YPMC) (Mallek et al. 2013), this would result in a range of about 180 000 to 550 000 ha burned per year in YPMC forest types in the assessment area. North et al. (2012a) estimated fire areas for the Sierra Nevada sensu stricto, which does not include lands north of the North Fork Feather River or east of the eastern Sierra Nevada foothills. Their "active-management" forest types, which essentially conform to YPMC plus some hardwood forests, were estimated to experience between 77 000 and 203 000 ha of burning per year before Euro-American settlement, or 5 to 18 percent of the total land area in the YPMC forest types (North et al. 2012a). Mallek et al. (2013) carried out an assessment of fire area for the same study area as the bioregional assessment, basing their calculations on fire rotation data found in the scientific literature. Mallek et al. (2013) found that presettlement burning probably affected about 4 percent of the land area in the YPMC forest types in an average year, or around 145 000 ha. Stephens et al. (2007) suggested that their low-end estimates of burning were probably more trustworthy than their high-end estimates, so it seems reasonable to suggest that somewhere around 5 percent of the area of YPMC forest types probably burned in an average year (and there was likely very high variability, year to year), or somewhere between 150 000 and 175 000 ha across the assessment area.

Comparison to current**—**Mallek et al. (2013) used the California Fire Perimeter Geodatabase (see footnote 4) to calculate the total area of fire within yellow pine, dry mixed-conifer and moist mixed-conifer forests in the assessment area for the period 1984 to 2009. During the period, 489 000 ha of fire are recorded in the database for these forest types, which comes to an annual average of about 18 800 ha in YPMC forests. This is between about 10 and 13 percent of our presettlement estimate above. Using data up to 2010, North et al. (2012a) suggested that current wildfire in the Sierra Nevada proper (about 60 percent of the assessment area) accounts for 10 to 30 percent of presettlement fire area. Note that since these publications, the area burned by wildfire in the Sierra Nevada has increased dramatically. Between 2013 and 2015, the three largest fires—Rim, King, and Rough—burned over 200 000 ha on their own, principally in YPMC forests. According to the California Fire Perimeter Database, the average annual burned area in YPMC forests for the period 2010-2017 was more than twice the average annual burned area between 1984 and 2009 (~39 000 ha vs. 18 800 ha). Even so, this accounts for less than 1/3 of the average annual burned area before Euro-American settlement.

Components of the fire regime: fire season—

NRV and comparison to current**—**The concept of "fire season" refers qualitatively to the average period of the year during which wildfire activity can be expected. Qualitatively or quantitatively, there are a variety of ways to define the fire season. For example, Westerling et al. (2006) defined fire season as the number of days between the first wildfire occurrence of the season and the final wildfire control date. Thonicke et al. (2001) defined the annual length of the fire season by summing the probability of at least one fire in a day across the calendar year.

The assessment area experiences one of the longest fire seasons in North America because of the combination of fuels fed by winter and spring moisture and the 3- to 6-month period of drought that coincides with the warm season (Keeley et al. 2012, Sugihara et al. 2006). Years of widespread burning in the assessment area are driven strongly by drier-than-average years, and this pattern stretches back to the beginning of the fire scar record (Trouet et al. 2010).

The fire season is driven to a great extent by temporal patterns in fuel moisture, which are in turn largely dependent on winter and spring precipitation. YPMC forests in the assessment area receive from about 25 to 50 percent of their precipitation as snow (Minnich 2007), depending on elevation and latitude, among other things. Fire season in YPMC forests north of the Tehachapi Mountains (i.e., north of approximately latitude 35° N) is generally considered to run from late June to October (Fried et al. 2004, Sugihara et al. 2006), but the average length varies with latitude, elevation, topography, and of course annual precipitation and temperature. Fire season tracks and slightly lags the climatic dry season. An approximation of the fire season length and timing can be derived from the Walter climate diagrams in figure 2. Because of fuel and soil moisture carryover from the wet season, coarse forest fuels are typically too moist to burn for some time after the beginning of the climatic dry season, and they remain dry enough to burn for some time after the beginning of the wet season (see fig. 2); fine fuels respond much more rapidly to meteorological wetting and drying. Thus, the fire season may be reasonably approximated with a 2- to 4-week lag on either end of the climatic dry season. The fire scar record shows that fires historically tended to occur late in the fire season (after cessation of summer tree growth) in the northern assessment area, but more in the middle of the fire season in the southern assessment area; areas farther south continue the earlier trend, with fires in the Baja California YPMC forests tending to occur in the early to middle fire season (Skinner 2002, Skinner et al. 2008, Stephens and Collins 2004).

In a study of wildfire in the Western United States, Westerling et al. (2006) found that fire season length had increased by more than 2 months during the period between 1970 and 2003. They attributed the earlier start of the fire season to earlier snowmelt from higher spring and summer temperatures.

Future fire regimes—

Flannigan et al. (2009) summarized the results of dozens of future fire activity projections under different climate change scenarios and concluded that most evidence pointed to increased fire occurrence and area burned. Referring to North American in general, Gedalof (2011) similarly noted that “nearly all… (modeling) efforts predict a substantial increase in wildfire activity over the next century…” Bachelet et al. (2007) concluded that “despite imprecise knowledge of future climate and human behavior, it is reasonable to conclude that fires will likely increase in the West.” Safford et al. (2012b) stated that “modeling studies specific to California expect increased fire activity to persist and possibly accelerate under most future climate scenarios." Miller and Urban (1999a) noted that the altered water balance that results from climate change can influence fire regimes both directly, through its influences on fuel moisture, and indirectly, through its influences on forest structure, composition, and fuel loads. Miller and Urban (1999a) concluded by stating, "If GCM predictions of future climate prove true, fires could be both more frequent and of greater spatial extent at certain sites." Many modeling efforts have been undertaken that either focus on or include California, and we summarize these efforts below.

***Fire frequency and fire rotation*—**Miller and Urban (1999a) simulated the effects of climate change on forest biomass, composition, and fire regimes across an elevational gradient in Sequoia & Kings Canyon National Parks. For their lowest two sites, which occur within YPMC forests, fire frequencies rose markedly during the first century of their climate change simulations, then dropped over time as woody biomass was increasingly lost. By the end of their 400-year climate change simulations, woody biomass had decreased at the 1800-m site from 0 to 4 m^2/ha overall, leaving little fuel to burn; under their most extreme scenario, forest fuels at this site were completely replaced by fine (grassy) fuels, and fire frequency rose. At the 2200-m site, biomass loss was also high but not as extreme as at the 1800-m site, and fire frequencies remained similar to the baseline conditions, although fire area decreased with the decrease in biomass (Miller and Urban 1999a). The 2600-m site, which is currently in red fir forest but was predicted to transition to a mixed-conifer composition, experienced very large increases in fire frequency.

Loudermilk et al. (2013) used LANDIS to model carbon and fire dynamics under future climates for the Lake Tahoe Basin. Under their more severe future climate scenario (+4.6 °C and –22 percent precipitation compared to today), the projected fire rotation period dropped by 18.6 percent compared to today. Under a more benign future climate scenario, the rotation period dropped by about 6 percent. Both of these projections assumed similar fire behavior to today, however, as well as continued success of fire suppression efforts, such that fire rotations continued to be quite long even under the much warmer future scenario (around 200 years).

Yang et al. (2015) used a averaged spatial point process modelling approach to project future "fire occurrence density" for the Lake Tahoe basin. Using the same future climate scenarios as Loudermilk et al. (2013), they found that—compared to today—the density of fires per unit area increased by 210 percent under the more extreme future climate and 70 percent under the more benign scenario.

***Fire severity and intensity*—**Flannigan et al. (2000) modeled the seasonal severity rating (SSR) across North America under two global circulation model (GCM) scenarios for the year 2060. SSR measures the difficulty of fire control. Flannigan et al. (2000) found that SSR increased by an average of 10 percent under both GCM scenarios for California. Lenihan et al. (2003a, 2003b) modeled vegetation and fire response to different GCM-based future climate scenarios for California, using the MC1 dynamic vegetation model. One of their mid-stream outputs was fireline intensity, measured as Btu/ft/sec (see Lenihan et al. 2003b). Lawler et al. (2012) summarized the fireline intensity outputs for the range of the California fisher in the southern Sierra Nevada (most of the west slope of the Sierra Nevada in the assessment area southern region), under a moderately warmer, slightly drier future climate scenario. They found that Lenihan et al.'s (2003a, 2003b) model projected higher fire intensity across about 35 percent of the fisher range, lower intensity on 15 percent of the area, and similar fireline intensity on 50 percent of the area.

Fried et al. (2004) modeled fire behavior while accounting for suppression response for lands under state of California fire management. Under a conservative future climate scenario, Fried et al. (2004) found that decreased fuel moistures and increased seasonal windspeeds under climate warming led to faster burning and more intense fires. Most of their increased fire activity was due to an increase in the number of fires burning under extreme conditions. Flannigan et al. (2013) linked the Canadian Forest Fire Weather Index to three GCMs and predicted the cumulative severity rating (CSR), a fire danger metric based on weather conditions, for the Northern and Southern Hemispheres for the periods 2041–2050 and 2091–2100. They projected that severity as measured by CSR would increase by 10 percent to ~30 percent by the later period over most of the assessment area. Yue et al. (2013) modeled trends in biomass consumption, which scales with severity, for the Western United States. They projected mean increases of 80 to 90 percent in biomass loss by the middle of the 21st century for their Pacific Northwest region, with the largest changes projected for the Sierra Nevada and coastal forests in northwestern California and western Oregon. Van Mantgem et al. (2013) showed that high prefire climatic water deficit increases the probability of postfire tree mortality, thus—aside from their well-known effects on fuel moisture—climate warming and increasing growing season drought can enhance fire severity independently of fire intensity. This suggests that future fire severities could be even higher than predicted by most climate modeling studies.

***Burned area*—**In Miller and Urban's (1999a) model, area burned at their 1800-m and 2200-m sites rose strongly during the first century of their climate change simulations, then decreased over time as woody biomass was gradually lost. At the lowest site, little woody biomass remained at the end of their simulation, and the abundance of grassy fuels led to a large increase in area burned. At the 2200-m site, fire area decreased as biomass was lost over time (Miller and Urban 1999a). Their red fir-forest site at 2600 m experienced very large increases in area burned. Fried et al. (2004), using a relatively conservative future climate scenario, compared 6-year simulations for current and future conditions. Their future simulation burned 43 percent more area in mixed-conifer forest than the current scenario.

Lenihan et al. (2008) simulated fire and vegetation dynamics in California under three future climate change scenarios. In all three of their scenarios, the assessment area experienced some of the greatest increases in simulated area burned (20 to 50 percent increases), especially on the Modoc Plateau, at higher areas of the southern Cascade Range, and in middle- to high-elevation forests along the Sierra Nevada axis. Spracklen et al. (2009) built regression models linking observed climate with observed wildfire area burned and used a GCM to project burned area out to 2050. They projected an increase of about 180 percent in annual area burned for their Pacific Northwest region, which included most of the assessment area. National Research Council (NRC 2011) modeling projected that compared to the average for the 1950–2003 period, median annual area burned would increase by more than 300 percent for the assessment area with a 1 °C increase in average temperature. The report also noted that, over time, extensive warming and wildfire could ultimately exhaust the fuel for fire in some regions, as forests were completely burned (NRC 2011).

Westerling et al. (2011) modeled burned area across California under a range of future climate and development scenarios. They found that, under the most realistic future climate and emissions scenarios and compared to the average for the period from 1960 to 1990, area burned by wildfire would increase by more than 100 percent by 2085 for most of the forested area of northern California. Middle and higher elevation forests in the assessment area would be among the most severely affected, with some future climate scenarios producing increases in burned area of more than 300 percent. Yue et al. (2013) used regression and parameterization approaches to project burned area under 15 GCMs for the Western United States for the middle of the 21st century. Their Pacific Northwest region, which included most of the assessment area, would experience projected median increases of 42 and 154 percent in area burned by wildfire, depending on the approach. Loudermilk et al. (2013) used LANDIS to model carbon and fire dynamics under future climates for the Lake

Tahoe basin. They found that under their more severe future climate scenario, the mean annual area burned would climb by 43 percent by the year 2100.

McKenzie et al. (2004) calculated correlations between mean summer temperature and precipitation and annual burned area for 11 Western States between 1916 and 2002, then employed regression models to project burned area into the future under two emissions/climate scenarios. They found strong relationships between their summer climate variables and fire area for all states but California and Nevada, and concluded that most of the Western United States was likely to experience large increases in annual area burned by wildfire in the 21st century. However, they concluded that "fire in California and Nevada appears to be relatively insensitive to summer climate, and area burned in these states may not respond strongly to changed climate." In their study, McKenzie et al. (2004) made two errors with respect to their analysis in California. First, they neglected to account for California's Mediterranean climate, which features a summer drought of 3 to 6 months. Second, McKenzie et al.'s (2004) analysis combined southern and northern California, which each contribute about half of California's total burned area in an average year but which are extremely different in their fire-climate relationships, and often do not share the same extreme years. Their analysis thus buried the relatively strong relationship that exists between fire and summer climate variables (in this case, temperature) in the assessment area and other parts of central and northern California (Miller et al. 2009b, Trouet et al. 2006, Westerling et al. 2006) under the southern California fire-climate relationship, which is essentially independent of summertime temperature or precipitation (Keeley 2004). In summary, changes in summer temperature and precipitation may not have strong effects on southern California fire area, but McKenzie et al.'s (2004) predictions for the Western United States in general are likely to have validity for most of the assessment area.

Fire ignitions—Because the human population of California is expected to increase to nearly 50 million by 2050—and a large proportion of that increase is forecast for the Central Valley and Sierra Nevada foothills (http://www.dof.ca.gov/Forecasting/Demographics/projections/documents/P1_County.xlsx)—it is reasonable to conclude that the density of human fire ignitions will also increase over time. Educational efforts can help to reduce fire ignitions and improve public safety, but more people usually means more fire (Syphard et al. 2009).

Ignitions by natural causes may also increase through the 21st century. Price and Rind (1994) simulated lightning distributions and frequencies under a GCM-based future climate scenario incorporating 4.2 °C global warming by 2100. They projected that lightning incidence could increase by up to 30 percent globally. Romps et al. (2014) found similar results, based on the linear relationship between lightning flash rate and the product of precipitation (per hour) times convective available potential energy (which measures atmospheric convective instability). Romps et al. (2014) projected a 12 percent average increase in lightning per degree celcius of temperature rise. This could translate into 50 percent more lightning across much of the United States by the end of the 21st century. Although neither study highlighted the assessment area as a global "hotspot" for increased lightning occurrence, the combination of greater lightning incidence, warmer climates, and drier fuels inexorably leads one to conclude that fire activity will likely rise in most semiarid areas currently supporting forest. Yang et al. (2015) found that lightning ignitions could increase in the future even without an increase in lightning occurrence, as the lengthening of the fire season, loss of snowpack, and drying of fuels combine to expand the conditions under which lightning strikes led to fuel combustion.

Fire effects on vegetation—Fire is a major driver of vegetation change in both space and time. Fire activity and behavior are tied strongly to fuel amount, fuel moisture, and weather conditions at the time of burning (Agee 1993, Sugihara et al. 2006). All these factors are influenced by both temperature and precipitation. There is near-universal agreement that the assessment area climate will become notably warmer through this century, but projections of future precipitation patterns are much less certain (Dettinger 2005). The effects of fire on vegetation in the assessment area will depend greatly on precipitation trends, but Bachelet et al. (2007) noted that in either wetter or drier conditions, forest could be notably reduced in much of the Western United States in a warmer future. Under drier conditions, enhanced fire frequency could favor drought-tolerant grasses, which would further enhance ecosystem flammability and reduce woody cover. Under wetter conditions, expansion of woody plants might promote more intense fires and high mortality when drought conditions occur, ultimately reducing tree biomass.

Bachelet et al. (2007) projected that most of the assessment area would see an increase in biomass consumption by fire during the 21st century, whether warming was extreme or moderate, and whether carbon emissions were relatively high or low. Most pixels in the assessment area experienced increases in biomass loss of 25 to 67 percent when compared to the 1961–1990 period.

Using the same deterministic vegetation dynamics model as Bachelet et al. (2007), Lenihan et al. (2008) simulated the future distribution of terrestrial ecosystems in California under three GCM-based future climate scenarios (see fig. 10). The "MC1" model used by Lenihan et al. (2003a, 2003b) explicitly models fire and its effects on vegetation; modeling results were driven to a notable extent by fire. Total annual area burned in California increased under all three scenarios, ranging from 9 to 15 percent above the 1961–1990 mean by the end of the 21st century

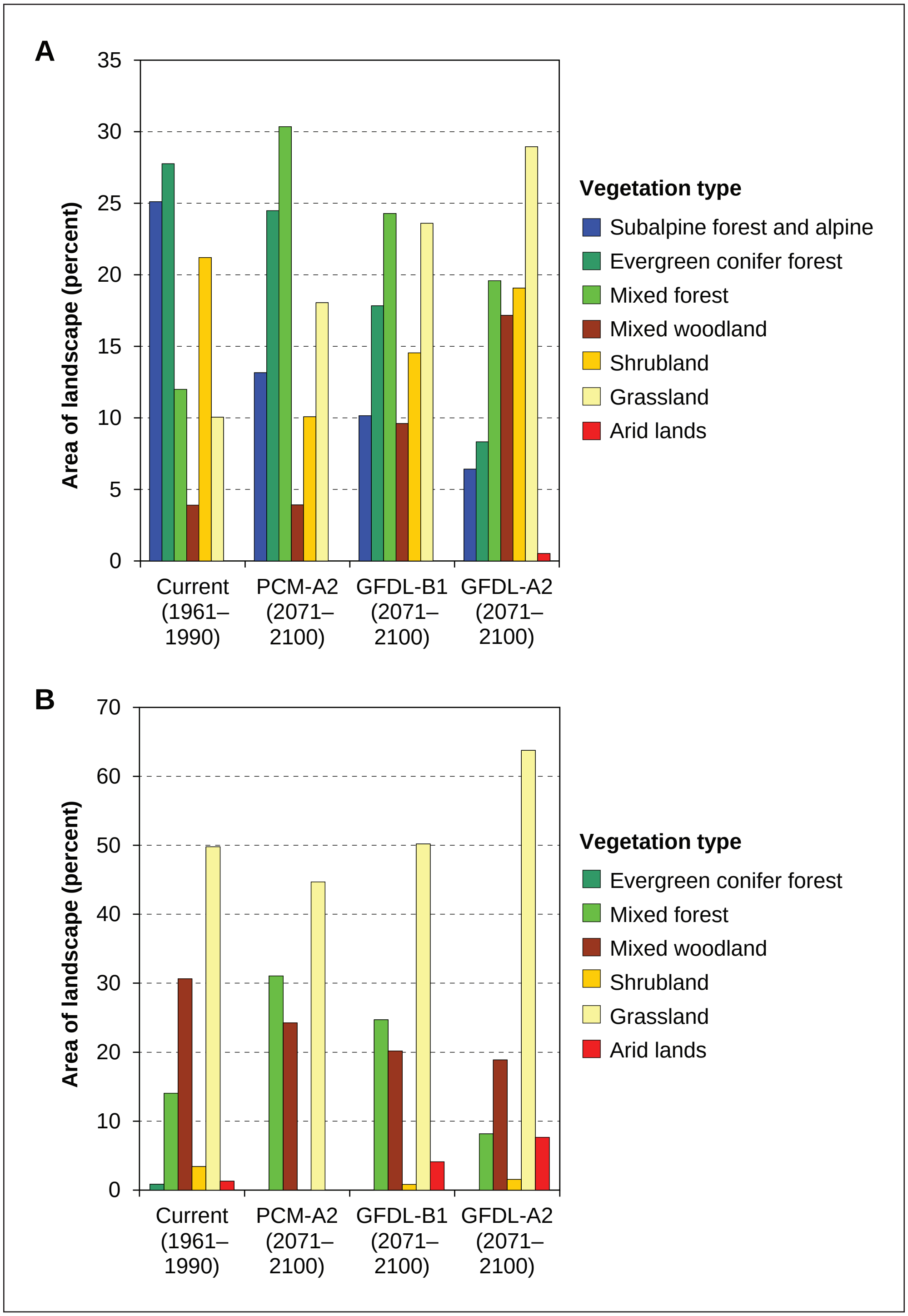

Figure 10—Lenihan et al. (2008) modeling results for the Sierra Nevada (A) and Sierra Nevada Foothills (B) ecological sections, comparing current conditions to future projections of vegetation extent. These ecological sections include most of the Sierra Nevada western slope. The GFDL-B1 scenario = moderately drier than today, with a moderate temperature increase (<3.1 °C); PCM-A2 = similar precipitation to today, with a <3.1 °C temperature increase; GFDL-A2 = much drier than today and much warmer (>4 °C higher). All scenarios project significant loss of subalpine and alpine vegetation. Most scenarios project lower cover of shrubland (including west-side chaparral and east-side sagebrush), owing principally to increasing frequencies and extent of fire. Large increases in the hardwood component of forests are projected in all scenarios except for the hot-dry scenario in the Foothills section. Large increases in grassland cover are projected for the Sierra Nevada section. The drier scenarios project moderate expansion of arid lands. In the Sierra Nevada section, coniferous forest decreases in cover under all scenarios. Illustration is adapted from Safford et al. (2012b).

Broadleaf woodland and forest replaced large areas of evergreen conifer forest under all three scenarios, with fire playing an important role in the transition, especially in the relatively warmer and drier scenarios.

(Lenihan et al. 2008). Fire drove grassland expansion into former shrublands and woodlands, even under the coolest and wettest future scenario; by 2099, under the warmest and driest scenario, grassland almost completely replaced shrublands on the Sierra Nevada west slope and also expanded greatly in the California portion of the Great Basin. Broadleaf woodland and forest replaced large areas of evergreen conifer forest under all three scenarios, with fire playing an important role in the transition, especially in the relatively warmer and drier scenarios (Lenihan et al. 2008). Under the more moderate climate scenario, annual consumption of biomass by fire by the end of the 21st century across California was about 18 percent greater than the 1961–1990 mean. Under the two drier and warmer scenarios, simulated biomass consumption by fire was greater at first, but as woody biomass was burned, vegetation type conversions led to large reductions in overall biomass available for burning by the end of the century.

Fire season**—**Although overall precipitation in much of the assessment area has been steady to rising slightly over the past three-fourths of a century, the snow:rain ratio and snowpack depth and persistence have all been decreasing (Safford et al. 2012b). Combined with warming temperatures, these negative trends in snow amount and storage result in fuels drying earlier. Current trends and projections of future patterns in the snow:rain ratio and snowpack persistence thus portend longer fire seasons (Mote 2006, Mote et al. 2005, Safford et al. 2012b, Westerling et al. 2006).

Liu et al. (2010) projected future changes in "wildfire potential" by modeling the Keetch-Byram Drought Index under a number of different future GCM-based scenarios. Under their projections, fire season will be a couple of months longer for much of the contiguous United States, including the assessment area, by the end of the 21st century. Flannigan et al. (2013) projected that fire season length would increase by more than 20 days for most of the assessment area by 2050, and for all of the assessment area by 2100. Basing their work on 15 GCMs, Yue et al. (2013) projected a median increase of more than 3 weeks in the fire season for the Pacific Northwest, which included most of the assessment area, by the middle of the 21st century.

Fire Suppression

The evolution of many plant species has been greatly influenced by their long-term relationships with fire (Bond and van Wilgen 1996, Keeley et al. 2012, Sugihara et al. 2006). Human-caused changes to natural fire regimes can have significant impacts on the diversity and composition of native plant and animal communities (Hobbs and Huenneke 1992, Mutch 1970). Because of the high ecological and evolutionary importance of frequent fire to assessment area YPMC forests, it has been argued that the **exclusion of fire** from most of the assessment area for the last century is one of the most significant human-caused ecological disturbances currently in play (Barbour et al. 1993, Fites-Kaufman et al. 2007, Sugihara et al. 2006). The scientific and management literature is overflowing with assessments of, and references to, the deleterious effects of fire exclusion on assessment area ecosystems (summaries in Agee 1993; Barbour et al. 1993, 2007; Erman and SNEP Team 1996, Keeley et al. 2012; Sugihara et al. 2006, and others.). These include altered species composition and dominance patterns, increased fuels and forest density, impacts to soils and hydrological cycles and carbon sequestration, loss of important wildlife habitat, increased fire intensity and severity, decreased human safety, threats to infrastructure, and so on.

The exclusion of fire from most of the assessment area for the last century is one of the most significant human-caused ecological disturbances currently in play.

Cermak (2005) provided a detailed consideration of the development of the fire control organization and policies in California. The desire to control fire came largely as a response to the destructive burning practices of early settlers, and also the belief that frequent fires were destroying timber and reducing the capacity of the forest to regenerate. Controversies surrounding the use of “light burning” to reduce forest fuels and protect old growth developed in the 1910s and 1920s, and again in the 1950s, but in both cases proponents of fire exclusion prevailed. In 1910, Region 5 (Pacific Southwest Region) Regional Forester Coert DuBois directed his forest supervisors that fire control was the top management priority in the Forest Service’s Pacific Southwest Region. He followed this with the 1914 publication of *Systematic Fire Protection in the California Forests*, which Cermak (2005) called the “most influential single document in U.S. fire control history.” It set fire control standards (forest fires were to be controlled before they reached 10 ac [4 ha]), and it described the outlines for a formal fire control organization and the processes for coordinated fire planning. In 1919, Region 5 directed forest supervisors to suppress all fires, even on neighboring private land. In 1924, the California Board of Forestry endorsed “fire exclusion” from forest lands as state policy. A policy of overnight fire control was discussed at a national Forest Service meeting in 1935, and emerged as the famous “10 a.m.” rule in May of that year (whereby Forest Service units were expected to have fire starts controlled by 10 a.m. the day after discovery).

Federal land managers were already actively working to extinguish fires when the first forest reserves were established in California at the end of the 19th century, but the lack of training, coordination, planning, and technology meant that their ability to stop large fires was very limited (Cermak 2005). The first trained fire crews were established in the late 1920s, and the adoption of more modern techniques and technologies gradually led to increasing success in fire suppression. Consultation of the California Fire Perimeters database (see footnote 4) shows a strong drop in fire frequency and annual burned area in the 1930s and 1940s. This was helped by a series of wet years in the late 1930s, but by the end of the 1940s a number of innovations had markedly improved firefighting success, including the deployment of tanker trucks and bulldozers, the institution of “hotshot” fire crews and “smokejumpers,” and the expanded use of planes and helicopters in patrols and aerial water drops (Cermak 2005).

Since 1910, 15 fires have exceeded ~20 000 ha (~50,000 ac) in size in the assessment area, but 14 of these have occurred since the late 1970s, and 12 since 1995.

Patterns in fire frequency show remarkable success in fire control through most of the rest of the 20th century (the Forest Service succeeds in extinguishing 98 percent of all ignitions before they reach 300 ac [120 ha;] [Calkin et al. 2005]), but beginning in the 1980s, the area of forest burned began to climb. By the 1990s, 10-year running averages for annual burned area and average fire size were at their highest points since formal recordkeeping began in 1908, and the upward trend continues (Calkin et al. 2005; see figures in Miller et al. 2009b). Since 1910, 15 fires have exceeded ~20 000 ha (~50,000 ac) in size in the assessment area, but 14 of these have occurred since the late 1970s, and 12 since 1995.

Part of the trend in area burned and fire size is due to changed federal fire management policies. In the face of research and management reviews showing the detrimental ecological effects of fire exclusion on Western forest ecosystems (e.g., Biswell 1961, Leopold et al. 1963), the National Park Service began permitting prescribed fires in California in the late 1960s and early 1970s, and allowed some lightning ignitions to burn under prescribed conditions (van Wagtendonk et al 2002). At the same time, Forest Service wilderness areas experimented with management, rather than suppression, of naturally ignited fires (Stephens and Ruth 2005). The Forest Service changed its policy from strict fire control to fire management in 1974, and formally abandoned the 10 a.m. rule in 1978 (Pyne 1982). By limiting direct attack on difficult fires, and taking greater advantage of topography, natural barriers, and weather to “indirectly” control fires, fire management agencies themselves have played a role in the growth of large fires since the late 1970s.

Nonetheless, the evidence is overwhelming that accumulated fuels and changes in forest structure resulting from a century of fire exclusion have led to major ecosystem changes in forest types that experienced frequent, primarily low-severity fires before Euro-American settlement (e.g., Agee 1993; Barbour et al. 1993, 2007; Erman and SNEP Team 1996; Leopold et al. 1963; Parsons and DeBenedetti 1979; Steel et al. 2015; Sugihara et al. 2006; etc). In interaction with climate warming, these forest changes are now resulting in larger and more severe fires throughout the YPMC forest belt, not only in the assessment area but across the southwestern United States (Dillon et al. 2011, Mallek et al. 2013, Miller and Safford 2012, Miller et al. 2009b, Skinner and Chang 1996). In summary, fire suppression is a major disturbance factor in assessment area YPMC forests, both in its direct modification of ecosystem composition, structure, and function, and in its contribution to increased forest fuels amounts and continuity, which are leading to deleterious effects when forest fires escape control. Nearly every other section in this chapter contains additional information pertaining to the negative ecological effects of fire suppression on YPMC forests.

Grazing

American Indian inhabitants of the assessment area did not herd animals, and livestock grazing occurred only after Euro-American settlement. A short summary of the grazing history of YPMC forests is offered here to provide context to current conditions and to the early observations that Euro-Americans made of the assessment area. For additional grazing-related information, see "Grass and forbs" on page 153.

Appreciable livestock grazing began in assessment area YPMC forests after the arrival of Euro-American settlers after 1849. By the 1860s, valley and foothill ranchers were using public lands in the Sierra Nevada on a seasonal basis to graze their herds of cattle (Dasmann 1965, Jackson et al. 1982, Pease 1965). Sheep grazing was also practiced in much of the Sierra Nevada after about 1860 (McKelvey and Johnston 1992). The herding habits, huge numbers, and more general diet of sheep caused major effects on Sierra Nevada ecosystems, especially riparian areas and meadows, and probably affected fire regimes as well by reducing fine fuels. Leiberg (1902) viewed grazing, especially by sheep, as a "destructive agent to the forest by preventing reforestation." Muir (1894) referred to sheep as "hoofed locusts." Sudworth (1900) militated for stricter control of sheep grazing. Conflicts developed between cattle ranchers and shepherds; and public concern with the effects of grazing, particularly by sheep, was one of the factors leading to the designation of the forest reserves in the 1890s and early 1900s. Shepherds and cattlemen also often set fire to the forest in the late summer or fall to clear the forest understory and ostensibly to improve forage; in some cases these fires caused major damage to YPMC and red fir forests, mostly where previous logging had increased surface fuel loads (Cermak 2005, Greeley 1907, Jackson et al. 1982, Leiberg 1902, Sudworth 1900).

Vankat and Major (1978) noted that livestock grazing, especially by sheep, had affected most of Sequoia National Park. However, their references to specific records of overgrazing refer almost exclusively to montane meadows and high-elevation forests, and they do not list grazing as a major change agent for YPMC forests. Sheep grazing in the park ceased in the early 20th century, so there has been nearly a century for park ecosystems to recover.

Brewer's memoirs from 1861 to 1864 (Brewer 1930) referred to the scarcity of good grass cover in the Sierra Nevada, and lush areas of grass were highlighted where they occurred. Brewer's team traveled on horseback, so they were reliant on the availability of forage. Brewer's time in the Sierra Nevada predated heavy cattle or sheep grazing, although he mentioned grazing in his memoirs. Sudworth's team also relied on pasturage, and Sudworth (1900) noted that unfenced forest land supported very "short forage" and expressed the opinion that sheep grazing had decimated herbaceous and grass cover in much of the central and southern Sierra Nevada, basing his statement on the "study of long-protected forest land in the same region" and conversations with older settlers. Most of Sudworth's unpublished notes refer to higher elevation locations, however, not mixed conifer. Leiberg (1902) also primarily referred to higher elevations (red fir, principally) when discussing the deleterious effects of grazing.

The period between 1894 and 1904 was extremely dry across southern California (but not as catastrophically dry in northern California, except between 1897 and 1899) (USDI 1951); most of the oft-cited observations of deleterious impacts of heavy grazing on Sierra Nevada ecosystems are from this period (e.g., those cited in McKelvey and Johnston 1992). Note also that the years in which Sudworth (1900) and Leiberg (1902) conducted their field studies coincided with the third longest recorded period of profound drought in California (as measured by the Palmer Drought Severity Index—PDSI), which included the 2nd driest year on record (1898), and the 3rd driest 2-year span (1898–1899) (NOAA National Climate Center data for 1895 to 2015: https://www.ncdc.noaa.gov/cdo-web/search?datasetid=GHCND). The extreme dryness of the soil and depleted herbaceous cover noted by observers during this period was ascribed by many of them entirely to sheep grazing, but the extreme climatic conditions certainly played a major role. Old settler's memories were of times before significant sheep grazing but also of much more abundant rainfall.

Whatever the case, heavy grazing in much of the assessment area clearly reduced understory cover and affected soil in parts of the assessment area for many decades. It probably also reduced fire frequency in some parts of assessment area YPMC forests by reducing the amount of fine fuel. Swetnam and Baisan (2003) noted that many Sierra Nevada fire histories show a virtual absence of fire after the 1850s, which they attributed to the introduction of large herds of sheep into the range after the 1859–1860 drought. A soon to be published fire history study from the southern Modoc Plateau (Adin Pass area) shows a very early cessation of fires that coincides closely with the introduction of cattle to the study area, and other studies showing very low local FRIs (<8 years) also suggest that herbaceous fine fuels would have been necessary to support such high fire frequencies (see footnote 8). These studies are in northern and northeastern assessment area forests dominated by ponderosa pine, and may follow the model suggested for the Southwestern United

States (Arizona and New Mexico) by Swetnam and Betancourt (1998), where fire regimes in ponderosa pine forest were hypothesized to respond strongly to herbaceous fuel production, while fire regimes in mixed-conifer forests were suggested to be driven primarily by woody fuels. Note, however, that the general lack of summer precipitation in the assessment area results in much less grass cover on average than in yellow pine forests in the Southwestern United States, which receives much summertime rainfall; see "Forest understory and nonforest vegetation" on page 146.

Given that most heavy (especially sheep) grazing ceased before World War I, one question is to what extent the effects of this disturbance have lasted over the ensuing century. Grasses are extremely resilient to disturbance, and their seeds are very easily dispersed. A further issue is that the institution of fire suppression and the cessation of heavy grazing happened at about the same time. This complicates our ability to discern the independent effects of the two disturbances. It also means that forests were densifying (and reducing understory light availability) just as understory plant communities were being freed from decades of heavy pasturage. This probably stalled understory recovery and possibly led to different patterns of succession than would have occurred had fire not been suppressed.

Insects and Disease[9]

Background information—

Table 5 lists major insects and diseases found in tree species of assessment-area YPMC forests. A more complete listing and description of injurious insects and diseases can be found at http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_046410.pdf.

Noteworthy increases in ponderosa pine, Jeffrey pine, and sugar pine mortality in the Sierra Nevada range can usually be attributed to moisture stress, high tree density, and elevated bark beetle activity (Young et al. 2017). The primary bark beetles associated with ponderosa pine mortality are western pine beetle (*Dendroctonus brevicomis*) and mountain pine beetle (*Dendroctonus ponderosae*). Mountain pine beetle also kills sugar pine. Jeffrey pine beetle is the primary killer of Jeffrey pine. Dwarf mistletoe (*Arceuthobium* M. Bieb.) and *Heterobasidion* root disease cause additional stress on host trees; the spread of *Heterobasidion* is abetted by logging when cut stump faces are not treated with borax (Slaughter and Rizzo 1999). Black stain root disease is scattered throughout the northern Sierra Nevada range and can be found in ponderosa and Jeffrey pine. White pine blister rust has been devastating to sugar pine since the disease entered northern California around 1930.

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[9] "Insects and Disease" text primarily by Sheri Smith, USDA, Forest Service, Pacific Southwest Region regional entomologist, Lassen National Forest, 2550 Riverside Drive, Susanville, CA 96130.

Table 5—Major insects and diseases found in tree species of assessment-area yellow pine and mixed-conifer forests[a]

	Host tree [b]							
Agent	**Pp**	**Pj**	**Pl**	**Ac**	**Cd**	**Pm**	**Qk**	**Sg**
Heterobasidion root disease, *Heterobasidion* spp.	x	x	x	x	x	x		x
Black stain root disease, *Leptographium wageneri*	x	x	x			x		
Armillaria root disease, *Armillaria* spp.	x	x	x	x	x	x	x	x
Dwarf mistletoe, *Arceuthobium* spp.	x	x	x	x		x		
White pine blister rust, *Cronartium ribicola*			x					
Western pine beetle, *Dendroctonus brevicomis*	x							
Jeffrey pine beetle, *Dendroctonus jeffreyi*		x						
Mountain pine beetle, *Dendroctonus ponderosae*	x		x					
Fir engraver beetle, *Scolytus ventralis*				x				
Douglas-fir beetle, *Dendroctonus pseudotsugae*						x		
Douglas-fir tussock moth, *Orgyia pseudotsugata*				x				
Flatheaded fir borer, *Melanophila drummondi*				x		x		

[a] Table courtesy of Sherri Smith, USDA Forest Service Pacific Southwest Region regional entomologist.

[b] Host species and codes: Pp = ponderosa pine, *Pinus ponderosa*; Pj = Jeffrey pine, *P. jeffreyi*; Pl = sugar pine, *P. lambertiana*; AC = white fir, *Abies concolor*; Cd = incense cedar, *Calocedrus decurrens*; Pm = Douglas-fir, *Pseudotsuga menziesii*; Qk = California black oak, *Quercus kelloggii*; Sg = giant sequoia, *Sequoiadendron giganteum*.

White fir mortality throughout the Sierra Nevada is typically attributed to fir engraver beetle, moisture stress, and *Heterobasidion* root disease. High tree density and true fir dwarf mistletoe (*Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens) also contribute toward decline in some areas. Douglas-fir tussock moth readily defoliates white fir in the Sierra Nevada. Population cycles trend upward every 7 to 10 years, and significant levels of tree mortality have been recorded during past outbreaks.

Insects rarely kill incense cedar. Bark beetles that attack incense cedar are not considered aggressive tree killers; however, when combined with drought stress, they can cause mortality. During drought periods in some areas of the Sierra Nevada range, small incense cedars are the first trees to decline and die. *Heterobasidion* root disease and true mistletoe also weaken incense cedar.

Douglas-fir in the Sierra Nevada can be heavily affected by insects or diseases typical of more northerly latitudes, but their incidence in the Sierra Nevada is reduced. However, Douglas-fir beetle, flatheaded fir borer, and black stain root disease can be found in some Douglas-fir stands. Both insects are capable of killing trees, particularly drought-stressed ones. The detected incidence of black stain root disease in Douglas-fir in the Sierra Nevada is low.

Several insects and diseases can be found on native oaks. Typically the extent or severity of their effects are not widespread or protracted. Foliar injury can result from a variety of diseases, insects, and mites. Wood-boring beetles are usually restricted to dead or dying branches, although the recent emergence of gold spotted oak borer in southern California is a worrying sign, as it readily kills adult black oak, canyon live oak, and coast live oak. Damage by these agents is normally secondary in nature, rather than the primary cause of branch or tree decline. *Armillaria* root disease and true mistletoe can commonly be found on oaks.

Uprooting and stem breakage of giant sequoia is not uncommon and can be a problem along roads and in recreation areas. *Heterobasidion* root disease is sometimes found infecting the roots of fallen trees. Tree killing of giant sequoias by insects or diseases is rare.

***NRV and comparison to current*—**We have little information on insect or disease occurrence in presettlement YPMC forests in the assessment area. Based on insect and forest ecology, however, some inferences can be made about probable changes over time. Fettig (2012) provided a list of the bark beetle species that cause "significant" mortality in the assessment area. Within YPMC forests, most research has been done on the beetles affecting yellow pine species, especially beetles from the genus *Dendroctonus*, as they can have major impacts on mortality rates in commercially important stands of trees.

It has been understood for some time that tree stand densities have a strong relationship to bark beetle-induced mortality. Higher density stands increase competition for resources (especially water and light) and reduce tree vigor, which makes individual trees less able to withstand insect attack. Various studies demonstrate that lower density YPMC stands are much less susceptible to bark beetle attack and subsequent mortality (Fettig et al. 2007, Young et al. 2017).

In the current absence of frequent understory fire, bark beetles have become one of the principal agents of tree mortality in the assessment area (Fettig 2012, Manley et al. 2000). Under reference conditions, frequent fire would have interacted with insects and disease, as well as abiotic and biotic site conditions, to drive stand structure (Bonnicksen and Stone 1982, North et al. 2012b). Much more open and heterogeneous forest structure resulted, and—based on the strongly inverse stand density versus bark beetle relationship—we can infer that bark beetle-caused mortality was probably lower than under current conditions.

Evidence from comparisons between contemporary forests in the assessment area and reference sites in Baja California support this inference. The Lake Tahoe Watershed Assessment compared modern disease and insect incidence in old-growth forest versus mid-seral forests in the Lake Tahoe basin and also versus old-growth forests in the SSPM (Manley et al. 2000). Mid-seral forests in the Lake Tahoe basin generally supported more mortality (29 percent mortality), more pest incidence, and more dwarf mistletoe infestation than old-growth stands (21 percent mortality; note that these values are overall standing mortality and not annual mortality rates). Assessment was made after a 5-year drought (1987 to 1992), and compared to conditions in the SSPM, which experienced similar levels of drought. Overall mortality in the SSPM, which was not logged and has seen frequent fire throughout most of the 20th century, was only 12 percent. Savage (1997) assessed mortality in the SSPM versus mortality in YPMC forests in the Transverse Ranges of southern California. In her stands, she found only 4 percent mortality in the SSPM forests versus 14 percent in the southern California sites. Her interpretation was that low densities of trees in the Mexican sites (kept low by recurrent fire) reduced soil moisture competition and thus tree stress. Stephens and Gill (2005) measured mortality before and after a major drought, and found that cumulative mortality in Jeffrey pine/mixed-conifer forests in the SSPM ranged from 2.7 to 3.6 percent. It is unclear why there is such a discrepancy between the Savage (1997) and Stephens and Gill (2005) mortality measures and the Manley et al. (2000) number. Manley et al. (2000) concluded that fire continues to be responsible for most stand thinning in the SSPM, but insects have replaced fire as the major thinning agent in the Lake Tahoe basin.

One assessment area insect species for which presettlement outbreak dynamics have been documented is the pandora moth (*Coloradia pandora*), which is a defoliator of yellow pines in and around areas with very loose, usually pumice-based soils (which are required for pupation); such soils occur frequently in the northern and eastern portions of the assessment area. The pandora moth is generally not a mortality agent, but serious defoliation can result in significantly slowed growth among affected trees. Data are not from the assessment area itself, but rather from central Oregon in ponderosa pine forests. Pohl et al. (2006) identified six major outbreaks between 1800 and 2000 (mostly at 40- to 50-year intervals) and demonstrated a strong correlation between outbreaks and the occurrence of drought, which weaken trees' resistance and increases susceptibility to herbivory. It seems likely that similar drought-driven dynamics also characterize pandora moth outbreaks in the east side of the assessment area.

Most recently, as a result of the interactions of high stand densities with 4 years of below-average precipitation and the warming climate, YPMC stands in the southern Sierra Nevada have begun to exhibit very high levels of beetle mortality, both in terms of local intensity as well as the geographic extent. Ponderosa pine, sugar pine, and white fir are being the hardest hit, but direct drought-driven mortality is beginning to be evident in species like incense cedar as well. Some smaller watersheds in the southern Sierra Nevada have seen >75 percent of their ponderosa pine die over the past few years. As this mortality wave moves northward, large areas of YPMC forest are being left in conditions that have no precedent in the historical (i.e., since 1850) record.

As a result of the interactions of high stand densities with 4 years of below-average precipitation and the warming climate, YPMC stands in the southern Sierra Nevada have begun to exhibit very high levels of beetle mortality, both in terms of local intensity as well as the geographic extent.

Future—Fettig (2012) noted that climate warming may benefit bark beetles in multiple ways. For example, warming may allow extra generations to complete their life cycles each year, and adult beetle emergence and flight could occur in the season and continue further into the fall. Under warming temperatures, cold-induced mortality during the winter may also decrease. Bentz et al. (2010) maintained that future thermal regimes, assuming continued warming, will be very favorable for many bark beetle species. Mountain pine beetles are likely to become especially damaging to higher elevation conifer forests. Huge warming and drought-driven beetle outbreaks have recently occurred in the United States and Canadian Rockies, and such events may become more common in the future. Bark beetles currently restricted to the southwestern-most United States or Mexico will also likely move northward as climates warm.

Kliejunas (2011) carried out a risk assessment of the likelihood that current and projected future climate change trends would lead to increased adverse effects by eight pathogens on Western U.S. forests. Kliejunas (2011) estimated risk potential as the likelihood of increased disease damage multiplied by the potential consequences (which included both ecological and economic components) of increased disease damage. High to very high risk potentials were identified for dwarf mistletoe and *Armillaria* root disease under both drier and wetter future climate projections; both pathogens affect numerous conifer species in the assessment area. A moderate risk potential was identified for white pine blister rust (which affects sugar pine and western white pine) under both precipitation scenarios. Swiss needle cast (which affects Douglas-fir) and *Dothistroma* needle blight (which affects pines and Douglas-fir) were assigned moderate risk potentials under wetter future conditions, but low potential under drier future conditions.

Logging

Although American Indians used trees for a variety of purposes, large-scale timber harvest did not begin in the assessment area until after Euro-American settlement. Like grazing, a short summary of the history of Euro-American logging in the assessment area is provided here in order to provide some context to current conditions, and to the observations of forest conditions that were made by Euro-Americans in the late 19th and early 20th centuries.

McKelvey and Johnston (1992) summarized the logging history of the Sierra Nevada up to about 1900. Most logging before the turn of the 19th century was done to support mining and the communities that arose to support mining. Timber was cut to build homes and commercial buildings, tunnels, mine and ore processing infrastructure, and railroad lines, and it was the fuel for heating, railroad engines and other machines, and the various types of mills used for processing ore; in some areas, a very valuable market in sugar pine shakes (for roofing or siding) also arose (McKelvey and Johnston 1992). The great majority of timber harvest both before and after 1900 occurred in yellow pine and mixed-conifer forest.

According to McKelvey and Johnston (1992), most 19th-century logging occurred on private lands near the mines and communities, at elevations below the eventual national forests. Exceptions to this rule included the canyon of the South Fork American River, the Yuba River watershed, the Tahoe National Forest (which supported a high density of mines even at higher elevations and was crossed by the transcontinental rail line) (Jackson et al. 1982), and the basin of the Truckee River including Lake Tahoe. Where cutting did extend into what would become national forest lands, it was often selective rather than general, and focused on the most valuable trees, usually sugar pine and yellow pine (Leiberg 1902, Sudworth 1900), although less valuable species might be cut for fuel for steam engines or smelting (see footnote 3).

Between the 1890s and 1920s, railroad lines were extended throughout the lower and middle elevation Sierra Nevada to allow access to timber resources that were beyond reach of animal-drawn transport. More than 80 private railroad logging companies existed at one time (Beesley 1996). Use of railroads for transport allowed for much more generalized and intensive logging to take place, and the northern assessment area was particularly affected, as well as areas of the Truckee River basin and Lake Tahoe, the South Yuba River, and the Eldorado and Stanislaus National Forests (Conner 1997, Jackson et al. 1982, Laudenslayer and Darr 1990, TCHS 2016). According to Beesley (1996), by 1934 more than half of the mixed-conifer forest land in the “north-central” Sierra Nevada had experienced some level of harvest, primarily of the more valuable pine species. Private lands were the focus of most of the harvesting, and by the 1940s, almost all the remaining uncut forest land in the Sierra Nevada was found on national forests or national parks.

After World War II, demand for timber from federal lands increased dramatically, and the Forest Service greatly expanded its involvement in the timber industry. As an example, harvest on the Eldorado National Forest expanded from about 3.8 million board feet per year between 1902 and 1940, to 35.1 million board feet during the war, to more than 56 million board feet per year between the end of the war and 1959 (Beesley 1996). Before the war, Forest Service lands provided about 5 percent of the nation’s supply of lumber. By the end of the war the total had risen to 10 percent, and by 1970 Forest Service lumber supplied almost one-third of the U.S. need (Beesley 1996). In the Sierra Nevada, the period of the heaviest timber harvest occurred in the 1950s and 1960s. Harvest techniques were more generalized than before the war, and large areas of forest were clearcut. Since the 1960s, national legislation, regulations, changing economics, and environmental concerns have acted in concert to greatly reduce the amount of logging on public lands in the Sierra Nevada and elsewhere, although private lands have made up some of the difference. In the end, Barbour et al. (1993) estimated that, "half the original acreage of the mixed-conifer forest has been… cut at least once in the last 150 years."

The effects of logging on forest stand structure have been sufficiently described in the literature and will only be summarized here. Historically, most cutting in the assessment area has been at least partly selective, with the largest and most valuable trees from a handful of species (mostly sugar pine and yellow pine) being targeted. Areas of clearcutting also occurred, mostly between the 1950s and 1970s. In both cases the tree canopy is opened up, increasing light incidence in the understory and often resulting in a pulse of herbaceous and then shrub growth, followed by ingrowth of mostly single-aged tree regeneration (either planted or not). In selectively cut areas, smaller and less valuable trees were retained, usually from fir species or incense cedar, which greatly increased their relative presence in the forest stand. Without further management and in the absence of fire, harvested stands, which may originally have been dominated by fire-tolerant species like sugar pine or yellow pine, mature to much denser stands of more evenly aged individuals of shade-tolerant/fire-intolerant species, sometimes with scattered remnant overstory pines. Most of the shade-intolerant/fire-intolerant tree species are competitively dominant in the absence of recurrent disturbance (Burns and Honkala 1990, USDA FS 2013b) (see "Introduction"). Compared to the original, preharvest forests, these forests tend to be much denser, structurally much more homogeneous, more shaded, and less biodiverse (Agee 1993, Barbour et al. 1993, Fites-Kaufman et al. 2007). Fuel structure in these secondary forests is also highly altered. Fuel continuity is often greatly increased over the preharvest condition in both horizontal and vertical directions. Surface fuels are often increased owing to accumulation of timber harvest "slash," in addition to the accumulation of fuels resulting from fire exclusion. Fir species support low canopy-base heights and often grow under the canopy of overstory dominant trees; should fire occur, fir species are easily ignited from surface fuels and act as "fire ladders" into the canopy of large trees that are otherwise protected by their thick bark or lack of lower branches. Modern timber harvest practices are designed to avoid or even to mitigate many of these negative effects, but many forest stands in the assessment area harvested before the last few decades are highly departed from structural and compositional conditions that characterized presettlement forests.

Without further management and in the absence of fire, harvested stands, which may originally have been dominated by fire-tolerant species like sugar pine or yellow pine, mature to much denser stands of more evenly aged individuals of shade-tolerant/fire-intolerant species, sometimes with scattered remnant overstory pines.

Nutrient Cycling

NRV and comparison to current—

Like most of the semiarid Western United States, tree growth in assessment area ecosystems is primarily limited by water availability rather than by nutrients (Major 1988, Stephenson 1990). However, in some situations and on some substrates significant nutrient limitation may occur, such as on ultramafic (“serpentine”) rock types, or where water availability is sufficient to permit dense vegetation growth. Where nutrient limitation does occur, it is usually for nitrogen (N) or, much less commonly, phosphorus (P). We know of no studies of nutrient dynamics in YPMC forests that have not experienced long-term fire exclusion. Because fire is such an important contributor to decomposition and nutrient flux (Johnson et al. 2009, Wohlgemuth et al. 2006), we focus on studies that (1) have investigated the nutrient dynamics of YPMC forests that have experienced fire, and (2) provide some insight into how fire suppression may have changed nutrient dynamics.

Compared to other temperate and boreal forest types, assessment area YPMC forests support very low rates of litter decomposition (Hart et al. 1992, Stohlgren 1988). This is due to the Mediterranean-type climate of the assessment area and general lack of precipitation during the growing season. Most decomposition occurs in the spring, often under snow, as temperatures begin to warm but soil moisture is still high (Johnson et al. 2009, St. John and Rundel 1976, Stohlgren 1988). Nitrogen and phosphorus are immobilized in needle litter and slowly released. Because of the near absence of precipitation in the growing season, trees in upland YPMC forests do not tend to generate extensive roots in the soil O horizon, and the slow decomposition rates of litter in most of the assessment area mean that nutrients mineralized from the O horizon and not taken up by plants are often leached into runoff waters (Johnson et al. 2009). Spatiotemporal variability in nutrient pools and fluxes is very high in YPMC forests in the assessment area. Spatial and temporal variation in moisture availability (mostly from seasonal snowmelt) is a major driver of nutrient dynamics, but fire is an even greater source of variability in some types of nutrient flux. Johnson et al. (2009) noted that fire exclusion has allowed large increases in the depth of the O horizon and subsequent buildups in N and P, which are released to stream waters by overland flow during rain events and may be significant contributors to the deterioration of Lake Tahoe water quality.

St. John and Rundel (1976) studied the effects of fire on nutrient dynamics in a giant sequoia/mixed-conifer forest. Phosphorus, cations (calcium [Ca], potassium, and magnesium), and pH levels were all higher in burned plots, while nitrogen and carbon (C), as well as cation exchange capacity (CEC), all decreased in burned plots. St. John and Rundel (1976) noted that although the cations were made available for plant uptake by fire, they were also susceptible to loss by runoff unless they were taken up by plants or held in exchange sites, which are in low supply after fire owing to the loss of much of the prefire organic layer and needle litter. The loss of N to volatilization could potentially also be balanced over time by any increase in N fixation promoted by fire, such as the postfire succession of N-fixing shrubs (e.g., *Ceanothus* spp.) or herbs (legumes) (Wohlgemuth et al. 2006).

Other studies have found similar results. For example, Chorover et al. (1994) studied soil solution chemistry before and after prescribed fire in YPMC forests in Sequoia National Park and documented very large increases in cation concentrations in soil water, and a drop in ammonium (a source of N) to below prefire levels within the year after fire; however, nitrate, another important source of N, rose and remained elevated for 3 years (Chorover et al. 1994). Stephens et al. (2004) found that prescribed fires in YPMC forests in the Lake Tahoe basin released Ca and raised pH of both soil and nearby stream water. Oliver et al. (2012) studied the effects of a severe wildfire on stream chemistry in a YPMC forest and found that P, nitrate, and cations (measured with electrical conductivity) were all elevated after fire.

Sobota et al. (2013) recently reported on geographic patterns of anthropogenic N input in the United States. Western portions of the assessment area are affected by atmospheric deposition of N from automobile exhaust and Central Valley use of synthetic fertilizers, especially in the central and southern sections. Central California is highlighted as one of the most heavily affected areas for N input in the entire United States. Maps in Sobota et al. (2013) indicated that the western portions of the southern assessment area are receiving from 5 to 10 times (or more) the annual input of N than they probably received before Euro-American settlement. In terrestrial ecosystems, high levels of N are known to increase invasion and survival of fast-growing annual weeds (Porter et al. 2013), which compete strongly for water, light, and nutrients with native plants, and in some cases have major effects on fire regimes (e.g., cheatgrass [*Bromus tectorum* L.]). High levels of N input can also have major effects on tree ecology, including stimulation of growth, changed root:shoot ratios, induced nutrient deficiencies or imbalances, and reduced drought tolerance (Bytnerowicz and Fenn 1996). Gaseous N can also act as a pollutant, and various forms of toxic and acidifying N compounds are formed with oxygen. Effects of N deposition on YPMC forests in the assessment area are not as extreme as in southern California. In both places, most N arrives as dry deposition, and the summer drought and limited dry season stomatal conductance mean that plant utilization of gaseous N is more limited than in more humid regions (Bytnerowicz and Fenn 1996).

Future—

Current trends in the assessment area are for continued suppression of most fires, with escaped fires becoming larger and more severe over time. This is a fundamentally different situation than what characterized presettlement YPMC forests, where fires were frequent and largely of lower severity and intensity. It is very difficult to generalize about how these trends may affect nutrient cycling in assessment area YPMC forests. One of the most significant outcomes of continued fire suppression is likely to be the enhancement of the nutrient pool in the forest litter layer and its episodic release by severe fires. Further enhancement of nutrients will continue to be carried by wind in the form of nutrient deposition (mostly N) from human sources to the west. Higher levels of soil N will likely abet further invasion by annual invasive weeds and subsequent changes in forest understories and fire regimes.

Miesel et al. (2009) conducted an interesting study in which they compared belowground soil and microbial variables in forest stands mechanically treated to favor ponderosa pine versus stands treated to favor large trees regardless of species. They found notable differences between the two treatment strategies, especially in soil organic C content and N availability, and pH. This work suggests that future soil nutrient status may depend to some degree on the tree species favored in forest management.

Successional Processes

Surprisingly little empirical and quantitative documentation of successional patterns in YPMC forests in the assessment area has been published. Nonetheless, early observers of YPMC forests in the assessment area were already well acquainted with the different ecological tolerances and successional tendencies of the major tree species. For example, Sudworth (1900), Leiberg (1902), and Greeley (1907) all referred to the strong potential within YPMC forest for dense seedling recruitment of the shade-tolerant/fire-intolerant species in the absence of fire (see chapter 1). The species differences referred to in tables 1 and 2, and figures 3 and 4 interact with the environment and ecological disturbances to drive successional processes in YPMC forests.

Leiberg (1902) stated that the relative proportion of tree species in assessment area YPMC forests was changing because of timber harvest and fire. In general, he noted that the relative proportions of sugar pine and yellow pine were decreasing, as recruitment of young trees was not keeping up with their removal from the overstory by logging (one exception was the northern part of his central survey area). At the same time, he described “a uniform increase” in the proportions of incense cedar and white fir across the survey area. Overall, the YPMC forests that Leiberg surveyed had low densities of tree seedlings and saplings, owing to the effects of frequent fire. However, he noted that stands of YPMC forest that had escaped fire for 12 to 15 years were often filled with stands of saplings "so dense that a man can with difficulty force his way through" (Leiberg 1902: 43). Sudworth (1900) also noted that, "The frequent open spaces in yellow pine forests are sooner or later covered with dense patches of young trees, but these thickets may in turn be swept off by fire." Show and Kotok (1924) made the same point, namely that fire protection in the pine belt in the Sierra Nevada had resulted in "an enormous number of young forest trees that have appeared as individuals and in groups, or, in the more open virgin stand, as a veritable blanket under the mature timber."

The rate of forest infilling in the absence of fire varies along environmental gradients. For example, studies in assessment area YPMC forests have found that seedling recruitment, survival, and growth are inversely related to elevation (Hunter and Van Doren 1982, van Mantgem et al. 2006), and topographic exposure and insolation are also major drivers of seedling survival and growth rates (Kolb and Robberecht 1996, Maguire 1955). Local soil conditions and topographic- and vegetation-defined (e.g., nurse plants) microhabitats can also play a major role in seedling survival, young tree growth, and rates of forest succession and densification in the absence of frequent disturbance (Gomez et al. 2002, Tappeiner and Helms 1971). In the assessment area, dense shrub cover can have a major effect on future forest composition as well, as shade-tolerant trees (e.g., white fir) are more likely to survive the decades it may take to overtop the shrub canopy (assuming that fire can be kept out of the stand, in which case succession will be reset) (Stark 1965). Another major driver of seedling density and forest infilling is temporal coincidence between large seed crops and years with favorable climate (high precipitation, occurrence of summer thundershowers, low summer temperatures, etc.) (Burns and Honkala 1990).

Bonnicksen and Stone (1982) provided a summary of successional dynamics in moist mixed-conifer forest (including giant sequoia). Bonnicksen and Stone (1982) popularized the notion of the "shifting mosaic" of successional stages on the landscape, where neighboring sites of the same ecological "potential" could be in dissimilar vegetation states owing to different spatiotemporal processes and their rates. They stressed that the nature and rate of different successional pathways depended on abiotic and biotic conditions of the site in question. That said, a generally recognized truism is that white fir is the competitive dominant in most YPMC forests in the assessment area, and the long-term absence of fire will ultimately lead to white fir forests (or Douglas-fir at lower elevations in the north assessment area). Fires in the presettlement period were frequent and mostly of low severity, but some aggregations of mature trees would nonetheless be periodically killed by fire, while others were left untouched, and in yet others the understory vegetation and tree regeneration would be consumed by the passage of fire. Such patches of high-severity fire would often be succeeded by dense areas of fire-promoted shrubs, and return to forest in such areas might take many decades (Show and Kotok 1924). Although fire was frequent, there were always tree clumps that had escaped fire for several FRIs, and thickets of shade-tolerant species (white fir, incense cedar) would often develop in these places. Regeneration of species like giant sequoia and the yellow pine requires mineral soil and canopy gaps large enough to bring sunlight to the forest floor (Burns and Honkala 1990, Meyer and Safford 2011). Recruitment of these species thus required fire intense enough to kill clumps of canopy trees; sugar pine tends to favor smaller gaps (Burns and Honkala 1990, Oliver and Dolph 1992). Note that Bonnicksen and Stone's (1982) ideas were applicable to patchiness at a very fine scale (they explicitly state that they are referring to patches between 0.0135 and 0.16 ha). As is noted in multiple locations throughout this document, coarse-grained patchiness on the order of thousands, hundreds, or even tens of hectares was uncommon in YPMC forests before Euro-American settlement.

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Overall, the general picture is one of very high potential for forest recruitment, especially by shade-tolerant species, with frequent fire or soil conditions maintaining the dominance of the pine (and in some places, giant sequoia) overstory and a more open forest condition (Bonnicksen and Stone 1982; Kilgore and Taylor 1979; Leiberg 1902; North et al. 2002, 2005; Show and Kotok 1924, Sudworth 1900).

Models of YPMC forest successional dynamics—

Kercher and Axelrod (1984) developed a Monte Carlo-based model of YPMC forest succession (SILVA) at the stand level to better understand the effects of fire on forest dynamics in the Sierra Nevada. The SILVA model is complex, and includes more than 30 subroutines that model such phenomena as species-specific demographic rates (recruitment, growth, death, injury, etc.), stand structures, fire, and brush and litter dynamics. Fire effects on trees were estimated as a function of scorch height and tree diameter, but weather inputs were mostly held constant, so the simulated fire regime was relatively crude (Agee 2000). Kercher and Axelrod (1984) used SILVA to compare forest succession after a simulated clearcut for 500 years at two different elevations, 1520 m (5,000 ft) and 1830 m (6,000 ft). The lower elevation site is at the upper reaches of YPMC forests historically dominated by ponderosa pine; the upper site is nearer the upper limits of YPMC forests in the Sierra Nevada and historically included a significant component of fir species.

The time-averaged results of Kercher and Axelrod's (1984) lower elevation simulation are shown in figure 11. Figure 12 shows the successional progression of the lower elevation YPMC stand through the 500 years of the SILVA simulations.

Fire was modeled as a stochastic process with a mean return interval of 7 years. Ponderosa pine and black oak dominate the stand immediately after the initial stand-replacing fire, but black oak becomes subordinate to incense cedar and then white fir by 70 to 100 years and almost completely drops out of the stand by 300 years (fig. 12). After 200 years, overall basal area varies between 50 and 54 m^2/ha, and the relative dominance of species changes but the proportions of shade-intolerant to shade-tolerant species fluctuate around 70:30 until after 400 years, when the proportion of ponderosa drops. Simulations without fire supported much higher basal area of shade-tolerant/fire-intolerant species like white fir and incense cedar. The higher elevation simulation is in the "fir zone" and supported much more white fir than ponderosa pine, even under frequent fire (Kercher and Axelrod 1984).

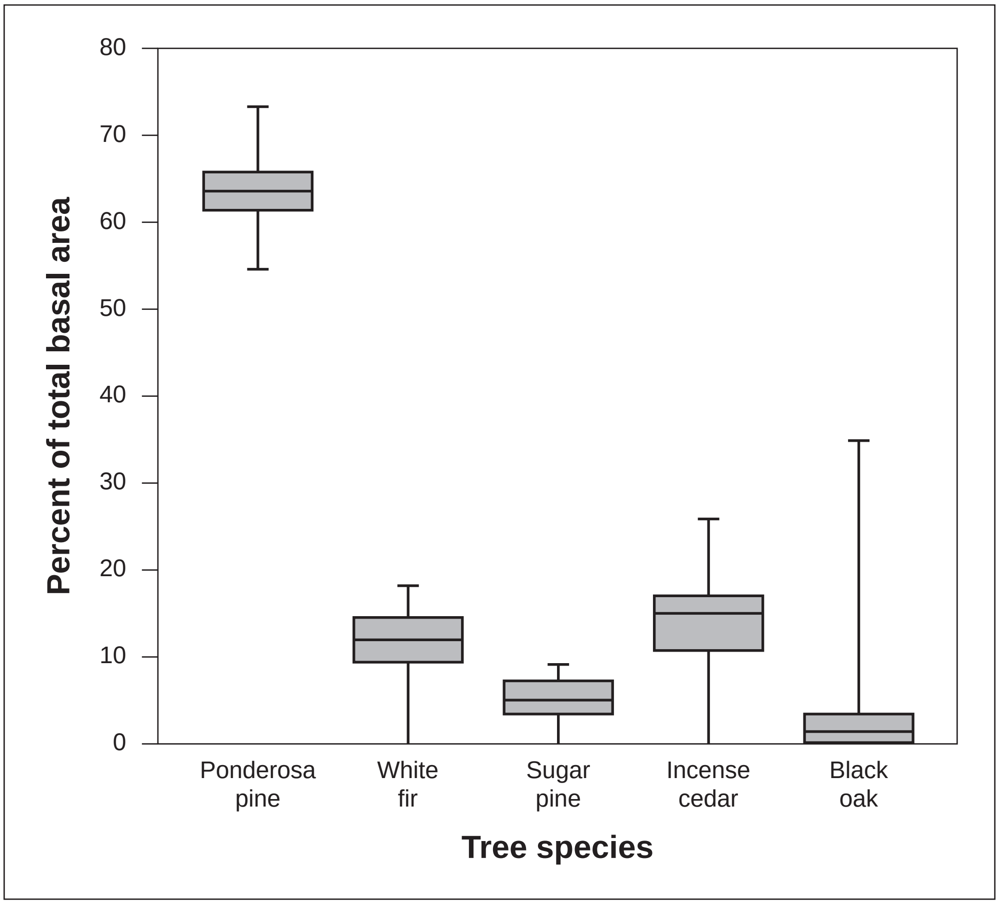

Figure 11—Box plots of upper and lower quartiles for basal area of five tree species modeled by Kercher and Axelrod (1984) for a yellow pine–mixed-conifer forest at 1524 m elevation with a mean fire return interval of 7 years. Values are from temporal distributions of basal areas as predicted by the SILVA forest succession model, averaged over 10 runs of 500 years. Horizontal lines within quartile boxes represent the median; the "error bars" represent upper and lower ranges for each species. Douglas-fir was also modeled but accounted for only about 1 percent of the basal area. Illustration adapted from figure 6 in Kercher and Axelrod (1984).

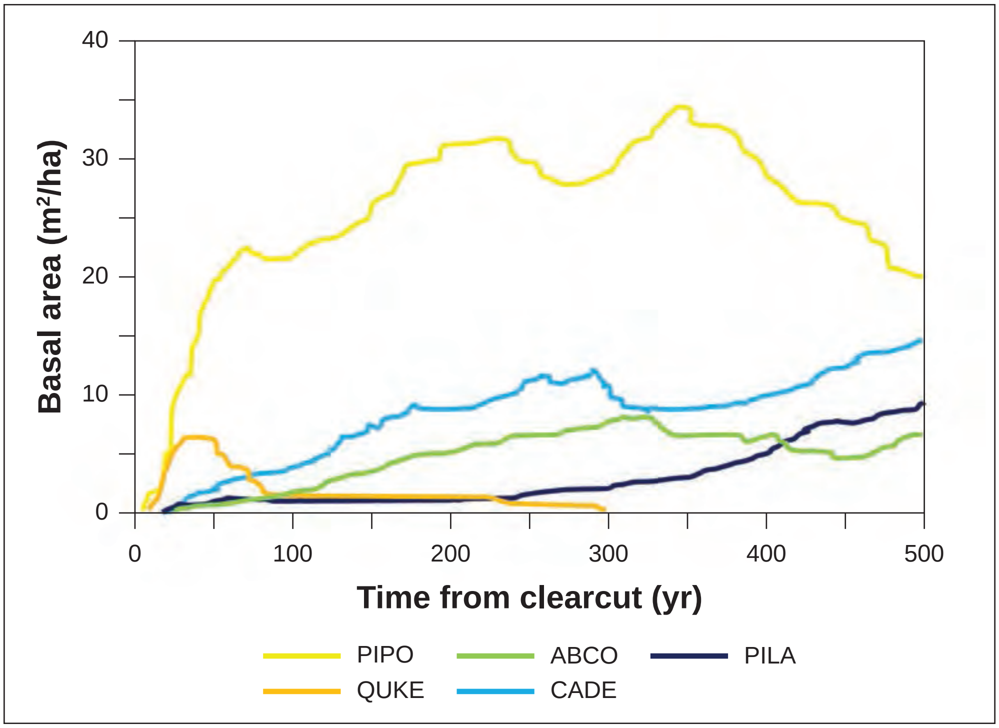

Figure 12— Composite of SILVA simulation results for five tree species in a yellow pine–mixed-conifer forest at 1524 m elevation, under a mean fire-return interval of 7 years. Douglas-fir was also simulated but accounted for very little of the basal area. Data are from Kercher and Axelrod (1984).

Van Wagtendonk (1984) carried out simulation modeling of YPMC forest succession using an improved version of the FYRCYCL stand-level forest dynamics model. The model included subroutines on vegetation, fuels, fire, weather, and lightning ignitions. Historical fire weather was used to drive the fire regime, and fires could be of any intensity. Van Wagtendonk (1984) carried out 200-year simulations under three management conditions: no fire, natural lightning ignition regime, and fire suppression (which permitted fires to burn under certain extreme conditions). Starting conditions were a seedling patch of 40 percent (by basal area) ponderosa pine, 25 percent sugar pine, 20 percent white fir, and 15 percent incense cedar. Under the no-fire scenario, ponderosa pine increased to >55 percent of basal area by 90 years (taking advantage of originally open stand conditions), then began to drop as white fir accrued individuals and basal area; white fir dominated the stand after 150 years. Under the lightning-ignition scenario, fires occurred on average every 8.9 years (the first fire occurred at 34 years) and ponderosa pine comprised more than 90 percent of stand basal area by the end of the simulation. Sugar pine was the most important codominant species in this scenario, but by the end of the simulation it was less than 8 percent of the stand as reckoned by either basal area or density. Stand densities varied widely in the lightning-ignition scenario, depending on fire frequency and intensity (van Wagtendonk 1984). Under the fire-suppression scenario (basically a modern business-as-usual scenario), two moderate- to high-severity fires occurred, reducing white fir density much more than basal area (as some white fir had reached sufficient size to survive intense fire), and resulting in a system dominated by a fluctuating balance of ponderosa pine and white fir (but with ponderosa pine always dominant in terms of basal area). Sugar pine and incense cedar were only minor players in all three scenarios.

Keane et al. (1990) developed the FIRESUM successional process model as an upgrade to SILVA and applied it to understanding successional dynamics in ponderosa pine/Douglas-fir forests in the inland Northwest under different fire regimes. Keane et al.'s (1990) study area includes the northern tip of the assessment area, and four of the forest types ("fire groups") modeled by FIRESUM either occur in assessment-area YPMC forests or are similar (warm, dry ponderosa pine; grand fir [*Abies grandis* is ecologically similar to white fir]; warm, dry Douglas-fir; moist Douglas-fir). In Keane et al. (1990), FIRESUM was used to carry out a 200-year model of successional dynamics in a semiarid ponderosa pine-dominant stand beginning in 1900. The major findings were that Douglas-fir was able to establish in the stand only when FRIs reached 50 years, but ponderosa pine still dominated the site under these conditions, with about 50 percent of the basal area at year 200 (*Larix occidentalis* and Douglas-fir comprised the remainder). Under no fire, Douglas-fir comprised one-third of the total basal area by year 100, and dominated the stand by 130 years; at the end of the simulation, Douglas-fir was about 65 percent of the total basal area (65 m^2/ha). Under the frequent fire scenarios (<50-year FRIs), most basal area was contributed by large trees, but at FRIs of 50 years and above, fuels accumulated and fires were intense, which resulted in stands of small to intermediate trees at high densities.

Miller and Urban (1999a, 1999b) and Urban et al. (2000) described an adaptation of the ZELIG forest gap model for forests along an elevational gradient in Sequoia & Kings Canyon National Parks in the southern Sierra Nevada. In various publications, Miller and Urban and colleagues employed the modified ZELIG model to study climate change scenarios, carbon dynamics, the effects of fire on stand parameters, the importance of the physical habitat and moisture availability, and so on, but they did not publish results on the actual successional dynamics between species within their simulations. We refer to these studies in various other places in this assessment.

All the simulation models referred to above make clear the initial advantage that the yellow pine species have in frequent fire scenarios. Seedlings and saplings of ponderosa pine and Jeffrey pine (and sugar pine) grow rapidly in high light environments (fig. 3), and as young trees they support thicker bark than their competitors (fig. 4). Both adaptations provide for higher survival under recurrent fire. Where fire is not frequent, or overstory cover is high, the yellow pines are ultimately outgrown by shade-tolerant species.

***Future*—**It is unknown how future climates and conditions may affect basic successional processes in assessment-area YPMC forests. If future environmental conditions differentially affect key species in YPMC forest, then successional relationships among species may change. An example is the effect of white pine blister rust on the five-needle pines, which in YPMC forests are represented by sugar pine, and, to a lesser extent, western white pine. Aside from these sorts of effects, it appears likely that warming temperatures and increasing fire activity on some of the landscape, but continued fire exclusion on most of the landscape, will simply accelerate the sorts of successional changes we have already witnessed for the past half century.

Tree Mortality

NRV and comparison to current—

We have little historical information on tree mortality processes or patterns in assessment-area YPMC forests. Peter Decker, an observant miner whose journal from his 1849 to 1851 trip to California has been published (Giffen 1966), noted after 3 years in the Sierra Nevada that “the woods in California seem like the original or first growth. How seldom to be seen a dead tree unless fired.” Greeley (1907) came to a different conclusion, but his viewpoint was certainly colored by his formal silvicultural training. Greeley decried what he saw as “high densities” of dead, broken-topped, and fire-hollowed trees. Greeley’s (1907) estimate was that 1 to 5 percent of the stems in sugar and yellow pine were dead. Because this is a cumulative mortality estimate and snags remain standing for years, the actual annual mortality rates in the forests Greeley visited were probably very low.

Although periodic drought and high interannual variability in precipitation are characteristic of the California climate, assessment-area YPMC forests are generally much denser today than under presettlement conditions. Higher stand densities lead to higher competition for light, nutrients, and water. In the standard scenario, “self-thinning” ensues, in which younger, smaller, or weaker individuals succumb to competition and die, while larger, healthier trees benefit from the release of competition (Barbour et al. 1987, Westoby 1984). Although the mortality rates of smaller trees tend to be higher, recruitment in the small size classes is also higher, and many recent studies documented surprisingly high mortality rates of large trees in YPMC and other forests in and around the assessment area, even before the 4-year drought and subsequent mortality wave (e.g., Dolanc et al. 2013, 2014b; Dolph et al. 1995; Fellows and Goulden 2012; Lutz et al. 2009; Smith et al. 2005; van Mantgem et al. 2009; Walker et al. 2006). Most researchers have concluded that some combination of water stress, stand density, and insect-driven mortality are to blame.

The few data available suggest that background mortality rates (averaged over multiple years) in assessment area forests are between about 0.25 and 1.4 percent for fire-excluded forests and less than 0.5 percent for contemporary reference forests with a largely intact fire regime (Ansley and Battles 1998, Maloney and Rizzo 2002, Stephens and Gill 2005). Modern plantation studies broadly corroborate these numbers, and show large increases in annual mortality between low- and high-density stands. Data in Zhang et al. (2006), for example, give annual mortality rates of between 0 and 0.8 percent in thinned stands of fewer than 332 trees/ha, versus rates of 0.6 to 2.3 percent in stands of more than 2,450 trees/ha.

Van Mantgem et al. (2009) showed that mortality rates in Western U.S. forests have strongly increased over the last four to five decades. Of the three large regions compared—Pacific Northwest, western interior United States, and California (in California all of van Mantgem et al.'s [2009] study sites are located within the bioregional assessment area)—the assessment area experienced the highest mortality rates, and the greatest rate of increase in mortality rates. Averaged over many sites, the rate changed from less than 1 percent in the 1980s to about 1.6 percent in the early 2000s. Furthermore, the greatest rates of increase in mortality were found in species of pine, in (formerly) frequent-fire forests, within the elevation belt occupied by YPMC forests; overall, the highest annual rate of mortality was found in the studied species of pine, which died at an annual rate of about 2 percent during the early 2000s (van Mantgem et al. 2009). Of course, mortality rates, especially among the pines, have skyrocketed since 2014, with tens of millions of dead trees mapped by the Forest Service as a result of the 4-year drought and subsequent beetle outbreak.

Future—

Adams et al. (2009) showed that increases in temperature increased mortality in two-needle pinyon (*Pinus edulis* Engelm.) in the Southwestern United States via carbon starvation. When coupled with drought and other factors, such as insect outbreaks, Adams et al. (2009) concluded that future warming will increase background mortality rates, and also greatly increase the risk of regional die-off events. They called for similar experimental assessments of other tree species. Carnicer et al. (2011) studied tree species responses to increased temperatures in the Iberian Peninsula, which supports a similar Mediterranean climate to much of California. They assessed

16 species, mostly pines and oaks. They found that interactions between drought, temperature, forest density, insects, and disease were resulting in increased defoliation and mortality among the studied species, and they noted that climate change-driven drought pressures on Mediterranean tree species were likely to lead toward increased damage and mortality in the future. Allen et al. (2010) summarized the results of about 150 worldwide studies of tree mortality and concluded that the data were consistent with an increase in mortality resulting from climate warming and drought.

Wind

NRV and comparison to current—

There is little information on the effects of windthrow on YPMC species in the assessment area. YPMC stands were historically relatively open, and species adapted to these conditions must have some resistance to high winds. Larsen and Woodbury (1916) noted that wind was not generally an important disturbance factor in sugar pine stands. According to maps in Peterson (2000), California and neighboring states are subject to fewer major wind events like tornados and convective wind events (“downbursts”) than any other part of the contiguous United States. Very high winds are common when winter storms arrive at the Sierra Nevada crest, but these elevations support red fir and subalpine forests for the most part. It seems unlikely that wind as a disturbance agent has changed significantly between presettlement and current times.

The most famous wind event to hit California was the 1962 Columbus Day storm, which was precipitated by a strong tropical storm entering northern waters and interacting with the jetstream (Lynott and Cramer 1966). Many windspeed records at northern and northwestern California meteorological stations were set by this storm, and gusts above 90 kph (56 mph) were common in the northwestern part of the assessment area (southern Cascades). Huge areas of forest were blown down, with the most damage done outside the assessment area (around 11 billion board feet were blown down in Oregon and Washington) (Lynott and Cramer 1966).

Hillmire et al. (2012) reported on what they termed the most extensive windthrow event on record in the Sierra Nevada sensu stricto. An event with winds exceeding 145 kph (90 mph) occurred in the central Sierra Nevada in the upper San Joaquin River basin in the fall of 2011. Thousands of mature trees were downed, mostly red fir, white fir, and lodgepole pine. In some areas, more than 70 percent of live trees were downed. Large trees were more susceptible to uprooting than small trees, and the effects were relatively evenly distributed across species. Larger snags were also more likely to uproot than small ones (Hillmire et al. 2012). This size-dependent effect has a very different impact on forest structure than fire, which preferentially kills smaller trees.

Future—

Changing weather patterns resulting from climate change may increase windthrow as large-scale pressure systems shift at the continental scale (Peterson 2000). However, in the assessment area, it seems likely that windier conditions would have greater effects on fire effects to forest than directly on the forest itself. For example, Fried et al.'s (2004) model of future fire activity under fire exclusion showed that increased windspeeds during the fire season were an important factor behind the increased number of modeled fire escapes. High winds during the wet season can also influence the outcome of future fires. The 1999 Megram Fire in northwest California burned primarily through a landscape full of wind-thrown trees and broken tops that resulted from a strong wind event a few years earlier. This led to more severe fire effects to the soil in some places and hampered fire control efforts (see footnote 3).

Structure

Forest Landscape Structure

NRV—

Analyzing landscape structure in assessment-area YPMC forests is difficult. Historically YPMC forests were not characterized by large, stand-replacing disturbance events, but rather by highly frequent, low- and moderate-severity events that did not generally leave a coarse-grained pattern on the landscape that could be easily mapped. Even after a century of fire exclusion, an increase in forest density, and the vestiges of logging and increased occurrence of high-severity fire, it can be challenging to conduct the sorts of classic landscape structure assessments that are routinely done in forests of the Eastern United States or northern Europe. Because of that, we urge some caution in interpreting "patchiness" in assessment-area YPMC forests from standard vegetation maps or model outputs that track successional/seral stages.

Historically YPMC forests were not characterized by large, stand-replacing disturbance events, but rather by highly frequent, low- and moderate-severity events that did not generally leave a coarse-grained pattern on the landscape that could be easily mapped.

Although it may have been difficult to find much coarse-grained patchiness in presettlement YPMC forests, gradients of soil depth, moisture, temperature, and insolation combined to drive differences in forest structure between cool and warm aspects, high and low elevations, and upper, middle, and lower slopes (species changes across these gradients are treated in the "Forest composition and species diversity" section under "Composition" below). Such landscape differences in forest structure are still noticeable today (Barbour et al. 2007; Fites 1993; Lydersen and North 2012; North et al. 2002, 2012b). The major driver of this variation is water availability, but it was greatly modified by fire before fire exclusion. See chapter 1 for a summary of the effects of topography on forest structure in the assessment area. In general, areas with higher water availability (north aspects, higher elevations, lower slopes) tend to support higher forest density and cover (and other related variables) than areas with lower water availability (south and west aspects, lower elevations, upper slopes). When exposed to fire, more densely forested areas tend to exhibit a more coarsely grained landscape structure than open forest areas, because fire effects are more severe where fuels are more continuous and fuel loadings higher (Agee 1993, Sugihara et al. 2006).

Soil depth and texture are the long-term products of interactions between topographically driven water availability and vegetation, and both of these variables also play a major role in driving vegetation conditions. Aside from the few truly unproductive soil types (serpentine soils, for example), the major effect of soil on vegetation in assessment-area YPMC forests is its contribution to water availability (see chapter 1). Meyer et al. (2007) found that soil depth had a strong influence on the basal area and canopy cover of YPMC forest at a site in the southern Sierra Nevada, and North et al. (2012b) described soil depth as a major driver of forest structural and compositional heterogeneity at the landscape scale.

Fire is also an important driver of forest landscape structure in assessment-area YPMC forests. When high-severity fire occurs, it normally results in a successional process dominated in its initial stages by montane chaparral, which includes shrub species that germinate in response to fire (van Wagtendonk et al. 2012). The boundaries between forest and chaparral stands are quite abrupt in the first decades after fire, but in the absence of further burning, trees slowly reoccupy these sites. This process can take many decades. If the sites burn again, the process may take centuries, or the chaparral may become a semipermanent feature in the landscape (Nagel and Taylor 2005, Show and Kotok 1924, Skinner and Taylor 2006). The denser forests typically found in areas of higher water availability are more likely to burn at high severity owing to high fuel loadings and fuel continuity (unless fire has been very frequent in the stand over sufficient time to reduce fuels), and owing to the enhanced presence of fire-intolerant species like white fir (Agee 1993, North et al. 2012b, Sugihara et al. 2006). Such environments are therefore more likely to support coarse-grained landscape structures than drier forests supporting higher densities of fire-tolerant species.

The proportion of presettlement landscapes occupied by defined patches of chaparral was certainly variable, but there are few sources of information to base an estimate on. Bonnicksen and Stone (1982) carried out a reconstruction study in a YPMC-giant sequoia forest in Kings Canyon National Park, and estimated that about 19 percent of the study site in the 1890s was occupied by shrub "aggregations" (shrubfields); by 1977, the proportion had dropped to 11 percent. Show and Kotok (1924) reported on the area of national forests in northern California that supported “brushfields” in the early 1920s, which were seral chaparral stands that had resulted from (often human-caused) fires in previously forested areas. Their estimate of 11.1 percent of the landscape on six national forests in the assessment area is slightly higher than the current area of montane and mixed chaparral that occurs on productive forest land on the same national forests (8.6 percent). See table 9 and “Shrubs” in “Forest understory and nonforest vegetation” for more detail.

Franklin and Fites-Kaufman (1996) used contemporary conditions in assessment area national parks (which were not logged) to estimate that a maximum of 55 percent of assessment-area conifer forests would have been in “old-growth” status before Euro-American arrival. It is important to qualify that Franklin and Fites-Kaufman’s (1996) concept of “old growth” was not restricted to areas of high canopy cover, and they explicitly noted that much assessment-area old growth would have been in areas of open canopy.

Models of landscape structure—The interagency LANDFIRE Program developed a nationwide map of potential vegetation representing the distributions of vegetation types as they are hypothesized to have existed prior to Euro-American settlement. The vegetation types are referred to as biophysical settings (BpS), and are linked to state and transition models (see “Fire severity” above for more detail). State and transition models are nonequilibrium, nonlinear models linking defined states (in this case, vegetation seral stages defined by tree size and canopy cover) via pathways that are driven by forces that can transition a site between states (e.g., successional processes, disturbances) (Stringham et al. 2003, Westoby et al. 1989).

Using Van de Water and Safford’s (2011) crosswalk between their presettlement fire regime types and the LANDFIRE BpS types, we determined that BpS models 610270 (Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland), 610280 (Mediterranean California Mesic Mixed Conifer Forest and Woodland), and 610310 (California Montane Jeffrey Pine–Ponderosa Pine Woodland) best represented dry mixed conifer, moist mixed conifer, and yellow pine, respectively (see http://www.landfire.gov for BpS descriptions). One of the outputs of the BpS state and transition models is an average end state for many runs of each model over a 500-year period. The end states are assumed to represent a snapshot of the average landscape condition during presettlement times, with the caveat that the landscape is greater than about 5000 ha.[10] LANDFIRE uses these reference values to compare to current conditions in order to develop a measure of departure (“fire regime condition class,” FRCC). Figure 13 provides the distribution of

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[10] Keane, B. 2009. Personal communication. Research ecologist, USDA, Forest Service, Rocky Mountain Research Station, 5775 W. Broadway Street, Missoula, MT 59808.

reference values for the three models above, portrayed as percentages of the landscape occupied by each of five seral stages: early successional (after severe fire), mid successional (closed canopy and open canopy), and late successional (open and closed canopy). The early-successional stage represents anything not dominated by trees >10 cm diameter at breast height (d.b.h.) (>4 in), and therefore includes areas dominated by herbaceous plants, shrubs, and seedling and saplings. The "open" mid- and late-successional stages include areas of medium and large trees with canopy cover <50 percent (<40 percent in the yellow pine type), the "closed" mid- and late-successional stages include areas of medium and large trees with canopy cover >50 percent (>40 percent in yellow pine).

The LANDFIRE BpS models predict that, under the presettlement fire regime, 15 to 20 percent of the average YPMC landscape would have been in early seral stages (herbs, shrubs, seedlings/saplings) and young forest, about 35 percent in areas dominated by trees between 12.5 and 53 cm d.b.h. (5 to 21 in), and 45 to 50 percent in areas dominated by trees >53 cm d.b.h. (fig. 13). Furthermore, the BpS models predict that most of the landscape was under open forests of less than 50 percent canopy cover ("open" stages), especially in the yellow pine and dry mixed-conifer types (fig. 13). Dense, older stands ("late closed") are predicted to have occupied around 5 percent of the landscape in the yellow pine and dry mixed-conifer types, but around 20 percent of the moist mixed-conifer type.

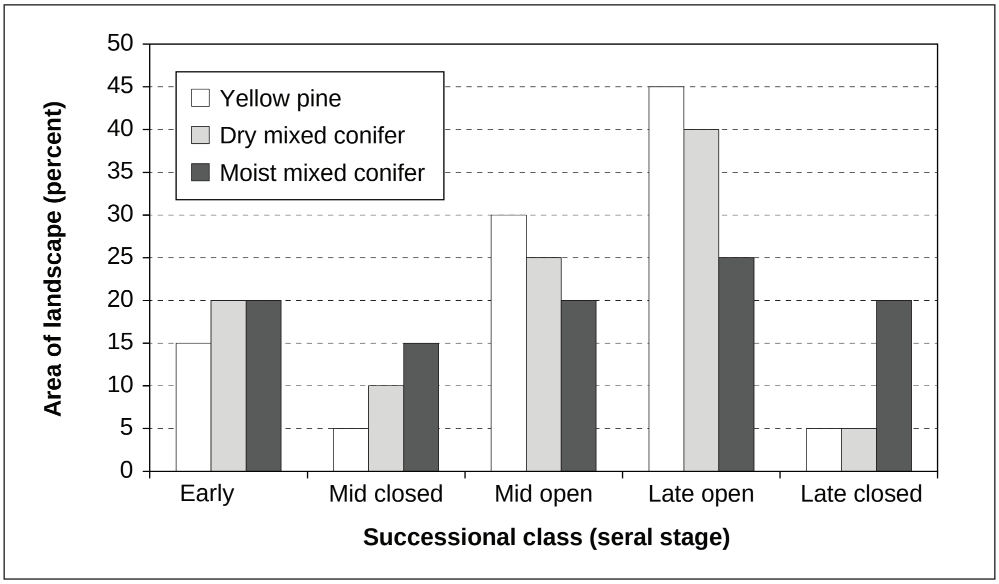

Figure 13—Average landscape conditions for presettlement yellow pine–mixed-conifer forests in the assessment area, as predicted by LANDFIRE BpS state and transition models for LANDFIRE modeling region 6. These are applicable only on landscapes greater than about 5000 ha in area. LANDFIRE BpS reference conditions do not include error bars and are rounded off to the nearest 5 percent by LANDFIRE for ease of use by managers. See text for definitions of successional classes.

The LANDFIRE BpS models are only models, but the BpS outputs are surprisingly close to other, independent estimates of presettlement forest landscape structure in assessment-area YPMC forests. Compare, for example, Franklin and Fites-Kaufman's (1996) estimate of around 55 percent of assessment area conifer forests in "old-growth" status before Euro-American arrival with the 45 to 50 percent of landscape in the BpS late-successional classes (fig. 13). Also, Bonnicksen and Stone's (1982) estimate of about 19 percent chaparral cover in their 1890 landscape is very close to the landscape proportion for early-seral vegetation projected by the BpS model, as is the 15 to 25 percent range in shrub cover found in studies of unlogged (and in some cases periodically burned) YPMC forests in and near the assessment area (see "Shrubs" on page 148). Overall, we urge some caution in applying the LANDFIRE outputs, as they assume that distinct seral stages can be mapped and followed through time. As noted above, this is a tenuous assumption in YPMC forests, which under reference conditions were characterized by fine-grained heterogeneity that does not lend itself well to landscape-level mapping of structure (forest densification and increased occurrence of high-severity fire in modern stands makes seral stage mapping and modeling somewhat more tractable).

***Comparison to current*—**Overall, it can be safely generalized that the landscape structure of current assessment-area YPMC forests is more coarsely grained (characterized by larger, more defined patches) than under presettlement conditions. This is largely due to the interacting effects of timber harvest and fire suppression. Early selective cutting removed the large pine trees from many areas of YPMC forest, and with the long-term absence of fire, natural succession has led to infilling by higher densities of young, mostly fire-intolerant species. More recent clearcutting, mostly on private lands, has increased the representation of coarse-grained and "hard-edged" patchiness in assessment-area YPMC forests. Fire exclusion has greatly increased forest fuel loadings and continuity, and driven a species dominance shift to fire-intolerant trees, which together have led to an increase in the occurrence of large, stand-replacing fires. Like clearcutting, these types of fires also lead to a much coarser-grained, more hard-edged pattern in assessment area forests than was typical before Euro-American settlement. Fry et al. (2014) documented a decrease in spatial complexity in fire-suppressed forests of the Sierra Nevada, compared with forests in the Sierra de San Pedro Mártir in Mexico with a relatively intact frequent fire regime. As noted in the "Fire regime" section above, because of human management over the past 150 years, assessment-area YPMC forests have largely

The landscape structure of current assessment-area YPMC forests is more coarsely grained (characterized by larger, more defined patches) than under presettlement conditions.

transitioned from Fire Regime I, characterized by frequent, low-severity fires and fine-grained heterogeneity in forest and fuels structure, to Fire Regimes III and IV, which are characterized by infrequent fires with a much greater high-severity component and a much coarser grained forest structure. More information on these fire regime and forest structure transformations is found in "Fire regime" above (see especially "High-severity patch size"), and "Forest structure" below (e.g., "Forest gaps and tree clumps").

Many studies and reviews refer to the high structural homogeneity of contemporary YPMC forests (Agee 1993, Barbour et al. 1993, 2007; Erman and SNEP Team 1996, Sugihara et al. 2006), and the return of more heterogeneous landscape structure is currently a major management focus (North 2012, North et al. 2012a, North et al. 2012b). The high homogeneity of fire suppressed YPMC forest landscapes in the assessment area is being increasingly broken up by large, severe wildfires, but most of the assessment area has not experienced fire in the past century (Safford and Van de Water 2014, Steel et al. 2015) (see fig. 13). The coarse-grained landscape structure that results from these fires is also very different from the fine-grained landscape structure that characterized presettlement forests. It is important to underscore that the forest "heterogeneity" referred to by North and colleagues (North et al. 2012a, 2012b; North 2012) is a fine-grained heterogeneity driven by the interactions between high frequencies of mostly low-severity fire and topographically driven variations in water availability.

***Future*—**The few models that have been run not only suggest increased transition of forest to chaparral, but increased transition of chaparral to grassland as well, both trends being driven by increased fire activity (Lenihan et al. 2003a, 2003b, 2008). Cole (2010) studied paleoecological data from earlier periods of rapid climate warming in the Pleistocene and suggested that current and projected future warming trends could be expected to greatly increase the amount of early-seral vegetation on the landscape. McKenzie et al. (2004) noted that, given current and projected trends in climate and fire, the long-term persistence of late-seral forest in much of the Western United States was questionable. Based on projections as well as trends already in play in southern California, it seems likely that—especially at lower elevations—some proportion of the YPMC forest belt will transition to shrubland and grassland over the next century. It also seems likely that forest landscape structure will become gradually more coarse-grained as fire frequency and severity continue to increase, and fire suppression efforts continue to lead to forest densification in the rest of the landscape.

Forest Structure

General forest structure—

***NRV*—**Early Euro-American visitors to assessment-area YPMC forests with interests in vegetation tended to focus on the large size of individual trees, and the generally open nature of the forest canopy. William Brewer was part of the California State Geological Survey of 1860–1864, and traveled across much of the state during that period. Brewer's memoirs (Brewer 1930) contain much reference to vegetation conditions. In general, Brewer was impressed by the large size of the trees in the Sierra Nevada and he noted in multiple places how they dwarfed anything he had been familiar with in the Eastern United States. Where Brewer (1930) refers to forest densities in the conifer belt, he often describes "open" conditions, or conditions of "scattered" trees. For example, his description of the Crane Flat area in current-day Yosemite National Park is of "open forests of enormous trees." Brewer also describes some areas of "dense" forest, however, and the general impression is one of a very heterogeneous forest landscape.

John Fremont's memoirs of his 1843–1844 expedition to California (Fremont and Smucker 1856) refers often to the immense size of conifer trees his group encountered in the Sierra Nevada. He also makes mention of open groves of pines in a number of locations, but does not once refer to forests he encountered as being dense or closed. Indeed, as his group left the San Joaquin Valley southwest of Bakersfield on their return journey to Colorado, he remarks, as they reenter the pine belt, that "we found ourselves again traveling among the old orchard-like places."

Miners' journals occasionally contain interesting and useful information about forest structure in the mid-19th century. Peter Decker's journals from 1849 to 1851 (Giffen 1966) refer periodically to forest conditions. He wrote both of thickets of trees and areas of open or regular spacing. J.G. Bruff's diary entries similarly contain short descriptions of both open and dense forest along the path of his travels, although—unlike other early observers—he described the latter condition more often.

Clarence King worked for Brewer's team on the geological survey, and his memoirs also contain much reference to vegetation conditions (King 1871). Referring to the Sierra-Cascade axis, which stretches from California to British Columbia, King noted the transition from more open and "grove-like" forests in California, where individual trees tended to be larger, to denser forests in Oregon and Washington, where pines ceased to be a major component. King noted that the transition was almost imperceptible from close range, but very clear at the broad scale. King (1871: 28–29) described the YPMC forest above Visalia thusly:

> Passing from the glare of the open country into the dusky forest, one seems to enter a door, and ride into a vast covered hall… You are never tired of gazing down long vistas, where, in stately groups, stand tall shafts of pine… Here and there are wide open spaces around which the trees group themselves in majestic ranks.

John Muir (1894; chapter 8) wrote that nowhere in the Sierra Nevada would one find, either "on the rocky heights (or) down in the leafiest hollows," anything approaching the dense forests found in the Amazon, or the Himalaya, the Black Forest, or the Douglas-fir forests of Oregon. In a classic passage reproduced innumerable times, he noted that:

> The inviting openness of the Sierra woods is one of their most distinguishing characteristics. The trees of all the species stand more or less apart in groves, or in small, irregular groups, enabling one to find a way nearly everywhere, along sunny colonnades and through openings that have a smooth, park-like surface, strewn with brown needles and burs.

In general, both Leiberg (1902) and Sudworth (1900) (see also Stephens 2000, Stephens and Elliott-Fisk 1998) described highly heterogeneous forest structure in the Sierra Nevada. Both surveyors referred qualitatively and quantitatively to the large size (height and diameter) of adult trees. Referring to the "middle timber belt," which occupied elevations between 2,000 and 6,000 ft (600 to 1800 m) and therefore corresponds approximately to the YPMC forest type, Sudworth (1900: 515) wrote: "As a rule the growth is continuous but rather open… there are, however, areas of considerable extent on broad benches where the forest is dense... The trees are usually of large dimensions."

Leiberg (1902: 32), made similar statements about the YPMC forests of the northern Sierra Nevada:

> In the eastern and trans-Sierran districts… the old-growth forests… are generally open on all slopes except the northern and on tracts with much seepage… In the central district, outside the canyon areas, the forest is of moderate density and is rarely what might be called open, except in stands of very old growth. Elsewhere large quantities of white fir and Douglas-fir with oak combine to form thickset stands. On the rocky slopes of canyons and in the great gorges of the rivers the forest is always very open and scattered.

Concerning yellow pine-dominated forests, Sudworth (1900) noted that they were rarely if ever dense, and single big trees or groups of three to six trees often stood far apart, forming a clumped but open stand structure. He observed that younger forests (up to 60 years old), which would establish in the frequent open spaces in the forest, were often very dense, but that successional processes and fire would thin them greatly over time. Incense cedar was a regular associate of ponderosa pine, and was often also in such open stands, although it was also a common riparian tree.

Manson (1906) wrote that the frequent burning in YPMC forests (he expressed the opinion that the American Indians annually burned everything) suppressed seedlings, and as a result the forests were "mainly composed of old trees, many badly burned at the butt." From his wide travels in the Sierra Nevada, he attested that lower and middle-elevation conifer forests of all types were "devoid of middle–aged and young trees… The light fires gave open forests through which one could readily see for great distances."

Greeley (1907) observed that the characteristic structure of YPMC forest was composed of smaller, often even-aged groups, usually with a core of pine. Weaver (1943) gave a very similar description, noting that when considered together these different-aged groups scaled up to an overall uneven-aged forest. Greeley (1907) wrote that:

> …in deep, moist soils… and on the north slopes, one sees bunch after bunch of six or eight mature sugar pines of nearly the same size. Where… seedlings and saplings occur at all they are usually in groups under broken cover or in narrow openings in the stand. On the same sites fir and cedar crowd the sugar pine closely and bunches or large patches of these species occur in among the groups of sugar pine. Yellow pine… seeks the drier and warmer sites… Here it is also commonly found in large even-aged groups, from open bunches of mature trees to dense thickets of saplings and seedlings.

In the tone of a forester, Greeley (1907) expanded on some of the unfortunate aspects of YPMC forests for silvicultural management. One of the chief unfavorable features was the "widespread over-maturity of the timber" (i.e., the general lack of regeneration and small trees), and the "high density" of dead, broken-topped, and fire-hollowed trees. He estimated that that 1 to 5 percent of the stems in sugar and yellow pine were dead, 10 to 25 percent were "decadent" (needed to be cut immediately to realize any timber value), 30 to 40 percent were "mature" (should be cut in 10 to 15 years), and only the remainder was composed of "thrifty" trees that were still vigorously growing and could be the basis for a 30- to 40-year cutting rotation. In fir and incense cedar, the percentage of dead and decadent trees was higher yet, and in many stands, 30 percent of the firs over 61 cm (24 in) d.b.h. were unmerchantable from decay.

According to Greeley (1907), other unfavorable features of the YPMC forest from the standpoint of a forester were the very open and "irregular" nature of the stand and the fundamental role of fire in reducing stand densities, and the very strong successional pressure of the shade-tolerant species, principally white fir, on YPMC forest composition. Regarding the former, Greeley decried the effects of intermittent fires that were common in YPMC forests, especially at lower elevations. These fires removed leaf litter and humus and killed young trees, while "simply scorch(ing) the butts of larger trees." The whole effect reminded him of the pineries of the Southeastern United States. The consequent open canopy resulted in much wasted growing space in YPMC forests. Greeley (1907), like Sudworth (1900) and Leiberg (1902), also described how dense stands of chaparral would arise where fires burned the tree canopy, and how such areas would be lost to tree production without human intervention.

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Areas of shrubs were an important component of YPMC forests, as fire stimulates germination of species of the most important shrub genera (especially *Arctostaphylos* and *Ceanothus*), and the open canopy meant that much light reached the forest floor. Even stands of sugar pine, which we tend to equate today with denser, more productive mixed-conifer stands, were often very open and with considerable underbrush (Knapp et al. 2013, Larsen and Woodbury 1916).

In summary, in comparison to today, early observers described YPMC forests that were generally more open, more heterogeneous, and more dominated by (clumps of) large trees (Agee 1993; Barbour et al. 1993, 2007; Brewer 1930; Greeley 1907; Jepson 1923; King 1871; Laudenslayer and Darr 1990; Leiberg 1902; Muir 1894; North et al. 2012b; Sudworth 1900; Sugihara et al. 2006; Vankat and Major 1978; Weaver 1943).

***Comparison to current*—**The Sierra Nevada Ecosystem Project executive summary (Erman and SNEP Team 1996) included the following statement about post-settlement human impacts on assessment area forest structure:

> **Forest Simplification.** The primary impact of 150 years of forestry on middle-elevation conifer forests has been to simplify structure (including large trees, snags, woody debris of large diameter, canopies of multiple heights and closures, and complex spatial mosaics of vegetation), and presumably function, of these forests. By reducing the structural complexity of forests, by homogenizing landscape mosaics of woody debris, snags, canopy layers, tree age and size diversity, and forest gaps, species diversity has also been reduced and simplified. At low elevations along the western boundary, ponderosa pine was preferentially removed, and throughout its range, sugar pine has decreased in abundance first through selection and

later by blister rust disease. Although the situation in the Sierra differs from that in forests in the Pacific Northwest, where fragmentation leaves remnant old-growth patches surrounded by large openings, functionally the Sierran forests have been fragmented to a lesser degree by simplification.

In the sections below, we refer more specifically to components of forest structure, including tree density, tree size and size-class distribution, tree basal area and volume, canopy cover, forest gaps and tree clumps, snags and coarse woody debris, and forest understory and nonforest vegetation.

Tree density—

***NRV and comparison to current*—**In the assessment area, the average YPMC forest stand today is much denser than during presettlement times. Figure 14 shows comparisons between historical reconstructions of stand conditions in the late 19th and early 20th centuries with current conditions at the same sites. In all cases, modern densities are much higher than the earlier reconstructed densities; differences range from 80 to 600 percent (fig. 14). These differences may be slightly inflated by the inability of reconstruction studies to accurately account for very small trees in the historical period, especially from species that rapidly decay such as firs (Barth 2014).

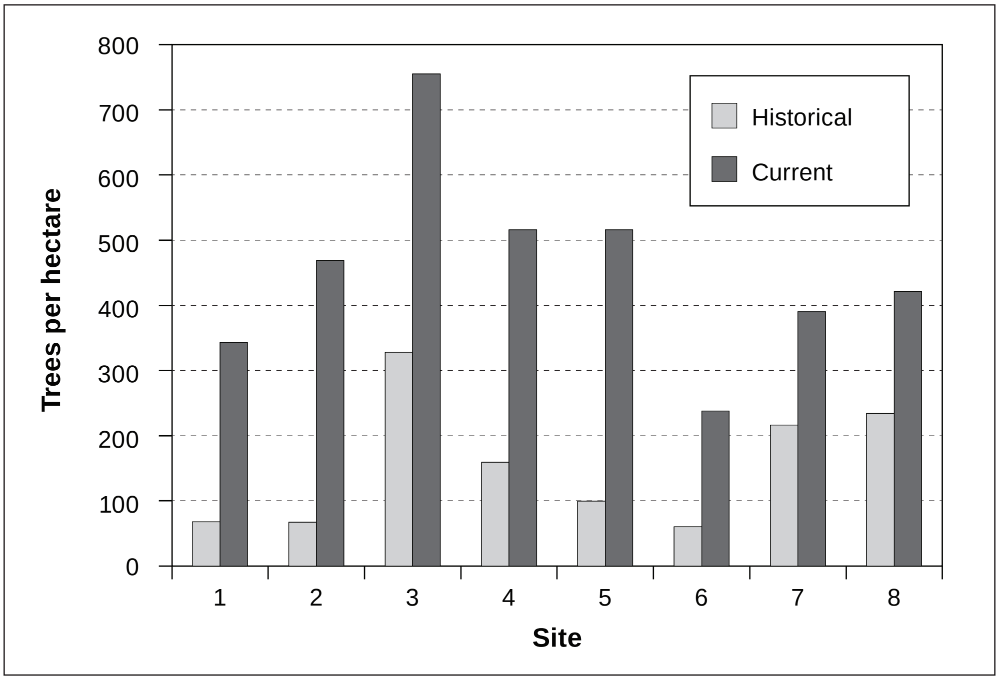

Figure 14—Comparisons of current and historical tree densities at eight yellow pine–mixed-conifer sites in the assessment area. 1 = Taylor 2004 (≥10 cm diameter at breast height [d.b.h.]); 2 = North et al. (2007) (trees ≥5 cm d.b.h.); 3 = Lydersen et al. (2013) (≥10 cm d.b.h.); 4 = Scholl and Taylor (2010) (≥10 cm d.b.h.); 5 = USDA (1911) vs. current from Scholl and Taylor (2010) (≥15.2 cm d.b.h.); 6 = Collins et al. (2011) (≥15.2 cm d.b.h.); 7 and 8 = Parsons and Debenedetti (1979) (≥12 cm d.b.h.).

Numerous other empirical studies in the assessment area have also documented similar patterns to those portrayed in figure 14. These include Ansley and Battles (1998), Beaty and Taylor (2007, 2008), Taylor et al. (2014), Knapp et al. (2013), Dolanc et al. (2014a, 2014b), and Barth (2014). Dolanc et al. (2014a) compared the 1930s Forest Service vegetation type mapping (VTM) inventory of the central Sierra Nevada (Wieslander 1935) with the modern FIA inventory, and found that mixed-conifer forests had experienced increases over the 70-year period of about 69 percent, and ponderosa pine had seen density increase by 40 percent. The VTM inventory ignored trees below 10 cm (4 in) d.b.h., so Dolanc et al. (2014a) also removed small trees from the FIA data to allow comparison. Including the smaller trees, we hypothesize that the overall increase in density would probably be much greater, because the major response to climate and management trends through the period has been in the smallest size classes.

Stephens and Gill (2005) sampled 49 0.1-ha plots in the Sierra de San Pedro Mártir (SSPM), in Baja California and found an average of 145.3 trees/ha (±10.4 SE, range 30 to 320). Dunbar-Irwin and Safford (2016) measured an average of 188 trees/ha (±15.1 SE) in a more widespread sample of the SSPM, and Rivera and Safford (unpublished data) measured 216 trees/ha in a similar assessment of Jeffrey pine forests in the Sierra Juarez, another Baja California site.[11] These values fall well within the reconstructed values in figure 14.

Baker (2014) used a complicated algorithm to suggest that GLO section-corner tree data (see “Tree size and size-class distribution” for more information) from four large areas in the Sierra Nevada showed mean densities of 293 trees/ha (±477 standard deviations [SD]; the median was 206). This is very much on the high end of prefire suppression estimates. Baker’s results run counter to early 20th century forest inventories that were conducted in the same areas. For example, Hagmann et al. (2014) summarized data from a 1922–1925 inventory in the eastern Oregon Cascade Range and found tree densities that were about four times lower than Baker’s estimates for the same area (in Baker 2012). The dataset Hagmann et al. (2014) analyzed had sampled >16,000 trees/mi^2 (6,265 trees/km^2), whereas the GLO sampling densities are at most 8 trees/mi^2 (a 0.004 percent sampling effort based on Baker’s density estimates). Hagmann et al. (2013) also found that Baker’s (2012, 2014) methodology notably overestimated density in YPMC-type forests in south-central Oregon. Collins et al. (2011) resampled a 1911 inventory in YPMC forest near Yosemite National Park and found an average of <70 trees/ha (only trees >15 cm d.b.h. included) over

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[11] Rivera and Safford. 2014. Unpublished data. On file with: Hugh Safford, USDA, Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592.

a 4000-ha area. Baker's (2014) GLO-based estimates for the same area suggested densities between 150 trees/ha and 450 trees/ha (>10 cm d.b.h.). Stephens et al. (2015) summarized a 1911 Forest Service inventory from the Greenhorn Mountains, west of Kernville, and found densities of 45 to 132 trees/ha (yellow pine and mixed-conifer stands [trees >15 cm d.b.h.]) in an area that Baker's (2014) GLO algorithm calculated 210 to 548 trees/ha. Stephens et al. (2015) summarized discrepancies between direct inventories in Oregon and California and Baker's estimates, and noted that (1) Baker's sampling effort is multiple orders of magnitude lower than the forest inventory studies from the same areas, and (2) Baker's methodology consistently overestimated forest densities by an average of more than 400 percent. Most recently, Levine et al. (2017) deconstructed Baker's algorithm and found that his methodology overestimated true tree densities from an array of 6-ha mapped forest plots by 1.2 to 4.8 times.

The compiled FIA data from YPMC forest plots (USDA FS 2013) show an average modern density (all trees greater than 10 cm d.b.h.) of 396.5 trees/ha (±292 SD). This is 2.75 times more dense than the reference density obtained by averaging the eight studies in figure 14, Taylor (2004), Stephens and Gill (2005), Minnich et al. (1995), and Dunbar-Irwin and Safford (2016): 143.8 trees/ha (±80.9 SD). Recall that the FIA plots include logged and severely burned areas, so the difference between FIA and reference site studies is less than it would be if we restricted the comparison only to undisturbed FIA plots.

Further information on density by species is found in "Forest composition and species diversity" on page 161. Information on tree densities by size class (diameter) is in "Tree size and size-class distribution" below.

Future—Continuation of current trends will lead to further increases in forest density, primarily among small- and medium-sized trees. Trends in fire and in forest mortality (see below) may counteract these tendencies to some extent.

Tree size and size-class distribution—

NRV and comparison to current—Average and maximum tree sizes in YPMC forest stands appear to have been much larger in presettlement times. Taylor et al. (2014), working in Jeffrey pine-dominated forests in the Lake Tahoe basin, found the average tree size (d.b.h.) in the modern forest to be only about 60 percent of the average tree size in the forest in 1873. Lydersen et al. (2013) compared stand conditions on the Stanislaus National Forest in 1929 with conditions in 2008 and found that mean tree diameter had decreased by about 26 percent.

Miners like Peter Decker and Joseph Bruff referred often to the large trees they encountered. In one place on the present-day Lassen National Forest, Bruff described a stand of pines "ten feet diameter, 200 ft high, straight as arrows" (Read and Gaines 1949: 204). For ponderosa pine, Muir (1894) suggested that the average size of “full-grown” trees on the western slope was over 65 m in height and from 1.5 to 1.8 m in diameter. Sudworth (1900) was somewhat less generous, estimating the averages to be 45 to 55 m in height and 0.9 to 1.2 m d.b.h. Sugar pine grew much larger; Muir (1894) listed a height of 67 m and 1.8 to 2.4 m d.b.h. as common measurements for full-grown trees, but Sudworth (1900) suggested that only the largest of all sugar pines reached those sizes. Table 6 lists the average sizes of “full-grown” adult trees provided by Sudworth (1900) for uncut stands in the central Sierra Nevada. These sizes are so large as to convince various investigators that Sudworth’s numbers can only refer to the best growing sites in his survey area (Bouldin 1999, Stephens 2000, Stephens and Elliott-Fisk 1998).

Early GLO land surveys also provide an idea of the sizes of trees on the late 19th century landscape. At section corners and halfway between section corners (1 mi apart), the original land survey teams took formal notes on “bearing” trees, which were the nearest trees >10 cm d.b.h. in each compass quadrant that were likely to survive over the long term. Trees between 25 to 36 cm d.b.h. (10 to 14 in) were apparently preferred if they were available (Hyde 2002). The survey teams identified the species, marked the tree, and measured the diameter, bearing, and distance from the section corner to each tree. At quarter-section corners along the section lines, two trees were marked and measured (Hawes 1882).

Hyde (2002) summarized GLO data from the Stanislaus, Sierra, and Sequoia National Forests. The average witness/bearing tree sampled by the GLO teams was <61 cm d.b.h., with the average sampled oak being between 38 and 50 cm d.b.h., the average sampled pine between 56 and 76 cm d.b.h., and the average sampled fir between 51 and 71 cm d.b.h. (values estimated from table 4.5 in Hyde 2002). On the Stanislaus National Forest, the average sampled pine was more than 78 cm d.b.h.; half of all pines sampled there were above 86 cm d.b.h., and more than one-third were

Table 6—Mean “full-grown” tree sizes (height and diameter at breast height [d.b.h.]) for major tree species in uncut yellow pine and mixed-conifer forests in the central Sierra Nevada at the turn of 19th century, according to Sudworth (1900)

Species	Height		D.b.h.	
	- - - Feet - - -	*- - Meters - -*	*- - - Feet - - -*	*- Centimeters -*
Yellow pine	150–180	45–55	3–4	90–120
Sugar pine	180–200	55–61	4–6	120–180
Incense cedar	80–100	24–31	5–7	150–210
White fir	175–190	53–58	3.5–5.5	110–170
Jeffrey pine	125–160	38–49	3–5	90–150
Douglas-fir	150–175	46–53	4–7	120–210

greater than 102 cm d.b.h.; fir on the Stanislaus were nearly as big on average, but the median was between 61 and 76 cm d.b.h. Trees on the Sierra and Sequoia National Forests were 15 to 30 percent smaller in diameter on average (Hyde 2002). General Land Office data from the Lake Tahoe basin give an average tree diameter of 61 cm in YPMC forests (Manley et al. 2000), and unpublished GLO data from the Eldorado National Forest show average yellow pine and sugar pine diameters between 76 and 83 cm d.b.h.[12] Baker's (2014) GLO-based study of forest structure in the northern and southern Sierra Nevada found that quadratic mean diameters (QMD) ranged from 50 to 59 cm (north and south), but Baker did not provide species-specific values.

Modern FIA data from the assessment area (USDA FS 2013a) for trees >10 cm d.b.h. give an average diameter of approximately 26 cm and a QMD of 32 cm.

The drop in the average size of trees in YPMC forests over the past century is the result of two trends: a great and general increase in the density of small trees, combined with a decrease in the number of large trees. Many studies have documented the former pattern (referenced throughout this assessment), but the latter may be ecologically just as significant. Figure 15 is reproduced from Dolanc et al. (2014b) and shows changes in density between the 1930s and early 2000s, as documented by the Forest Service VTM and FIA inventories. The pattern of increasing small tree density as well as the pattern of decreasing large tree density are seen clearly in the figure. Although overall forest density is up at all elevations, by far the greatest changes are in the YPMC belt (500 to 2000 m in figure 15), where fire suppression has played a major role. Other studies documenting the loss of larger trees in assessment-area YPMC forests include Dolph et al. (1995), Smith et al. (2005), Ritchie et al. (2008), Lutz et al. (2009), and van Mantgem et al. (2009); note that Collins et al. (2011) did not find this pattern. Although timber harvest certainly explains some of this trend across the assessment area (e.g., Lydersen et al. 2013, Taylor 2004), the patterns also occur in unlogged forests. Other factors might include insect outbreaks, pathogens, and drought stress, probably exacerbated by the much higher stand densities that characterize modern YPMC forests.

Figure 16 shows reconstructed size class distributions combined from four study sites in the assessment area. Figure 16 is given as the percentage of measured trees, to better allow comparison of the shape of the reference distributions among sites. Figure 17 reproduces size class distributions from three modern reference sites that were not logged and have not experienced total fire exclusion. In both figures, the roughly flat or even hump-shaped distribution of tree sizes in the historical reconstructions can

The roughly flat or even hump-shaped distribution of tree sizes in the historical reconstructions can be appreciated. This is very different from the classic "reverse J-shaped" age or size distribution that is typical of stable, self-replacing climax communities.

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[12] Fites-Kaufman, J. 2013. Personal communication. Regional planning ecologist, USDA, Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592.

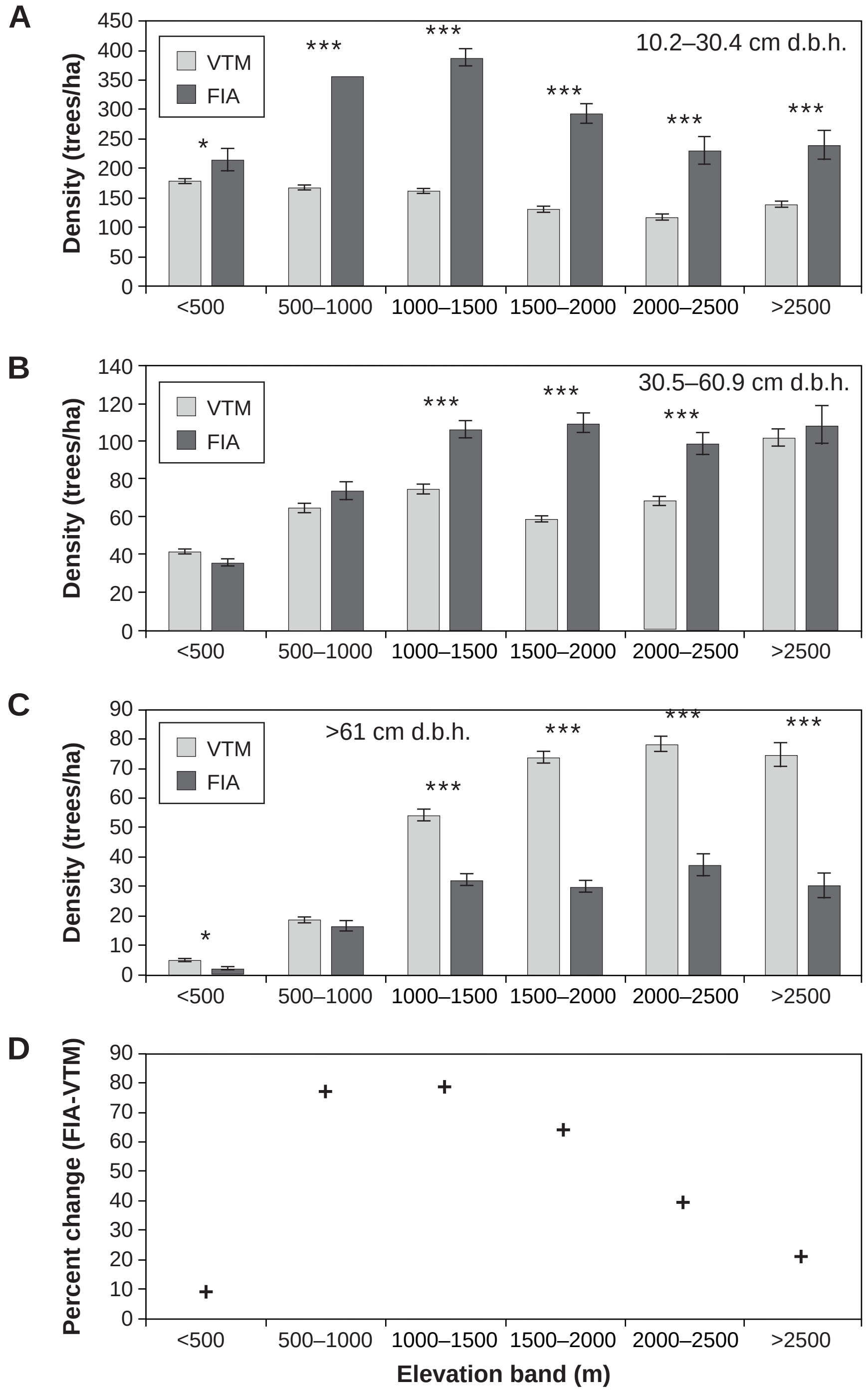

Figure 15—Change in density (trees/ha) between vegetation type mapping (VTM) plots (from the 1930s) and Forest Inventory and Analysis (FIA) plots (from the early 2000s) for all species combined, for six elevation bands (*x*-axis), and by size class: (A) 10.2 to 30.4 cm diameter at breast height (d.b.h.); (B) 30.5 to 60.9 cm d.b.h.; (C) >61.0 cm d.b.h.; (D) percentage change in density from VTM to FIA plots across all size classes. Statistically significant differences are indicated by * = $0.01 < p < 0.05$; ** = $0.001 < p \leq 0.01$; and *** = $p < 0.001$. Yellow pine–mixed-conifer forests are found principally between 500 and 2000 m. Illustration adapted from Dolanc et al. (2014b).

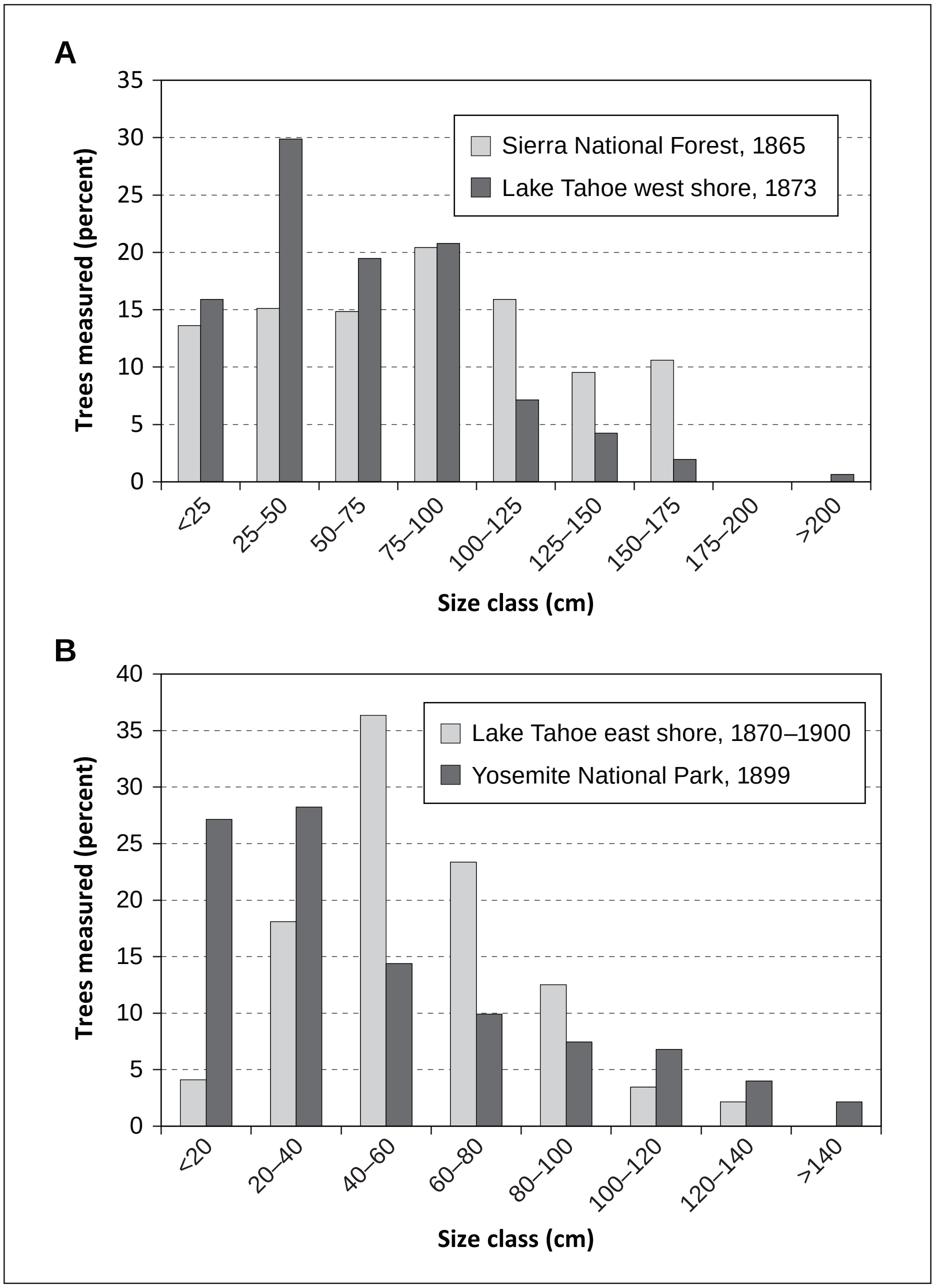

Figure 16—Historical tree-size distributions from four studies of yellow pine–mixed-conifer forest in the assessment area, standardized by percentage of trees measured. (A) Sierra National Forest, 1865 (North et al. 2007); Lake Tahoe west shore, 1873 (Taylor et al. 2014). (B) Lake Tahoe east shore, 1870–1900 (Taylor 2004); Yosemite National Park, 1899 (Scholl and Taylor 2010).

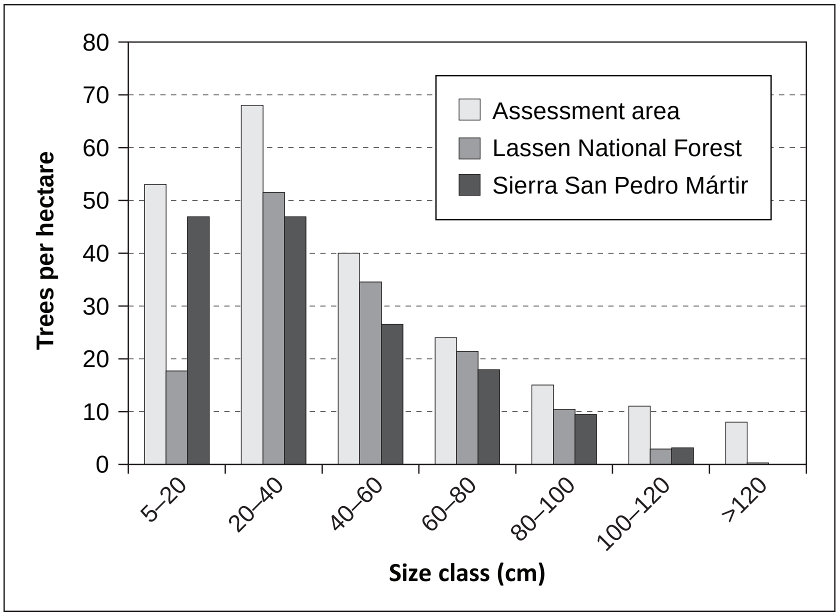

Figure 17—Modern size-class distributions from three unlogged reference areas with (partially) intact fire regimes through the 20th century. Assessment area = Lydersen and North (2012); Lassen National Forest (Beaver Creek Pinery) = Taylor (2010); Sierra San Pedro Mártir = Stephens and Gill (2005).

be appreciated. This is very different from the classic “reverse J-shaped” age or size distribution that is typical of stable, self-replacing climax communities (Barbour et al. 1987, Oliver 2001). Assuming that size is roughly correlated with age, the *x*-axes of figures 16 through 19 represent the spectrum from juveniles through immature, mature, and then senescent individuals. Given the relatively high probability of mortality for juveniles, a high number of young trees is usually necessary to replace the relatively few adults that die in any given period. This leads to the J-shaped (or “hockey stick”) size distribution in the contemporary forest stands in figure 18. Such a distribution is typical of a forest community relatively free of disturbance (Smith et al. 2009). If a population is composed mostly of mature and senescent individuals, the population may be in decline (which is how early foresters interpreted the situation they encountered) (e.g., Greeley 1907, Sudworth 1900), or it may be one that is replaced only by episodically successful recruitment (Barbour et al. 1987). This was largely the case with presettlement YPMC forests in the assessment area, where recurrent fire killed most juvenile trees and successful recruitment was somewhat of a stochastic event, when seed production happened to coincide with a period of sufficient precipitation and little or no fire. Roughly flat or hump-shaped age or size distributions are characteristic of old-growth forests in areas that experience frequent, low-severity fire (Lydersen and North 2012, North et al. 2007, Oliver 2001). As a result, they are also found in stand reconstructions of presettlement ponderosa pine

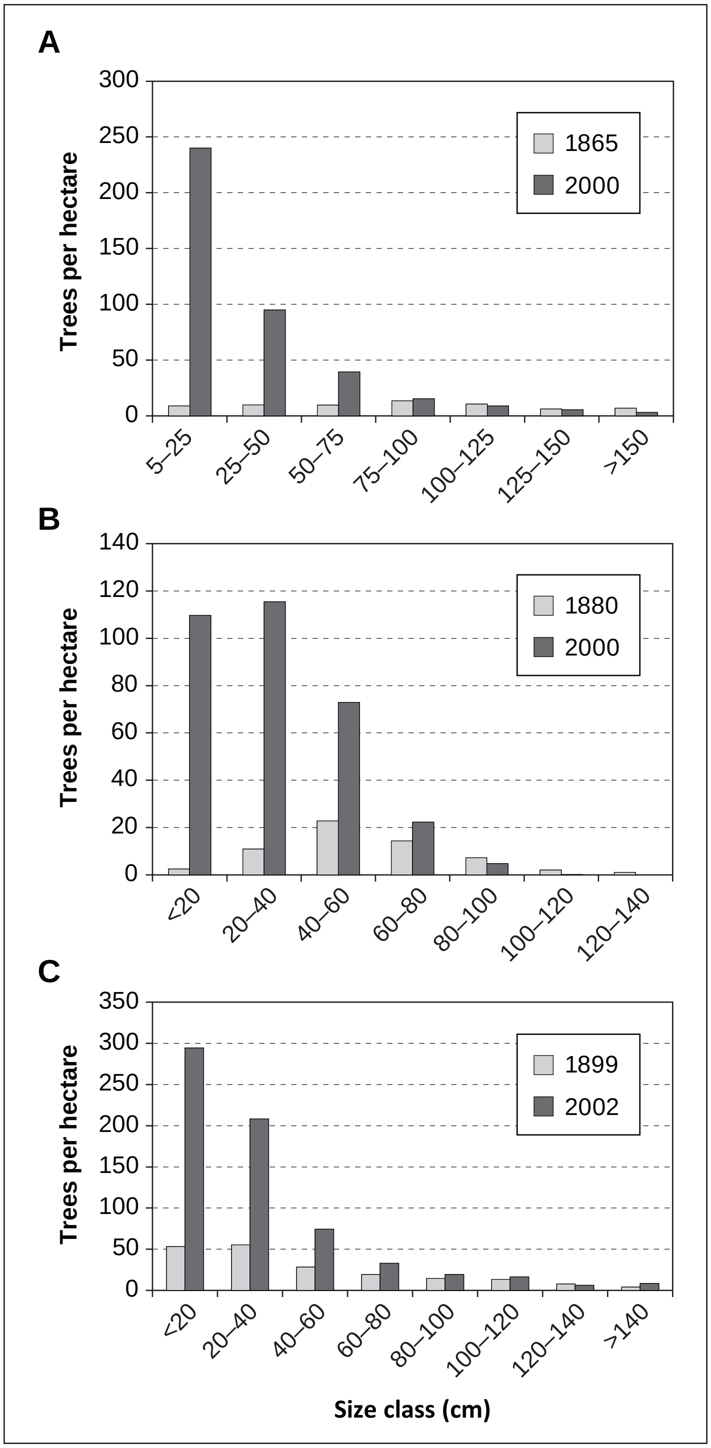

Figure 18—Comparisons of reconstructed historical tree size class distributions and contemporary distributions from three sites in the assessment area. (A) North et al. (2007); (B) Taylor (2004); (C) Scholl and Taylor (2010).

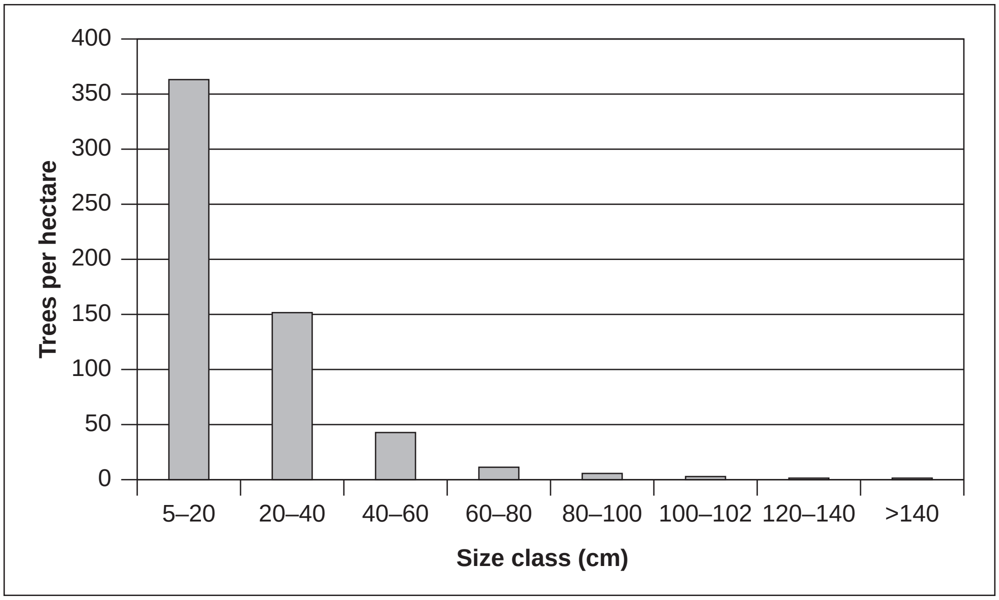

Figure 19—Average size-class distribution for compilation of most recent Forest Inventory and Analysis plot data in assessment-area yellow pine–mixed-conifer forests (USDA FS 2013).

forest in the U.S. Southwest (Mast et al. 1999), and in forests of longleaf pine (*Pinus palustris* Mill.) in the Southeastern United States (Heyward 1939). The distribution of size classes in the GLO data from the Lake Tahoe basin show a similar humped shape (Manley et al. 2000). Oliver (2001: fig. 2) graphed the size-class distribution from the Beaver Creek Pinery, a well-known reference ponderosa pine-black oak site in the northern assessment area that was not logged and experienced a number of fires in the 20th century; it is strongly hump-shaped. Using a project at Blacks Mountain Experimental Forest in the same general area, Oliver (2001) showed that prescribed fire could convert a reverse J-shaped distribution to a hump-shaped distribution. Taylor (2010) showed the same effect of fire in his study of the Beaver Creek Pinery and the nearby Devil's Pinery.

Not all reference YPMC forests show the hump-shaped distribution of tree size classes. In their array of plots in the contemporary Sierra de San Pedro Mártir, Stephens and Gill (2005) found a J-shaped distribution of size classes.

Figure 19 shows the average size-class distribution in 20-cm classes for the FIA plot data compilation (USDA FS 2013a). The obvious reverse J-shaped curve is very different from the more flat or hump-shaped size distribution found in presettlement forests.

***Future*—**Continued high levels of recruitment among shade-tolerant species, combined with increasing mortality among larger trees (see "Tree mortality" above), will likely intensify the tendency toward a reverse J-shaped size-class distribution.

Tree basal area/volume (forest biomass)—

***NRV*—**A number of stand reconstruction studies report late 19th century basal areas. Scholl and Taylor (2010) found that overall reconstructed basal area in 1899 was between 29 and 30 m^2/ha, depending on the smallest tree size considered. A U.S. Forest Service (USDA FS 1911) report referenced by Scholl and Taylor (2010) found basal areas in western Yosemite Park of about 21 m^2/ha. Taylor et al. (2014) reported an overall basal area of about 27 m^2/ha in YPMC forests in the Lake Tahoe basin (reconstructed date = 1893). Taylor (2004) reconstructed Jeffrey pine stands on the east shore of Lake Tahoe and found average basal areas of 25.5 m^2/ha for the period between 1870 and 1900. Parsons and Debenedetti (1979) provided data that produced basal areas (in 1875) of 38 to 89 m^2/ha in yellow pine and productive mixed-conifer forests in the southern Sierra Nevada. North et al. (2007) reported an 1865 basal area of about 51 m^2/ha for a moist mixed-conifer forest on the Sierra National Forest, and Knapp et al. (2013) found a mean basal area of 53.9 m^2/ha for a productive site on the Stanislaus National Forest. Using 1911 forest inventory data, Collins et al. (2011) reported basal areas of about 14 to 18 m^2/ha from the east side of Yosemite National Park. Collins et al. (2015) reported basal areas of 11 to 30 m^2/ha for the west side of Yosemite National Park, and Stephens et al. (2015) reported basal areas of 11 to 30 m^2/ha for the Greenhorn Mountains. Baker's (2014) GLO-based estimates were between 32.5 and 35.5 m^2/ha (north and south Sierra Nevada sites, respectively).

Outside of the assessment area but in similar forest, Avery et al. (1976) used long-term stand records in ponderosa pine forest in Arizona to determine that basal area in 1920, just as federal fire suppression was gaining traction, averaged about 14.2 m^2/ha across 16 forest inventory plots.

Data from contemporary reference sites give similar numbers. Lydersen and North (2012) found that modern old-growth stands with recent recurrent fire averaged 54 m^2/ha in a sample of 48 sites across much of the assessment area. Stephens and Gill (2005) measured stand characteristics in a limited area of Jeffrey pine/mixed-conifer forest in the Sierra de San Pedro Mártir in Baja California and found that basal area averaged 19.9 m^2/ha, but with an enormous range (5.7 to 50.7 m^2/ha). Dunbar-Irwin and Safford (2016) found an average basal area of 22.5 m^2/ha for Jeffrey pine and mixed-conifer stands across the plateau of the Sierra de San Pedro Mártir, and in an unpublished study they measured an average of 15.5 m^2/ha for Jeffrey pine stands in the Sierra Juarez,[13] which is at the lowest altitudinal limit of Jeffrey pine in Baja California. Taylor (2010) measured basal areas of 27.1 m^2/ha

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[13] Dunbar-Irwin and Safford. 2013. Unpublished data. On file with: Hugh Safford, U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592.

in the Beaver Creek Pinery on the Lassen National Forest, which is an old-growth ponderosa pine-black oak forest with multiple 20th century fire entries.

Outlying values are given by Sudworth (1900, and in his unpublished notes), who sampled plots in highly productive sites in the central and southern Sierra Nevada. Mean basal areas from plots in mixed-conifer stands ranged from 130 to 270 m^2/ha. The representativeness of Sudworth's (1900) plot data has been questioned (Baker 2014, Bouldin 1999, Stephens 2000, Stephens and Elliott-Fisk 1998).

***Comparison to current*—**A compilation of the most recent FIA data in the assessment area (USDA FS 2013a) suggests that mean basal area in YPMC forests has not changed dramatically over the past 100+ years. The average of the reference values given above (not including Sudworth and Avery) is 31.7 m^2/ha (±18.5 SD), while the average of the 2,508 FIA plots in YPMC forests included in the compilation is 32.9 m^2/ha (±20.4 SD; all trees >5 cm d.b.h.). Mean basal area in YPMC FIA plots on the west side of the assessment area (north, central, and south subregions) is 34.6 m^2/ha; on the east side (northeast and southeast subregions), it is 26.5 m^2/ha.

Obviously, it is statistically somewhat tenuous to compare the results of 14 local studies with an average derived from 2,508 plots regularly spaced across the entire assessment area, especially when the latter comprise all stand conditions, including logged and severely burned areas. Studies that have directly reconstructed early stand conditions on a site and then compared them to the current forest stand have mostly found that basal area has increased, although not at the rate that tree density has increased (see above). Figure 20 summarizes temporal changes in basal area by species for four sites in assessment-area YPMC forests; the increase in basal area is nearly entirely in shade-tolerant/fire-intolerant species. Overall increases in basal area from these studies and others referenced above range from 10 to 150 percent, averaging about 60 percent across studies.

Studies that have directly reconstructed early stand conditions on a site and then compared them to the current forest stand have mostly found that basal area has increased, although not at the rate that tree density has increased.

Ansley and Battles (1998) compared modern YPMC forest structure to structure in a stand first sampled 40 years before. They found that basal area rose by 15 percent over the 40 years, and it increased for all species except for sugar pine (which remained the same) and ponderosa pine (which dropped). Lydersen et al. (2013) compared forest stand structure conditions in 1889 (estimated through reconstruction), 1929, and 2008 on the Stanislaus-Tuolumne Experimental Forest and found that basal area had increased from 52.8 to 56.6 to 70.5 m^2/ha, respectively. Increases in basal area were primarily in shade-tolerant species; the percentage of pine in the sampled stands dropped from 25 to 11 percent over the same period. Ritchie et al. (2008) also found that the contribution of pine to stand basal area dropped by about 12 percent over the 20th century in unlogged stands at Blacks Mountain on the Lassen National Forest.

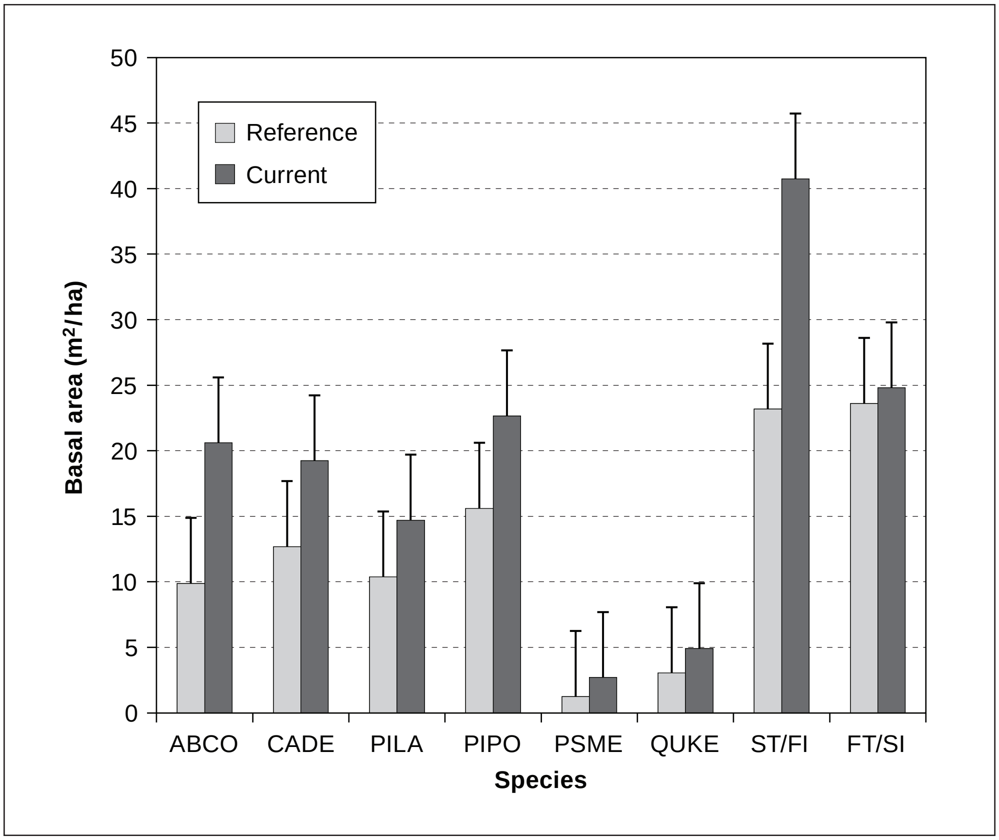

Figure 20—Basal area for reference and current yellow pine–mixed-conifer forests, means of four stand reconstruction studies from the western slope of the Sierra Nevada. Data are from Scholl and Taylor (2010), USDA FS (1911), and Parsons and Debenedetti (1979) (yellow pine and mixed-conifer sites). Error bars represent standard errors, based on n = 4. ABCO = *Abies concolor* (white fir); CADE = *Calocedrus decurrens* (incense cedar); PILA = *Pinus lambertiana* (sugar pine); PIPO = *P. ponderosa* (ponderosa pine); PSME = *Pseudotsuga menziesii* (Douglas-fir); QUKE = *Quercus kelloggii* (black oak); ST/FI = shade-tolerant and fire-intolerant group (ABCO + CADE + PSME); FT/SI = fire-tolerant and shade-intolerant group (PILA + PIPO + QUKE).

Because presettlement YPMC forests in the assessment area generally supported more large trees than current forests, a rise in basal area over time would be driven mostly by increases in small and medium tree densities. In places where those young tree densities have not risen as rapidly, or where large tree densities have not dropped (e.g., unlogged areas or areas where large tree mortality has not been otherwise high), basal areas of current forest may be similar to or even lower than presettlement forests (North et al. 2007).

Interestingly, comparisons between current FIA data and the Forest Service VTM dataset from the 1930s have mostly found that basal area and volume have **decreased** over time (e.g., Bouldin 1999, Fellows and Goulden 2008, McIntyre et al. 2015). It is difficult to determine why this is. There is some concern that VTM plots may have been preferentially sited in areas of better growing conditions or larger trees (Bouldin 2009), whereas the FIA data are a statistically unbiased sample. Little note is made in the VTM plot notes of previous logging, so it may be that they tended to avoid previously harvested stands. This would perhaps provide a better idea of natural forest conditions in the early 20th century, but it would complicate comparisons with modern inventories, which include all stand conditions to permit a statistically robust estimate of landscape-level conditions. Another issue with the VTM plots is that they did not sample any trees <10 cm d.b.h. The general understanding is that presettlement YPMC forests generally supported very low densities of saplings and small trees because of frequent fire. The VTM plots were sampled a few decades after the institution of fire suppression, so it seems likely that the absence of the smallest tree sizes in the VTM data does not constitute a major omission when calculating biomass. However, modern YPMC forests are highly enriched in the smallest size classes, and high densities of <10 cm d.b.h. trees can contribute measurable amounts of biomass to a forest stand. In the modern FIA data from assessment-area YPMC forests (USDA FS 2013a), the size class between 5 and 10 cm d.b.h. contributes an average of about 0.7 m^2/ha in basal area. Combining this with a rough estimate of the biomass in the 0 to 5 cm d.b.h. class (seedlings and small saplings), which is not measured in size by FIA but only enumerated, omission of trees <10 cm d.b.h. can reduce measured forest biomass from 1 to 2 m^2/ha or more. As a result, removing trees <10 cm d.b.h. from FIA plots to permit an unbiased comparison with VTM (a standard practice in FIA to VTM comparisons) may result in modern plots appearing to support less biomass than the early plots when they actually do not.

In summary, FIA data and local forest reconstruction studies suggest that modern basal areas are broadly similar to or slightly higher than basal areas in presettlement times. Local trends will depend on the relative effects of fire exclusion (which would increase basal area on its own) versus logging and other forest mortality agents (which decrease basal area). Remember that most (but not all) reconstruction studies are done in areas that did not experience logging, whereas the FIA dataset samples the forest without bias.

Future—Miller and Urban (1999a) simulated the effects of climate change on forest biomass and composition along an elevational gradient in Sequoia & Kings Canyon National Parks (see "Forest species composition and species diversity" on page 161 for more detail). At their two lowest elevation sites, which fall in YPMC forests, woody biomass was completely or almost completely lost by the end of the simulations. Under their less extreme warming and drying scenarios, basal area at 1800 m declined from 29 to 4 m^2/ha, and was completely lost under the more extreme scenarios. At 2200 m, basal area declined from 52 m^2/ha to 25–32 m^2/ha under the less extreme future scenarios, and to 8 m^2/ha under the most extreme scenario. Miller and Urban

Plates

The following 24 photographs provide an overview of the variety of stand conditions (except recently logged stands) found in yellow pine and mixed-conifer forests in the assessment area and a reference site in northwest Mexico. The approximate locations, forest types, and management agencies are identified, along with brief notes on site histories and conditions.

Plate title: Open mixed-conifer stand.

Plate Notes: Near the Wawona Hotel (Big Trees Lodge), Wawona, Yosemite National Park, Mariposa County, 1310 m (4300 ft). This stand is dominated by ponderosa pine, with sugar pine, incense cedar, and black oak. The understory is dominated by bear clover (*Chamaebatia foliolosa*), which is a common ground cover in open stands characterized by frequent fire. This area has experienced up to three prescribed fires over the last 35 years. Some ponderosa pine in the stand were being killed by western pine beetle when the photo was taken in 2015.

Plate title: Large patch of high-severity fire in moist mixed-conifer forest

Plate Notes: The Rich Fire (2008) burned across this south-facing slope above North Fork Feather River, Plumas National Forest, Plumas County. Elevation in the photo ranges from 1130 to 1800 m (3700 ft to 5900 ft). Prefire species composition was moist mixed conifer, with Douglas-fir, white fir, incense cedar, ponderosa pine, sugar pine, Jeffrey pine, black oak, and canyon live oak. This is an example of the very large patches of high-severity fire that are becoming common in yellow pine and mixed-conifer forests in the Sierra Nevada. The distance from the photo point to the top of the peak is about 2.7 km, the patch of nearly complete mortality is >600 ha. Before the Rich Fire, there was no fire here in at least 100 years, and much of the area was heavily logged in the late 19th and early 20th centuries.

Plate title: Smaller patch of high-severity fire in moist mixed-conifer forest

Plate Notes: The Meadows Fire (2004) burned within the Illilouette Creek Basin, Yosemite National Park, Mariposa County, 1980 m (6,500 ft). The predominant species are white fir and Jeffrey pine. This is an example of one of the larger high-severity patches seen in this wildland-fire-use area. Distance across patch is 140 m, patch size is about 2 ha. This site also burned previously in 1981, after at least 80 years of fire suppression.

Plate title: Large legacy trees

Plate Notes: Rubicon River drainage, Eldorado National Forest, Eldorado County, 1200 m (3,950 ft). This is one of the few remnant stands of older trees in the Rubicon River drainage; very light levels of cutting occurred here. Most of the forest in this area was heavily logged at least once since the mid-19th century. This stand is dominated by ponderosa pine, sugar pine, white fir, incense cedar, Douglas-fir and black oak, with buck brush (*Ceanothus cuneatus*) in the understory. Trees in the foreground are 80 to 140 cm diameter at breast height (32 to 55 in). No fire has burned here in at least 100 years, but stand conditions are still somewhat open owing to rocky, excessively well-drained soils. This stand escaped the very severe King Fire that burned much of this drainage in 2014.

Plate title: Jeffrey pine stand following fuel treatment

Plate Notes: Lake Tahoe Basin, just outside of Angora Fire perimeter, Eldorado County, 2010 m (6,600 ft). Stand dominated by Jeffrey pine, with some white fir, red fir, and lodgepole pine. This site on the left (panel A) experienced three forest fuel treatments between 1996 and 2005, beginning with a mechanical thin, followed by a hand thin and then a pile burn/prescribed fire. The shrub resprouts (greenleaf manzanita) are from 3 to 5 years old in the photo, and are a common understory response to opening of the canopy. Nearby stands with the same treatment history that burned in the Angora Fire suffered only 5 to 15 percent overstory mortality. The site on the right (panel B) is about 500 m SW of panel A, and was not treated before the date of the fire. The site is characterized by large Jeffrey pine and red fir in the overstory, with white fir and lodgepole pine dominating the smaller size classes. Nearby stands with the same forest structure that burned in the Angora Fire suffered 80 to 100 percent overstory mortality.

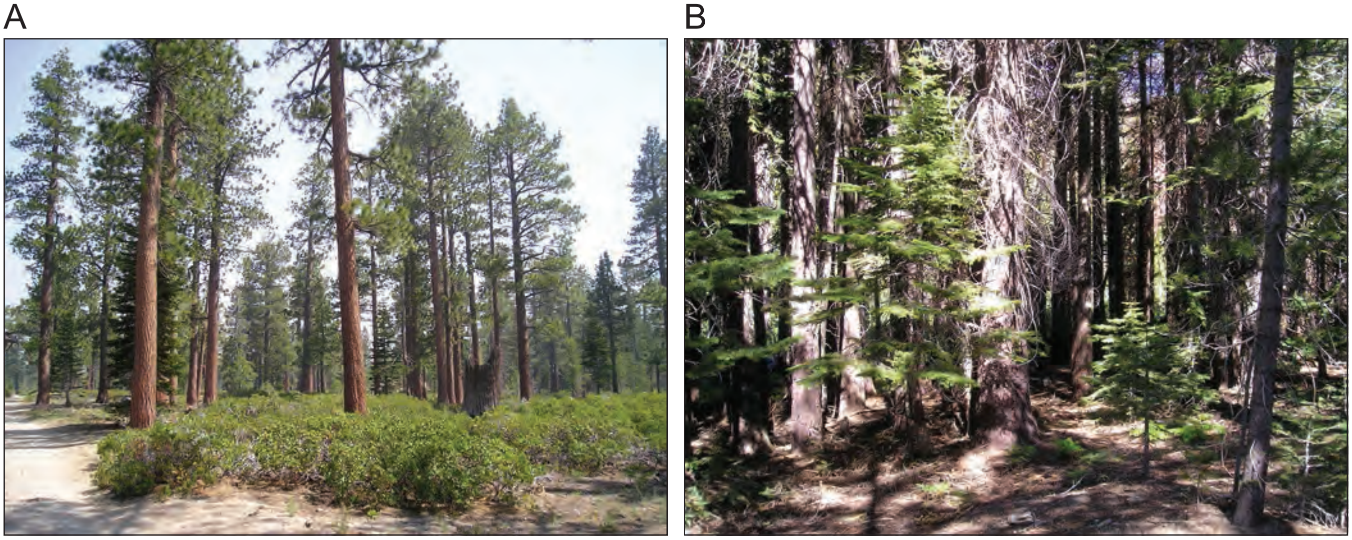

Plate title: Standard mixed-conifer stand, Sierra Nevada west slope

Plate Notes: Near Camp Nelson, Greenhorn Mountains, Sequoia National Forest, Tulare County, 1770 m (5,800 ft). This area was selectively logged more than once in the 19th and 20th centuries. The stand is dominated by ponderosa pine, incense cedar, white fir, sugar pine and black oak. There was some western pine beetle damage in the stand when the photo was taken in 2015; by 2016 there was widespread pine mortality. No fire has burned here in at least 100 years.

Plate title: Dry yellow pine-black oak forest

Plate Notes: Beaver Creek Pinery, Ishi Wilderness, Lassen National Forest, Tehama County, 870 m (2,850 ft), a well-known natural range of variation reference site. This low-elevation forest is dominated almost completely by ponderosa pine and black oak. The open canopy and low surface fuels of this site and other nearby unlogged "pineries" contrast strongly with nearby lands that were heavily logged and fire suppressed, which are now dominated by dense stands of shade-tolerant species (especially Douglas-fir). This site burned in 1903, 1924, 1990, and 1994. Recent fires in the area were suppressed. The current 22-year gap in the fire record has led to some fuels accumulations, and there is concern that the site could be lost to wildfire if prescribed burns are not instituted.

Plate title: Gap regeneration following fire

Plate Notes: Illilouette Creek Basin, Yosemite National Park, Mariposa County, 2200 m (7,200 ft). This stand is near the upper limits of yellow pine and mixed-conifer forests on the west slope of the Sierra Nevada. The stand is dominated by white fir and red fir with some Jeffrey pine, as well as lodgepole pine in wet undrained areas. This is a good example of the regeneration that occurs in forest gaps, in this case caused by a small lightning fire about 20 years previous to the photo.

Plate title: Sparse Jeffrey pine.

Plate Notes: Owens River Valley, Inyo National Forest, Mono County, 2410 m (7,900 ft). Pure Jeffrey pine stands occur at the eastern edge of its distribution in the Sierra Nevada rain shadow. Soils here are on volcanic rocks. Selective logging occurred in this area in the late 19th and early 20th centuries. When the photo was taken, no fire had burned here in at least 100 years. Then two fires burned the area in the summer of 2016. The photo foreground experienced very high tree mortality in a wind-driven fire after three years of drought.

Plate title: Mixed-conifer stand on a serpentine soil boundary

Plate Notes: Along Concow Road, Plumas National Forest, Butte County, 850 m (2,800 ft). A geological contact between ultramafic rocks (peridotite) and metasediments runs vertically through the middle of the photo. Site history is identical across the contact. The soils that develop on ultramafic rocks (often called "serpentine" soils) are usually critically low in macronutrients like nitrogen, phosphorus, and potassium, and enriched in magnesium, iron, and a number of heavy metals. As a result biomass accumulation is slow, woody plants are often stunted and much older than they appear, and there is high plant species endemism. Both soils support yellow pine and mixed-conifer forest, with the serpentine forest on the left dominated by gray pine and a thin and stunted complement of species from the more fertile soil to the right (Douglas-fir, sugar pine, incense cedar, ponderosa pine). Hardwoods are uncommon on serpentine soils (except where they have been hydrothermally altered). Photo taken in 2005 after more than 100 years without fire; the entire area of the photo burned in the 2008 BTU Lightning Complex Fire. Because of fuel differences, the dense forest to the right burned with nearly complete overstory mortality, the serpentine forest suffered about 30 percent mortality.

Plate title: Dense understory, mesic mixed conifer stand.

Plate Notes: Private property, North San Juan, Nevada County. 640 m (2,100 ft). The understory "jungle" that is common in mesic stands on unmanaged/unburned lands at low elevations on the Sierra Nevada west slope. This stand is dominated by ponderosa pine, incense cedar, Douglas-fir, black oak, interior live oak, and madrone (abundant in the understory), with some invasion by Spanish broom (*Spartium junceum*). This area was heavily logged in the mid to late 19th century and has not experienced a fire in at least 100 years.

Plate title: Low-elevation ponderosa pine-oak woodland

Plate Notes: Near Priest Reservoir, Tuolumne County, 760 m (2,500 ft). At very low elevations, ponderosa pine occurs as scattered individuals or small groves within landscapes dominated by oak species (interior live oak, blue oak, canyon live oak), other hardwoods, and gray pine. Chaparral stands are also common. The ponderosa pine in this photo had been attacked by western pine beetle that year (2015) and are now dead. This area was logged in the late 19th century.

Plate title: Open mixed-conifer forest.

Plate Notes: Illilouette Creek Basin, Yosemite National Park, Mariposa County, 2070 m (6,800 ft). This mixed-conifer stand is dominated by Jeffrey pine and white fir. The stand structure is an example of open forest maintained by frequent surface fire. This stand burned at low severity in 1981 and 2004.

Plate title: Open dry mixed-conifer forest

Plate Notes: Sierra de San Pedro Mártir National Park, Baja California, 2600 m (8,540 ft). This high-elevation stand is dominated by Jeffrey pine, with white fir, lodgepole pine, and sugar pine (white fir and sugar pine mostly occur on north slopes). Aspen is found along the drainage and also on north slopes. A few oak species, including canyon live oak, are also found in this stand. This site last burned in 1948, a previous fire occurred in 1929. There is also moderate grazing pressure here. Most of the national park, including this site, has never been logged. Since the 1980s, the Mexican Park Service has been aggressively suppressing fires in the park, and recent science is showing that fuel loads are increasing as a result.

Plate title: Sugar pine stand

Plate Notes: D.L. Bliss State Park, Lake Tahoe Basin, Eldorado County, 2070 m (6,800 ft). Sugar pine often dominates areas such as this with thin soils and rocky outcrops but decent precipitation. There are also white fir and some Jeffrey pine in this stand. White pine blister rust is killing many of the trees in the stand. This stand was one of few to escape the clearcut logging that pervaded the Lake Tahoe Basin in the late 19th century. No fire has burned here in at least 100 years.

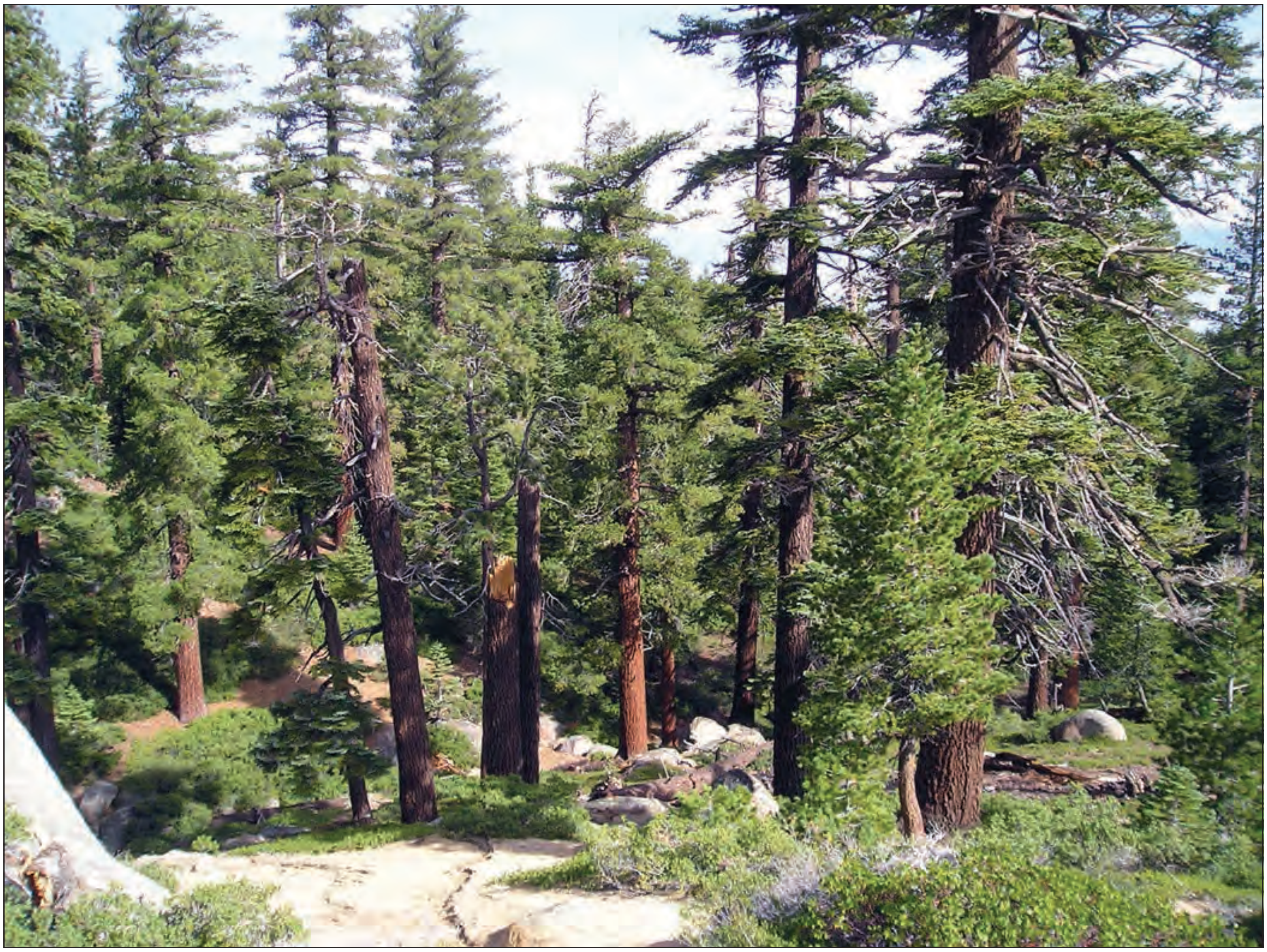

Plate title: Fire suppressed mixed conifer forest

Plate Notes: Plumas National Forest, Butte County, 1220 m (4,000 ft). Standard moist mixed-conifer stand after late 19th century logging and a century of fire suppression. Stand is dominated by Douglas-fir, with individuals of ponderosa pine, sugar pine, black oak, canyon live oak, incense cedar, and madrone also present. This is in the area of the highest conifer growth rates in the assessment area. No fire has burned here in at least 100 years.

Plate title: Regeneration in the absence of fire

Plate Notes: Buck Meadows, west of Yosemite National Park, Stanislaus National Forest, Mariposa County, 915 m (3,000 ft). Regeneration of ponderosa pine, incense cedar, and black oak is occurring in a gap left by fallen beetle-killed pine. No fire has burned here in at least 100 years; however, the area was logged in the early 20th century.

Plate title: High-elevation Jeffrey pine

Plate Notes: Big Pine Creek, Inyo National Forest, Inyo County, 2560 m (8,400 ft). Yellow pine stands follow drainages in these high-elevation, rain shadowed sites on the east side of the Sierra Nevada. The stand is dominated by Jeffrey pine, with a minor component of lodgepole pine and aspen. This is near the upper elevation of Jeffrey pine at this latitude, with lodgepole pine the dominant species at higher elevation. No fire has burned here in at least 100 years.

Plate title: Fire-suppressed moist mixed-conifer/white fir

Plate Notes: Illilouette Creek drainage, Yosemite National Park, Mariposa County, 2100 m (6,900 ft). Moist mixed-conifer stands such as this are typical in bottomlands and cold air drainages at higher elevations. This stand is almost entirely white fir and lodgepole pine, with a few scattered Jeffrey pine. None of the Illilouette Creek Basin was logged. No fire has burned here in at least 100 years.

Plate title: Invaded low-elevation ponderosa pine-oak woodland

Plate Notes: City property, Nevada City, Nevada County, 820 m (2,700 ft). The overstory in this stand is dominated by ponderosa pine with some Douglas-fir and black oak; the understory is heavily invaded by Spanish broom (*Spartium junceum*), a Mediterranean legume originally introduced as an ornamental. The species is actively invading yellow pine and mixed-conifer forests at lower elevations near seed sources and areas of disturbance, especially along roads and near urban areas. There are many other noxious weeds in this stand as well, including Himalayan blackberry (*Rubus armeniacus*), and a variety of Mediterranean grasses. This area was heavily logged in the mid to late 19th century. No fire has burned here in at least 100 years.

Plate title: Open Jeffrey pine forest

Plate Notes: Golden Trout Wilderness, Inyo National Forest, 2440 m (8,000 ft), Tulare County. Jeffrey pine dominates this high-elevation site, which last burned in a surface fire 5 years before the photo was taken. This area is subject to wildland fire use. The site is also within an active grazing allotment, with low levels of livestock use.

Plate title: Moist mixed-conifer stand

Plate Notes: Station Creek Research Natural Area, Eldorado National Forest, Eldorado County, 1650 m (5,400 ft). This moist mixed-conifer stand is dominated by white fir and sugar pine, with some Douglas-fir, ponderosa pine, and black oak. Soils are thin, over steep granitic bedrock, keeping forest densities somewhat lower than in nearby drainage bottoms. There was some logging here in the late 19th century. No fire has burned here in at least 100 years.

Plate title: Large legacy ponderosa pine

Plate Notes: Emerald Bay State Park, Lake Tahoe, Eldorado County, 1905 m (6,250 ft). This property is one of few uncut old-growth stands at lake level; the dominant trees are ponderosa pine, which is rare in the Lake Tahoe Basin. Other conifers include (in order of decreasing basal area) Jeffrey pine, incense cedar, white fir, and sugar pine. Ponderosa pine in the foreground are 100 to 150 cm diameter at breast height (d.b.h.) (40 to 60 inches), some ponderosa pine in this stand reach 220 cm d.b.h. (87 inches). No fire has burned here in at least 100 years.

Plate title: Low-density Jeffrey pine stand on serpentine soils

Plate Notes: North-facing slopes south of North Fork Feather River, near Red Hill, Plumas National Forest, Plumas County, 1250 m (4,100 ft). Ultramafic “serpentine” soils, on peridotite. Site is dominated by Jeffrey pine, with some incense cedar, Douglas-fir, and sugar pine. Although Jeffrey pine is normally a higher elevation species in the assessment area, it is a better stress tolerator than ponderosa pine, and it supplants ponderosa pine on serpentine soils as low as 1100 m. At the time of the photo, this site had not experienced a fire in over 100 years, but it burned in the 2008 Rich Fire. Windy conditions led to surprisingly high mortality, up to 50 percent in some stands in this area.

(1999a) included fire in their simulations, but only surface fires were modeled, so fire played little role in directly causing biomass loss. Miller and Urban's (1999a) results are thus probably conservative with respect to the velocity of change in biomass.

Bachelet et al. (2001) modeled the potential effects of climate warming on carbon budget using climate data from seven different GCMs. Their results varied widely, depending on the GCM used, the vegetation/carbon model used, the degree of future warming, and precipitation. Forested areas were especially sensitive to changes in temperature. Bachelet et al. (2001) found that most scenarios predicted increases in forest cover and forest biomass in the assessment area under moderate warming (+2 to 4 °C); their vegetation model, which included fire, resulted in less biomass gain. Their projections included a relatively large increase in precipitation, however; according to Dettinger (2005), the most common prediction among more recent GCMs (which are considerably more complex and realistic than the models available in the late 1990s) is temperature warming by about 5 °C by 2100, with precipitation remaining similar or slightly reduced compared to today. The newer GCMs thus cast some doubt on Bachelet et al.'s (2001) results. Under more extreme warming scenarios (>4 °C), Bachelet et al. (2001) found that increases in forest biomass were reversed. They referred to this temperature-driven pattern as the "early green-up, later browning" hypothesis. Overall, Bachelet et al. (2001) suggested that a temperature increase above a threshold of about 4.5 °C would result in more carbon loss than sequestration across the United States. In a subsequent modeling effort, Bachelet et al. (2007) projected that biomass consumption by wildfire would increase by 25 to 67 percent across most of the assessment area over current (1961 to 1990) rates.

Lenihan et al. (2008) modeled vegetation distribution and productivity in California under three future climate change scenarios. Under the most moderate warming scenario, which also featured similar precipitation to today, the extent of tree-dominant vegetation in the assessment area increased substantially (although some losses of conifer forest occurred), and California as a whole was modeled to be a significant carbon sink by the end of the 21st century. Under the two drier and warmer scenarios, significant loss of conifer forest occurred (much of it to fire), and broadleaf expansion was not sufficient to offset a large net loss of ecosystem carbon by 2099.

Loudermilk et al. (2013) modeled carbon sequestration in the Lake Tahoe basin under two future climate scenarios that included interactions with fire. Because the basin was heavily logged at the turn of the 19th and 20th centuries, their modeling suggested that forests in the basin would remain a carbon sink until the end of the 21st century under all modeled scenarios. Including the effects of fire, however (constrained to burn in similar fashion to current fires and under continued fire suppression), under the more extreme climate scenario, resulted in 30 to 40 percent less C storage.

Canopy cover—

Canopy cover is a measure of the percentage of the ground surface that is shaded from directly above by trees. A tree's "canopy" is a polygon whose perimeter coincides with the outer edge of the tree's foliage. The canopy is assumed to be whole, and gaps within the tree canopy perimeter are not subtracted. In this section, we refer to "relative" canopy cover, where overlapping tree canopies are not double-counted (or triple-counted, etc.), so the maximum canopy cover in a plot is 100 percent. Canopy cover is usually an overestimate of the amount of shade on the underlying ground because it ignores intercanopy gaps. "Canopy closure" is better correlated with actual light availability, but it must be measured on a plot-by-plot basis and cannot be easily modeled or estimated from plot tree data (see North and Stine 2012).

NRV—As indicated in the "General forest structure" section, observations of forest cover in the 19th and early 20th centuries are overwhelmingly characterized by remarks about the general openness of the canopy of YPMC forests in and near the assessment area, but it is clear from descriptions that conditions differed across the landscape (e.g., Brewer 1930, Greeley 1907, King 1871, Larsen and Woodbury 1916, Leiberg 1902, Muir 1894, Sudworth 1900; also see Pearson [1923]) for descriptions of yellow pine forests in Arizona). Recently, a number of researchers have undertaken plot-based reconstructions of stand structural conditions in the late 19th century, and data are also now available from a number of contemporary reference sites where logging did not occur and—in many cases—where fire was not completely suppressed during the 20th century. From these studies, we can now obtain a more quantitative idea of the levels of canopy cover supported by YPMC forest stands before timber harvest and fire suppression altered much of the landscape.

Historical datasets and reconstructions of presettlement or prefire suppression conditions do not generally report canopy cover. However, most of these datasets provide data on size class distributions of trees in the sampled plots. Where such data were available, we used two methods to generate canopy cover estimates. First, we used species-specific equations for crown-width (Keyser 2010: table 4.4.2.1) from the FVS (Dixon 2002) to estimate crown area, using the midpoint of the size class in our calculations, then multiplying by the number of trees in that size class. Percentage of cover was obtained by summing across the size classes and standardizing to square meters, then dividing the result by 10 000 (number of square meters in a hectare) and multiplying by 100 for the percentage. Second, cover was adjusted by applying a formula that assumes the random spatial location of the trees in the sampled area and subtracts overlapping canopies from the maximum cover value (Crookston and Stage 1999). In table 7, we report both the adjusted value and the

Table 7—Percentage of tree cover in historical and contemporary reference yellow pine and mixed-conifer (YPMC) stands in the assessment area and comparable reference sites, arranged from north to south

Site	Mean	Standard error	Method	Observations	Source
Lassen National Forest	25.2 (29) [a]		FVS modeled estimate[b]	Modern: ponderosa pine forest, Ishi Wilderness	Taylor (2010)
North and central assessment area	48.5 (79.9) [a]	1.2	FVS modeled estimate[b]	1930s: Forest Service vegetation mapping inventory, YPMC	Dolanc (2014b
Central assessment area	69.1 (89.1) [a]	4.1	FVS modeled estimate[b]	1899: timber inventory, mixed conifer	Sudworth (1900)
Lake Tahoe Basin	16.6 (18.1) [a]		FVS modeled estimate[b]	1870—1900: stump counts, Jeffrey pine forest, east shore	Taylor (2004)
Lake Tahoe Basin	35.7 (44.1) [a]		FVS modeled estimate[b]	1893: plot-based reconstruction, mixed conifer, west shore	Taylor et al. (2014)
Lake Tahoe Basin	45.3		Line intercept	Modern: uncut old-growth, YPMC, white fir, red fir	Barbour et al. (2002)
Stanislaus National Forest	36/45[c]		Tree canopy area equations	1889/1929: plot-based reconstruction, mixed conifer	Lydersen et al. (2013)
Yosemite National Park	22		FVS modeled estimate	1911: timber inventory, mixed conifer	Collins et al. (2011)
Yosemite National Park	41 (52.7) [a]		FVS modeled estimate[b]	1899: plot-based reconstruction, moist mixed conifer	Scholl and Taylor (2010)
Sierra National Forest	33.9 (41.4) [a]		FVS modeled estimate[b]	1865: plot-based reconstruction, moist mixed conifer, Teakettle Experimental Forest	North et al. (2007)
Sequoia National Forest	12.1	5.1	FVS modeled estimate	1911: timber inventory, ponderosa pine	Stephens et al. (2015)
Sequoia National Forest	25.2	7.1	FVS modeled estimate	1911: timber inventory, mixed conifer	Stephens et al. (2015)
Assessment area (mostly southern and central)	43.7	1.5	Densiometer	Modern: YPMC forest, uncut, with frequent or recent non-stand-replacing fire	Lydersen and North (2012)
Sierra de San Pedro Mártir	24.9	2.4	Ocular estimate	Modern: Jeffrey pine, mixed-conifer forests, Baja California	Dunbar-Irwin and Safford (2016)
Sierra Juarez	35.8	7.6	Ocular estimate	Modern: Jeffrey pine, Baja California	Safford, in preparation

[a] The first modeled canopy cover value reduces crown cover by removing canopy overlap under the assumption of random distribution of stems (Crookston and Stage 1999). The value in parentheses is the total cover of all trees in the sampled plot, assuming that no trees grow beneath others. This might be taken as a rough estimate of the mean maximum canopy cover in the analyzed dataset.

[b] Forest Vegetation Simulator (FVS) modeling carried out post facto on size-class distribution data provided in the cited paper.

[c] Values refer to 1889 and 1929 reconstructions.

value before adjustment, which assumes that no trees in the stand grow beneath any others and may therefore be seen as a rough estimate of the maximum possible canopy cover in the sampled stands.

Direct measurements of tree canopy cover in contemporary reference YPMC forests, and modeled canopy cover from historical datasets both strongly substantiate the oft-stated notion that presettlement forests were generally more open than modern forests in the assessment area (table 7). Average canopy cover values ranged from around 17 percent to less than 50 percent, except in the Sudworth (1900) dataset (16 YPMC plots from his table 1), which averaged almost 70 percent. The much higher canopy covers in Sudworth's data support the notion that his data were not a random sample of forest conditions (Bouldin 1999, Stephens 2000, Stephens and Elliott-Fisk 1998). Uncorrected modeled cover values suggested that values as high as 70 to 90 percent were possible in very dense forest stands (table 7).

With respect to the FVS modeled values, it should be noted that a few studies have found that FVS techniques tend to estimate lower cover values than field-based methods, especially in areas of higher canopy cover. Fiala et al. (2006), in Douglas-fir/western hemlock forests in western Oregon, found that FVS estimated lower canopy cover than four field-based methods by 11 to 27 percent in high canopy cover mature and old-growth forests. The sampled stands were almost entirely >60 percent cover, however, and the difference between FVS and the most precise field methods became nearly zero below 60 percent canopy cover. Because YPMC forests in the assessment area were highly heterogeneous and mostly open canopied, FVS modeling probably provides a reasonable "ballpark" estimate of canopy cover for historical and reconstruction plots. Another issue is that most of the modeled FVS values in table 7 were carried out on summary data that had been organized into size classes. This lessens the variability of the input data and could affect the calculated mean in either direction, depending on the distribution of tree sizes within the size class categories.

Comparison to current—Data from the compiled FIA plots (USDA FS 2013a) show that mean modern canopy cover in YPMC forests is 45.7 percent (±21.8 SD ; west-side mean = 50 percent, east–side mean = 38 percent). The average from the 15 reference values in table 7 is 34.4 percent (±14.3 SD) when including Sudworth, 34 percent when excluding Sudworth. The FIA canopy cover values were generated using the same FVS algorithm that produced most of the values in table 7. The modern average is about 33 percent higher than the presettlement average from table 7, but, as with all of the quantitative comparisons using the FIA data, it is difficult to statistically compare the two data sources given their different scopes and sample sizes. Generally, however, the data lend strong support to the idea that current canopy cover is higher on average than under presettlement conditions.

Future—Assuming that current trends in forest densification and fire exclusion continue, canopy cover will probably continue to increase across the YPMC forest belt. This will be offset to some extent if forest mortality agents, such as fire, insects, and disease, increase.

Forest gaps and tree clumps—

NRV—A “forest gap” is an opening or hole that exists within the forest canopy, or put another way, an area within a forest stand that is unoccupied by mature trees. Forman (1995) argued that gaps are small entities that exist within a mosaic of larger landscape “patches” (or what foresters refer to as “stands”), where a patch is a relatively large and homogeneous area that differs from its surroundings in its structure and composition. Essentially, patches are a component of coarse-grained heterogeneity, whereas gaps are a component of fine-gained heterogeneity. In assessment-area YPMC forests, the historical rarity of large-scale severe disturbances resulted in a very fine-grained structural heterogeneity that does not lend itself well to the recognition of landscape patches (Franklin and Fites-Kaufman 1996, USDA FS 2001). Given the generally low canopy cover and clumpy nature of YPMC forest stands, many presettlement forest stands were as dominated by gaps as by trees.

When gaps are created in the canopy, enhanced light is provided to the forest understory, which often results in a dynamic ecological response from both plants and animals. Gaps are important locations for tree, shrub, and herb regeneration, and they also serve a variety of roles in providing cover, forage, and other habitat for animals. Gaps are created through disturbance processes (“disturbance patches”), or they can also arise as a consequence of the physical habitat, e.g., soil type, rocks, and so on (“environmental patches”). The sizes and distributions of canopy gaps in forested ecosystems are important ecological variables (Agee 1993, Connell 1989, Spies and Franklin 1989), and over the past few decades it has become clear that the creation and maintenance of canopy gaps are important forest management objectives. Because open gaps in the forest canopy in a reasonably productive forest will quickly fill with regeneration, the size of “regeneration patches” can be roughly equated to the sizes of the original disturbance patches that led to the regeneration event. After growth to adult size, the surviving members of the regeneration patch will form an aggregation of trees, or a “tree clump” (Agee 1993). In general, canopy gaps are somewhat larger that the regeneration patches that arise within them, and mature tree clumps somewhat smaller than the regeneration patches that gave rise to them (Fry et al. 2014, Stephenson 1999).

Larson and Churchill (2012) outlined three components of local pattern in frequent-fire YPMC forests: tree clumps, widely spaced individual trees (usually large), and openings. Tree clumps could be composed of similar-aged overstory trees or multiaged aggregates, or they could be regeneration patches. In the studies that Larson and Churchill (2012) reviewed, the average number of trees in a clump ranged from 2 to 44 trees, and the average number of clumps per hectare ranged from 10 to 27. Fry et al. (2014) compared spatial clustering within reference YPMC forests in the SSPM of Mexico and forests in the Sierra Nevada of California, and found that the mean number of trees per clump ranged from 5.8 to 7.4 in Mexico and from 8.1 to 11.2 in California, with a larger proportion of trees found in large patches in California than in Mexico.

A number of studies in and around the North American Mediterranean climate zone have used stand-mapping techniques to estimate typical sizes of canopy gaps, regeneration patches, and tree clumps in YPMC forests. Table 8 provides a summary of the range of published gap-patch-clump sizes in the literature. Minimum sizes averaged about 0.04 ha, and maximum sizes averaged about 0.3 ha, with a maximum range from 0.07 ha to 1.17 ha. Larson and Churchill (2012) conducted an independent summary of tree clump sizes in YPMC forests across the Western United States, and found a range of 0.003 to 0.4 ha per clump. Their summarized range for regeneration patches was somewhat wider, but with a similar mean: 0.001 to 0.64 ha.

Table 8—Sizes of canopy gaps/regeneration patches/tree clumps in historical and contemporary reference yellow pine and mixed-conifer stands in the North American Mediterranean zone and the neighboring southwestern United States, arranged from north to south

Site	Minimum size	Maximum size	Observations	Source
	Hectares			
Central Oregon	?	0.16	Ponderosa pine; tree clumps	Youngblood et al. (2004)
Eastern Oregon	0.025	0.35	Ponderosa pine; tree clumps	Morrow (1985)
Lassen National Forest	0.003	0.14	Ponderosa pine-black oak; tree clumps	Taylor (2010)
Lassen National Forest	?	0.18	Ponderosa pine; tree clumps	Youngblood et al. (2004)
Lake Tahoe basin	0.003	0.07	Jeffrey pine-white fir; tree clumps	Taylor (2004)
Stanislaus National Forest	0.03	0.21	Mixed conifer; canopy gaps	Knapp (2012)
Kings Canyon National Park	0.014	0.16	Sequoia-mixed conifer; tree clumps	Bonnicksen and Stone (1980)
Sequoia National Park	0.16	1.17	Sequoia-mixed conifer; canopy gaps	Demetry (1995)
Northern Arizona	0.02	0.29	Ponderosa pine; tree clumps	White (1985)
Eastern Arizona	0.06	0.26	Ponderosa pine; regeneration patches	Cooper (1960)
Sierra de San Pedro Mártir, northern Baja California	0.001	0.07	Jeffrey pine-mixed conifer; regeneration patches	Stephens and Fry (2005)

Lydersen et al. (2013) described reference and current variability in canopy gaps and tree clumps in plots in a mixed-conifer forest in the central Sierra Nevada (same area studied by Knapp et al. [2012, 2013]). They found that, between 1889 and 2007–2008, the areal proportion of the studied stands occupied by canopy gaps fell from about 50 percent to nearly zero, and gap density dropped from 6.2 gaps/ha to 0.2 gaps/ha. Lydersen et al. (2013) also found that the average number of trees found in a definable clump rose from 5.2 trees/clump to 26.3 trees/clump over the same period, and the maximum number of trees per clump rose from 27 trees/clump to 543 trees/clump. Overall, the modern stands were extremely homogeneous in canopy cover, and completely lacked canopy gaps greater than 250 m^2 in area.

***Future*—**Increased forest densification will continue the trend of reducing forest openings/gaps. This will be offset to some extent if forest mortality agents continue to increase.

Snags and coarse woody debris—

***NRV*—**As he left the Sierra Nevada after 3 years of travel and mining, Peter Decker, in his diary from 1849 to 1851, wrote that dead trees were seldom seen and, “it is very rarely that timber is laying rotting” (Giffen 1966: 232). Arno (2000: 100) stated that, in western YPMC forests characterized by understory fires, “shrubs, understory trees, and downed logs were sparse, as testified to by dozens of historical photographs and narrative accounts.” In areas characterized by more moderate/mixed-severity fires, surface fuels, snags, and coarse woody debris (CWD) tended to be heterogeneously distributed, with concentrations found in scattered patches (Arno 2000). Skinner (2002) wrote that, because YPMC forests in California burned so often, “It is unlikely that much large woody material survived fire long enough to decompose fully in fire regimes that preceded the fire-suppression era.”

Stephens (2004) reported on fuel loads and snag densities in unlogged YPMC forests in the SSPM, which also have seen only recent suppression of fires. Stephens (2004) found that snag density in the sampled forests (all stems ≥2.5 cm d.b.h.) averaged 3.5/ha before a major drought, and 5.1/ha after a multiyear drought. Heterogeneity in snag distribution was very high: the modal snag density in the first sample (before drought) was 0 snags/ha (35 percent of plots), in the second sample (after drought) it was about 2.5/ha (27 percent of plots had no snags). The average snag measured 59 cm d.b.h. Coarse woody debris, measured as the 1,000-hr fuels (branches and logs >7.6 cm d.b.h.), averaged 15.8 tons/ha, but more than a third of plots had no CWD and only 20 percent of the plots supported 75 percent of the CWD. Eighty-one percent of the CWD was in a rotten state, and 19 percent was sound (Stephens 2004).

Stephens et al. (2007) reported on CWD over 15 cm in diameter and ≥1 m long from the SSPM. Thus defined, CWD averaged 15.7 tons/ha, with a large range (0 to 154.5 tons/ha). The median was only 1.4 tons/ha, and about half of the plots sampled contained no CWD of this size or above. Overall, the average density of CWD was about 108 pieces/ha (±16.3 SE). Most sampled logs were rotten.

Lydersen and North (2012) sampled assessment-area YPMC forests that had not been logged and had experienced at least two fires in the 65 years before the field work commenced. They found very high variability in snag and CWD measurements. Snag density for snags greater than 50 cm d.b.h. averaged 9.1/ha, and snag volume averaged 123 m^3/ha (±20.1 SE), with the highest densities and volumes of snags occurring on lower, northeast-facing slopes. Lydersen and North (2012) provided two measurements of CWD: logs ≥50 cm in diameter averaged about 10.3 pieces/ha (no measurement of variability given), while 1,000-hr fuels (>7.6 cm diameter) averaged 32.3 tons/ha (±3.4 SE).

Agee (2002), in a paper discussing the general relationship between fire regime and the creation and persistence of snags and CWD, suggested that a Fire Regime I forest with an undisturbed fire regime might typically support around five snags/ha, with the average snag size about 75 cm d.b.h. According to Agee (2002), CWD derived from the same average size of tree might total around 5 tons/ha. Because of very frequent fire in these forest types, both snags and CWD would fall or decompose at a higher rate than under conditions free of fire. For so-called mixed-severity fire regimes, Agee (2002) estimated that snag densities and CWD mass would be higher, as fires were more severe, which creates more snags and CWD, and less frequent, which allows them to persist longer on the landscape. Agee cited Wright (1998), who found an average of 40 tons/ha of snags and 55 tons/ha of CWD (ranging from 20 to 250 tons/ha) in Douglas-fir forests. Agee (2002) noted that modern fire-suppressed forests that used to experience frequent, low-severity fire might now support (much) more CWD than they did under presettlement conditions. Concerning these Fire Regime I forests, Agee (2002) stated that:

> Burning prescriptions designed to retain most coarse woody debris can produce a “non-window”: duff moisture levels so high that such moisture contents are rarely if ever attained on these sites. Constraints to preserve all or most coarse woody debris effectively eliminate the use of fire for restoration purposes and leave the dry forest types at risk for stand-replacing fire. When such high-severity fire occurs, it brings with it the “boom and bust” coarse woody debris dynamics of the high severity fire regimes. This is a

> classic case of the fine-filter (log preservation) trumping the coarse-filter (restoring the natural process), and in the long run is likely to result in a failed conservation strategy.

Harrod et al. (1998) used stand reconstruction and modeling techniques in an attempt to derive historical reference conditions for snag densities for an area of dry ponderosa pine/Douglas-fir forest in eastern Washington. They determined that, depending on the size classes included, snag densities under presettlement conditions probably ranged from about 14.5 to 34.6 snags/ha. Agee (2002) noted that Harrod et al. (1998) did not incorporate the effects of fire on snag-fall rates, implying that their numbers were probably biased upward.

Youngblood et al. (2004) studied three areas of old-growth ponderosa pine forest in eastern Oregon and northern California. All sites had experienced about a century of fire exclusion, although parts of the California site had recently experienced a prescribed fire. Youngblood et al. (2004) found that snag densities ranged from 8 to 12/ha (trees ≥15 cm d.b.h.), and CWD (≥15 cm diameter and 1 m long) averaged about 47 pieces/ha (±5.3 SE). Eighty-five percent of the CWD was between 15 and 65 cm in diameter, and most pieces were rotten (i.e., old). Youngblood et al. (2004) noted that the long-term demography of both snags and CWD in Western frequent-fire forests is largely unknown, with the current lack of fire in these stands a particular impediment. They suggested that, with respect to their ability to discern presettlement reference conditions from their data, fire exclusion over the previous century had probably biased their measurements of CWD (and snags) upward.

Comparison to current—Stephens (2004: 109) provided a table (his table 4) summarizing snag densities for seven studies in areas managed under fire suppression during the 20th century, two of which had also experienced timber harvest. The minimum sizes of measured snags differ from study to study, but the average snag density from these seven sites is 47.9 snags/ha, an order of magnitude higher than found in Stephens' (2004) study of the SSPM, and also much higher than two other studies of unlogged YPMC forests also summarized in the table (Savage 1997, Stephens 2000).

Dunbar-Irwin and Safford (2016) carried out a direct statistical comparison of snag densities and CWD in the SSPM versus an array of forest plots sampled in analogous YPMC forests on the Sierra Nevada east slope. In SSPM, Dunbar-Irwin and Safford (2016) sampled from a much broader geographic area than Stephens (2004) or Stephens et al. (2007). They found that snag densities (trees

>10 cm d.b.h.) averaged 12/ha in SSPM (±2.8 SE), while the fire-suppressed eastern Sierra Nevada plots averaged 31/ha (±8.7 SE). Coarse woody debris (1,000-hr fuels) was not significantly different between the two regions, and averaged 28.9 tons/ha in SSPM vs. 25.1 tons/ha in the eastern Sierra Nevada; the median CWD loading was higher in the eastern Sierra Nevada (5.9 tons/ha vs. 4.8 tons/ha in SSPM). Note that Dunbar-Irwin and Safford sampled 16 years after Stephens (2004), during which time SSPM suppressed every lightning-ignited fire in the park. This would partly explain the higher snag and CWD values found in the more recent study.

Studies of the effects of prescribed fire on CWD and snags in the assessment area provide more evidence that levels of both were probably lower on average in presettlement forests than in current, unlogged (but fire-excluded) forests. Kauffman and Martin (1989) summarized the results of 60 prescribed fires conducted at three experimental sites in the northern Sierra Nevada in the mid-1980s. Fires were ignited at four different times of year: early and late spring, and early and late fall. We summarize the results from late spring and early fall burns, as they best represent the natural fire season in the assessment area: fires reduced the mass of sound CWD (>7.6 cm diameter, i.e., 1,000-hr fuels) by 62 percent on average, and the mass of rotten CWD by 87 percent, resulting in an overall postfire mean of 11.3 tons/ha; CWD averaged about 28 tons/ha before fire.

Various other studies of the effects of prescribed fires on CWD and snags corroborate the Kauffman and Martin (1989) results in indicating that frequent fire in these forests would quickly consume most of the snags and CWD that have resulted from a century of fire exclusion. For example, Kilgore and Sando (1975) measured 15 tons/ha of 1,000-hr CWD after fire (down from 97.5 ton/ha prefire); Stephens and Finney (2002) measured 3.4 tons/ha (from 42.1 tons/ha prefire); and Knapp et al. (2005) reported 15 tons/ha postfire (from 66.2 tons/ha prefire) for their fall burn. Kilgore (1973b) measured the change in log (>15 cm diameter) mass after prescribed fire, finding a reduction to 2.8 tons/ha from 12.8 tons/ha prefire. Knapp et al. (2005) also measured losses in log mass (>15 cm diameter) to a fall prescribed fire: postfire = 7.4 tons/ha, prefire = 47.2 tons/ha. Kilgore (1973b) reported that snags were almost entirely reduced to charred stumps and cavities in the prescribed fire he studied. Uzoh and Skinner (2009) investigated the effects of prescribed fire on CWD (≥7.6 cm diameter) at Blacks Mountain Experimental Forest in the northern subregion of the assessment area. A single fall burn reduced CWD mass by 1.5 to two times more than the mechanical treatment effects, which also reduced CWD. In the burned plots, overall reductions of CWD ranged from 57 to 90 percent, with higher losses in the more decayed CWD classes. Uzoh and Skinner (2009) concluded that "restoration goals that include large amounts of decayed, CWD do not appear to be appropriate for these dry pine forests of northeastern California."

An important point is that these large reductions in CWD (and snags) were the result of single prescribed fires under moderate conditions at times of the year when naturally ignited fires are uncommon because of higher fuel moisture. They were also all carried out in stands that had not experienced fire for 50 to 100 years or more. Average fire return intervals in presettlement assessment-area YPMC forests were between 10 and 20 years, and such frequent fire would likely have rapidly reduced snag densities and CWD loadings.

Average fire return intervals in presettlement assessment-area YPMC forests were between 10 and 20 years, and such frequent fire would likely have rapidly reduced snag densities and CWD loadings.

The most recent FIA data compilation (USDA FS 2013a) gives an average of 23 tons/ha (±12.9 SD) for CWD measured as 1,000-hr fuels (≥7.6 cm diameter) in contemporary YPMC forests. The average of Kauffman and Martin (1989), Kilgore and Sando (1975), Knapp et al. (2005), Lydersen and North (2012), Stephens (2004), and Stephens and Finney (2002), all of which we interpret to broadly represent reference conditions, is 15.5 tons/ha (±9.4 SD). The FIA cutoff for measurement of logs is a diameter of 25 cm, which does not perfectly correspond to any of the studies we found in the scientific literature. Nonetheless, the FIA average density for logs ≥25 cm in diameter is 42.6 pieces/ha, which is comparable to the density of 44.8 pieces/ha (logs ≥30 cm diameter) found by Stephens et al. (2007) in the SSPM.

FIA data give an average snag density (≥15 cm d.b.h.) of 37.2 snags/ha (±69.5 SD; mixed-conifer mean = 47.7 snags/ha, yellow pine mean = 20.2 snags/ha) for contemporary assessment-area YPMC forests. For the same size categories, Stephens (2004) found 4.4 snags/ha in the reference forests in the SSPM, and Youngblood et al. (2004) found 8 to 12 snags/ha in the old-growth pine forests they studied. Harrod et al.'s (1998) estimate of presettlement yellow pine forests in eastern Washington, which did not account for fire consumption of dead trees (see above), was in the range of 14 to 36 snags/ha.

Based on these data sources and considerations, we conclude that the levels of CWD and snags in modern YPMC forests in the assessment area are somewhat higher on average than in the average presettlement YPMC forest stand. Note that this statement does not pertain to the area of intensive beetle mortality that has occurred since 2014–2015. In this area, snag densities and CWD are both orders of magnitude higher than under average presettlement conditions.

Future**—**Continuation of current trends toward more snags and CWD seems likely, especially if nonfire forest mortality agents increase substantially. Increases in fire frequency will increase snags and CWD initially, but will reduce them as areas are reburned.

Forest Understory and Nonforest Vegetation

Few of the early observers of assessment-area YPMC forest provide more than passing reference to nonforest vegetation, except with respect to seedling and sapling densities and an occasional reference to shrubs.

Tree seedlings and saplings—

***NRV and comparison to current*—**The very low average density of tree seedlings and saplings in YPMC forests alarmed early foresters in the assessment area, but it was clear to them that recruitment potential was high and fire was the main factor reducing recruitment (e.g., Greeley 1907, Leiberg 1902, Show and Kotok 1924, Sudworth 1900). Sudworth (1900) wrote that:

> The frequent open spaces in yellow-pine forests are sooner or later covered with dense patches of young trees, but these thickets may in turn be swept off by fire. So continuous and widespread are these forest fires that… they keep a very large percentage of the seedling growth down… The forest floor looks clean swept. But the remarkable productive power… is seen only in localities where fences and the exclusion of fire have protected the incoming seedlings. Here the stand is so dense as to be quite impenetrable.

Where seedlings and saplings successfully survived (usually because of longer intervals without fire), shade-tolerant species tended to dominate. Greeley (1907) wrote:

> The very large proportion of fir and cedar in its reproduction is the worst feature of the west Sierra Forest. Both of these species are prolific seed bearers… Except at lower elevations and on very warm exposures, where yellow pine grows in pure stand, dense thickets of fir and cedar crowd the young pine down to one fifth or less of the reproduction.

Bonnicksen and Stone (1982), in one of the first modern stand reconstruction studies, noted that the 1890s landscape at their study site supported much more open ground with seedlings and saplings than the current forest. Around 50 percent of the area covered by seedling and sapling “aggregations” was dominated by white fir, which surprised the authors, as they had expected shade-intolerant species to dominate recruitment into gaps.

What emerges is an ecosystem in which conditions were greatly determined by the frequency and nature of fire. Frequent fire substantially reduced reproduction, and the resulting bare mineral soil and open forest conditions favored species like yellow pine and black oak, which could better survive low-intensity burns and did better under high light conditions (Barbour et al. 2007, Burns and Honkala 1990, Moghaddas et al. 2008, Pearson 1942).

Modern reference sites like the SSPM or Beaver Creek Pinery (Lassen National Forest) show very high heterogeneity in seedling densities, which is similar to the conditions described by early observers. The mean seedling density in the SSPM was measured by Stephens and Gill (2005) at 125 seedlings/ha, with about 50 percent of the sampled plots supporting <100 seedlings/ha and 10 percent supporting >300 seedlings/ha. Sixteen years of fire exclusion later, Dunbar-Irwin and Safford (2016) found mean seedling densities in SSPM of 420 per hectare, but the median was zero; the coefficient of variation for seedling density in SSPM was more than twice as high as in the eastern Sierra Nevada plots that were compared to it. Mean seedling density in the Beaver Creek Pinery was measured by Taylor (2010) at about 660 seedlings/ha, including ponderosa pine and black oak. More than two-thirds of the ponderosa pine seedlings were found in high light conditions in forest gaps and variation in densities was very large, ranging from 37 to 1,408 seedlings/ha. It was observed that surviving seedlings after fire in the Beaver Creek Pinery tended to be associated with open canopy gaps that did not burn because of the lack of surface fuels, whereas seedlings were killed where they grew in gaps with some canopy cover that supported sufficient needle litter to carry fire (see footnote 3).

It was observed that surviving seedlings after fire in the Beaver Creek Pinery tended to be associated with open canopy gaps that did not burn because of the lack of surface fuels, whereas seedlings were killed where they grew in gaps with some canopy cover that supported sufficient needle litter to carry fire.

Compilation of the most recent FIA data (USDA FS 2013a) gives a mean of 1,820.6 seedlings/ha (± 3.973 SD) for yellow pine and mixed-conifer plots. The coefficient of variation (CV) is 2.2, which indicates high variance in seedling density among plots. We conclude from the data and from inference based on successional processes that current mean seedling densities are almost certainly higher than mean seedling densities under presettlement conditions.

Future—Seedling composition will largely reflect the overstory composition (van Mantgem et al. 2006). The very high proportion of shade-tolerant species in current YPMC forests in the assessment area suggests that future forest recruitment will be dominated by species like white fire and incense cedar. Even where repeated, prescribed fires have been employed in order to enhance pine and oak recruitment, the persistence of mature shade-tolerant species in the forest canopy has resulted in a strong dominance of these species in postfire seedling densities (Webster and Halpern 2010). If an increase in recruitment of fire and drought-tolerant species is desired, removal of shade-tolerant species from the overstory or direct planting of fire-tolerant seedlings may be necessary. If fire-tolerant species are already present at sufficient numbers in the overstory, the restoration of a frequent fire regime may accomplish this same objective.

Shrubs—

***NRV and comparison to current*—**Like tree cover, most evidence is that shrub cover in presettlement YPMC forests was relatively low but highly heterogeneous on the landscape. For example, Fitch (1900) described forests in the Yosemite area as: "…remarkably free from undergrowth… and only along streams, in the bottom of gulches, and on rocky southern slopes is the brush so thick as to impede progress." Marshall (1900), surveying the higher elevations of Yosemite National Park for the U.S. Geological Survey, which included some areas of moist mixed conifer, stated that the forest was "everywhere open without undergrowth of any kind." Decker, in his journal, wrote of the forests in the upper Mokelumne River drainage that there was "generally no underbrush" (Giffen 1966). On the other hand, Bruff, in his journal from the same time period refers to both open forests and forests with dense, bushy undergrowth (Read and Gaines 1949).

Leiberg (1902) stated that much of the forest understory in his survey area was more or less bare. At the same time, he noted that burned areas supported a "great amount" of undergrowth, mostly dominated by species of *Ceanothus*, which he ascribed to recent anthropogenic fire activity. According to Leiberg (1902), burned areas in YPMC forest often supported dense growths of montane chaparral, from 1.2 to 1.5 m in height. He was convinced that montane chaparral came only from fire in previously forested stands and counted such areas as representing destroyed forest even where there wasn't any evidence of previous forest (Miller and Safford 2017). Greeley (1907), referring primarily to fires set by Euro-Americans, decried the loss of valuable timberlands to montane chaparral. Contemporary data from the Plumas National Forest and Illilouette Creek basin in Yosemite confirm that fire-created chaparral patches are more likely to reburn at high severity, which can result in inhibition of forest succession and a (semi-) permanent conversion to chaparral (Coppoletta et al. 2016, van Wagtendonk et al. 2012).

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Mitchell (1913) noted that the quantity of brush (shrubs) in yellow pine forest tended to be minimal, but it was much higher in mixed-conifer stands (and even higher in red fir forests). Given that forest openings were much more prevalent in yellow pine stands, the difference was probably due to more frequent fire (which reduced shrub cover), less intense fire (which would result in less fire-induced germination of shrubs like *Ceanothus* or manzanita), and lower site productivity.

By using the section-line information recorded by crews doing GLO surveys, Baker (2014) found that >90 percent of the area surveyed had some mention of shrubs, mostly *Ceanothus* and *Arctostaphylos*. Surveyors neglected, however, to record entry or exit information from shrub patches on almost 30 percent of northern Sierra section-lines, and more than 55 percent of southern Sierra section-lines, so an estimate of shrub cover is not possible. Stephens et al. (2015) found that 54 percent of belt transects from a 1911 timber survey in the Greenhorn Mountains of the Sequoia National Forest contained shrub patches, and the average shrub cover within a given transects was 25 percent.

Show and Kotok (1924) decried the loss of forest to severe fires set by humans, especially in situations where logging slash was heavy. Severe forest fires in the assessment area normally result in postfire succession to shrublands (usually some form of chaparral), especially on the west side. In the absence of further fire, such shrublands will last for decades before succession to forest occurs. In the presence of further fire, such stands can become quasi-permanent features of the landscape, because chaparral generally burns at high intensity and kills most young trees (Nagel and Taylor 2005, Skinner and Taylor 2006). Show and Kotok (1924) produced a table providing summaries of the areas of the 10 northern national forests (minus the Modoc) that supported "brushfields" in the early 1920s. In their interpretation, these brushfields had developed in previously forested stands after fires set by Euro-American settlers. We reproduce that table for the six national forests in the assessment area in table 9, and compare it to modern areas of chaparral on the same national forests. Percentages of national forest area in brushfields in the early 1920s ranged from 7 percent on the Eldorado National Forest, to over 16 percent on the Stanislaus National Forest; the overall average was about 11 percent. Modern data (from the most recent Forest Service existing vegetation mapping, data at http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836), using "mixed chaparral" and "montane chaparral" California Wildlife Habitat

Table 9—Estimated percentages of the area covered by seral shrub fields in 1924 and the early to mid-2000s on six national forests in the assessment area

	Seral shrub fields	
National forest	1924[a]	2000s[b]
	Percent	
Lassen	11.8	8.5
Plumas	11.7	6.2
Tahoe	8.6	10.6
Eldorado	7.0	9.2
Stanislaus	16.2	9.9
Sierra	11.1	7.0
Average	11.1	8.6

[a] Data are from table 19 in Show and Kotok (1924).

[b] Data from most recent Forest Service existing vegetation maps, using "Classification and Assessment with Landsat of Visible Ecological Grouping" types of mixed chaparral and montane chaparral where growing in areas identified as having sufficient productivity to support forest. Imagery is from the early and mid-2000s.[17]

Relations types where they occur in sites identified as having sufficient productivity to support forest as our definition of shrublands, show that the overall averages are slightly lower on average. Four of the national forests experienced a decrease in the area occupied by shrubs, and two experienced increases. According to our comparison, the Eldorado National Forest experienced the greatest increase (+31 percent), the Plumas National Forest the greatest decrease (-47 percent). Note that the most recent vegetation mapping on the northern Sierra Nevada national forests (Lassen, Plumas, and Tahoe) was completed some time ago, using imagery from 2000 and 2005.[14] The values in table 9 thus exclude the large expanses of fire-caused shrubfields that have resulted from the high number of large, often very severe fires that have occurred in the northern Sierra Nevada and southern Cascade Range since 2005 (e.g., Rich, Butte Lightning Complex [BTU], Moonlight, Antelope Complex, Chips, Reading, Eiler). Including these numbers would raise the modern percentages substantially, especially on the Plumas National Forest. Note also that the techniques for measuring the areal extent of shrubfields in the two surveys were different (summary of ocular and land surveyed measurements in 1920s, versus remotely sensed imagery in 2000s), and the numbers in table 9 should therefore be viewed as approximations.

Modern studies of reference YPMC forests have found an average of about 15 to 25 percent relative shrub cover (but with high variability) in forests that have not been logged or have not experienced complete fire exclusion (table 10). Note that very large areas of chaparral would not have been sampled by these studies as they would not be considered forest for sampling purposes.

Contemporary FIA data on shrub cover are difficult to compare with other datasets, as shrub cover is computed by summing the species-specific covers without accounting for overlap (and therefore total cover can sum to more than 100 percent). Average absolute cover by shrubs in YPMC forest plots is 22.6 percent (±23.3 SD) (USDA FS 2013a). These values will be higher than the actual relative values.

Bonnicksen and Stone (1982) carried out a stand reconstruction in a small watershed of YPMC and giant sequoia forest in Kings Canyon National Park. They estimated that about three-fourths of the forest aggregations dominated by large and very large trees had some sort of shrub cover in their understory in 1890. They also found that about 19 percent of the watershed was covered by shrub-dominated “aggregations” in 1890 versus 11 percent in 1977, but these would have represented shrubfields rather than forest understory.

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[14] Ramirez, C. 2013. Personal communication. Vegetation mapping and inventory lead, U.S. Department of Agriculture, Forest Service, Remote Sensing Lab, 3237 Peacekeeper Way, McClellan, CA 95652.

Table 10—Percentages of shrub cover in reference yellow pine and mixed-conifer (YPMC) stands in the North American Mediterranean zone

Site	Mean	Median	Mode	Standard error	Observations	Source
	Percent					
Northeastern assessment area	21.4	8	8	1.0	Yellow pine forests, mature and old-growth, uncut	Smith (1994)
Northern assessment area	20.8	11.5	10	3.9	Mixed-conifer forests, mature and old-growth, uncut	Fites (1993)
Assessment area (mostly southern and central)	16.9			1.9	YPMC forest, uncut, with frequent or recent non-stand-replacing fire	Lydersen and North (2012)
Stanislaus National Forest	28.6			5.5	YPMC forest on productive site, 40 years after most recent fire	Knapp et al. (2013)
Sierra Juarez, northern Baja California	16.3	17.5	0	3.5	Yellow pine forests, mostly uncut, only recent fire suppression	Safford, in preparation
Sierra de San Pedro Mártir, northern Baja California	17.4	5	0	2.9	Mixed-conifer forests, uncut, only recent fire suppression	Dunbar-Irwin and Safford (2016)

Vankat and Major (1978) found that, in general, shrub cover had dropped in YPMC forests in Sequoia & Kings Canyon National Parks over the previous half century or more. They ascribed the changes to more light competition from trees, increased browse by ungulate populations, or less fire. The most affected shrub genera were *Arctostaphylos* and *Ceanothus*, both of which support species with fire-cued germination. Vankat and Major (1978) also noted some areas in which shrub cover had increased.

Laudenslayer and Darr (1990), studying areas where timber harvest had occurred, stated that shrub cover had increased in most places owing to greater availability of light and the long-term lack of fire, which they suggested had reduced shrub mortality.

Comparison of aerial photos from 1930s and 1940s with photos from today sometimes shows greater cover of shrubland in the early photos. It is difficult to determine whether the early photos are NRV, however, as there were many severe fires set by settlers in the late 1800s. For example, Nagel and Taylor (2005) found that the average area of six chaparral stands in the Lake Tahoe basin retracted by 62.4 percent between 1939 and 2000. Note that these comparisons are mostly focused on large stands of chaparral, rather than patches of shrubs found within the forest matrix itself.

Thorne et al. (2008) compared Forest Service VTM maps from the 1930s (Wieslander 1935) with modern Forest Service vegetation maps in the lower elevations of Eldorado County, on the west side of the central assessment area. They found that the extent of montane chaparral stands had declined by more than 90 percent over the 60-year period. Thorne et al. (2008) noted that some of these stands had potentially transitioned to hardwood stands, but others were large patches of chaparral from earlier timber harvest and fires that were reoccupied by conifer forest after the institution of fire suppression. As above, the extent of chaparral on the landscape in the 1930s was probably notably enhanced over presettlement conditions by human activities.

Kauffman and Martin (1990) reported on the effects on shrubs of 60 prescribed fires in the northern Sierra Nevada. We report only those results from the late spring and early fall burns (n = 30), as they best replicate the seasonality of natural fires. Kauffman and Martin (1990) found that fires at these times of year tended to consume more fuel and (mostly) burned more intensely than fires in the early spring and late fall. One year after fire, an average (across the three study sites) of 25 percent of shrubs within the burn plots had survived the early fall burns, and 36 percent survived the late spring burns. Kauffman and Martin (1990) also tracked 2-year survival of black oak and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehder) and found only 9 percent survival of black oak and 18 percent survival of tanoak in the early fall burn and, 28 percent and 21 percent survival, respectively, from the late spring burn. Survival was higher from the early spring and late fall burns. Seedling recruitment and sprouting from *Ceanothus* species was relatively strong, with hotter burns increasing mortality and reducing sprouting but increasing the number of seedlings. Kauffman and Martin (1990) concluded that intense burns could be used to reduce shrub cover on sites where that was a management goal.

Knapp et al. (2012) studied the shrub seed bank in 24 assessment-area YPMC sites. They found that seeds of *Ceanothus* were found at 88 percent of the unburned sites, at high densities (mean = 246 seeds/m^2 of soil surface), and as deep as 10 cm. *Arctostaphylos* and *Prunus* seeds were found at 64 and 45 percent of the unburned sites, respectively. The intrinsic potential for shrub response to fire is thus very high throughout assessment-area YPMC forests, and it has not been appreciably affected by fire exclusion.

Overall, considerations of shrub cover on assessment-area landscapes suggest that the overall portion of the YPMC landscape occupied by shrubs today is broadly similar to, but possibly somewhat lower than, the portion occupied at the beginning of the 20th century. Many early observers believed that shrub cover had been increased after Euro-American settlement, so it may be that the current overall areal extent of shrublands is actually somewhat higher than when Euro-Americans began arriving in the mid-19th century, but we have no quantitative data to substantiate this inference. At the same time, fire suppression, logging, and other management practices since the beginning of the 20th century have greatly homogenized assessment-area YPMC forests, resulting in higher canopy cover and denser stands, and less optimal conditions for shrub survival in the forest understory. In summary, the landscape extent of shrubfields and other early seral vegetation within the YPMC forest belt is probably within NRV, but shrub cover in the forest understory has probably been generally reduced by increasing tree density and canopy cover and decreasing understory light availability.

Future—The increase in fire area, fire severity, and high-severity patch size in assessment-area YPMC forests over the last quarter-century (Mallek et al. 2013, Miller and Safford 2012, Miller et al. 2009b) has led to a recent increase in the extent of early seral montane chaparral stands, especially in Forest Service lands in the northern half of the assessment area. Most future models and analyses of paleo-data suggest that future disturbance cycles and warming climates will further increase the amount of early seral vegetation on assessment area landscapes (e.g., Cole 2010, Lenihan et al. 2008, McKenzie et al. 2004).

Grass and forbs—

NRV and comparison to current—William Brewer's (1930) memoirs of his 1861–1864 travels with the Whitney Survey refer to the scarcity of good grass cover in the Sierra Nevada, and lush areas of grass are highlighted where they occur. Sudworth (1900) also referred repeatedly to the lack of good pasturage, and stated toward the beginning of his report that "…forage is exceedingly short on all the unfenced mountain ranges." Later Sudworth suggests that in many places, the lack of herbaceous growth is due to the effects of sheep grazing, although it is important to note that his field surveys also coincided with one of the worst California droughts on record. Interestingly, Fitch (1900), working adjacent to Sudworth's survey area, described "excellent pasturage" on high mountain slopes, meadows, and river valleys, as well as in open timber stands. None of Sudworth's photos from the YPMC forests, except perhaps one from the lower boundary with the oak-foothill pine belt, which supports much annual grassland, show any obvious areas of grass cover. Leiberg (1902) noted that humus layers were rare to nonexistent in the forests he surveyed, and the forest floor was usually bare, perhaps with a layer of needles "rarely exceeding two inches in depth."

Evett et al. (2007, 2006), studied soil phytoliths in mixed-conifer forests in the North American Mediterranean zone, looking to determine whether there was any support for hypotheses of substantial grass cover in presettlement YPMC forests. Phytoliths (also known as "grass opal") are small structures of silica left behind in the soil after death of the parent plant, and grass phytoliths are morphologically unique. Evett et al. (2006) found that the grass phytolith content of soils in a giant sequoia–mixed-conifer forest in the southern Sierra Nevada indicated a long-term (at least centuries-long) lack of a substantial grass component at the study site. However, the study found evidence of somewhat higher grass cover in some places on the landscape, such as in ponderosa pine-dominant forest on ridge tops, and in areas near stream channels. Evett et al. (2007) carried out a similar study in a Jeffrey pine/mixed-conifer forest in the SSPM of northern Baja California. As above, they found that grass phytolith levels were too low to indicate extensive cover of grass over the previous centuries.

Takahashi et al. (1994) studied volcanic soil development under mixed-conifer forests in northern California. Presence of melanic epipedons (humus) in forest andisols has traditionally been ascribed to periods in which the soils supported grassy vegetation, but phytolith analysis of the California YPMC soils showed very little to no grass component could have been present during the formation of the soils, i.e., over many centuries. According to Takahashi et al. (1994), the occurrence of frequent fire in their study forests may have been the key factor in forming melanic epipedons in the andisols they studied.

Modern surveys of YPMC forests in the California Mediterranean zone do not suggest that grass or forb cover is particularly high, even in relatively undisturbed stands with low canopy cover.

Modern surveys of YPMC forests in the California Mediterranean zone do not suggest that grass or forb cover is particularly high, even in relatively undisturbed stands with low canopy cover. Smith (1994) described 45 associations of yellow pine forests in the northeastern assessment area, sampling only from uncut stands that were at least 100 years old. Few of the sampled sites were heavily grazed.[15] Average overstory cover (relative) was about 53 percent (range = 13 to 82 percent), shrub cover 21.4 percent (range = 1 to 61 percent), forb cover 8.9 percent (range = 2 to 41 percent), and grass cover 6.5 percent (range = 2 to 20 percent). Fites (1993) conducted a similar survey of older and undisturbed mixed-conifer forests in the northern and southern Cascade Range. Canopy covers were much higher in these more productive sites (range = 25 to 96 percent), and forb and grass covers similarly low (relative cover means of 11.8 percent and 3.2 percent, respectively). Oliver (2000) described forest conditions

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[15] Smith, S. 2003. Personal communication. Sierra-Cascade province ecologist, USDA Forest Service, Modoc National Forest, 225 West 8th Street, Alturas, CA 96101.

at Black Mountain Experimental Forest on the Lassen National Forest. Perennial grass and herb cover was very low both before and after forest treatment (less than 4 percent total in both cases), although the cover of nonnative invasive annual grasses increased notably after treatment, especially prescribed fire. However, C. Skinner noted that grass cover has increased in the years since this study (see footnote 3). Barbour et al. (2002) sampled uncut old-growth mixed-conifer stands in the Lake Tahoe basin and found an average of only 0.5 percent (range = 0 to 10 percent) relative herbaceous cover, even though overstory tree cover was only 45 percent on average.

The contemporary FIA data provide measurements of herbaceous cover that are generated by summing the cover percentages of the different herbaceous species, thus total cover can sum to more than 100 percent. Comparison with relative cover data (which is what is typically reported in scientific studies) should be done with care, as the FIA summing practice ignores overlap among plants. The average cover of herbaceous plants reported from the FIA plots is 11.1 percent (± 12.5 SD) (USDA FS 2013a). Remember that the FIA dataset is a statistical sample of all stand conditions, whereas the reference values measured above are all from relatively undisturbed, old-growth-type stands.

The SSPM in northern Baja California has not been logged and has experienced more or less effective fire suppression only since the 1980s. Cattle are present but spend relatively little time in the upland forest at any distance from water sources and meadows (although it is true that low densities of cattle dung are present throughout forested areas in SSPM). A recent study of the understory vegetation in conifer stands in the SSPM found that relative forb cover averages 9 percent and grass cover less than 2 percent, under an average tree cover of 29 percent. Drier and lower elevation Jeffrey pine stands in the Sierra Juarez near the U.S. border show similarly low levels of understory cover: averages of 6.6 and 11.8 percent for forbs and grasses, respectively, under tree cover of 36 percent on average (see footnote 13).

Pearson (1942) described the effects of herbaceous vegetation on ponderosa pine recruitment and survival, and explained how the substantial cover of understory grass in southwestern (Arizona and New Mexico) ponderosa pine forests was highly dependent on the occurrence of monsoonal summer rain showers. He noted that, "Shallow-rooted herbs are dependent on summer showers, whereas the deeper rooted shrubs and trees are able to grow with little or no summer precipitation if the soil is well saturated during the winter months… A pronounced midsummer rainy season as well as relatively heavy soil favors the grasses."

Swetnam and Betancourt (1998) showed evidence from Arizona and New Mexico that fires in both mixed-conifer forests and ponderosa pine forests in that region tended to occur in years of low precipitation, but their analysis also suggested that fire in the latter forest type was positively correlated with precipitation in prior years. Swetnam and Betancourt (1998) ascribed this pattern to the increased importance of fine fuels—both live (grass) and dead (needles)—to fire dynamics in the more open and drier ponderosa pine stands, whereas moister mixed-conifer forests are more characterized by woody fuels that build up gradually over years and are less responsive to annual changes in precipitation. California supports a Mediterranean climate that is similar to the southwestern climate (Arizona and New Mexico) in its overall aridity but very different in its distribution of rainfall. For example, July and August are the driest months in California, but the wettest in Arizona and New Mexico; in much of New Mexico, the driest months are December through February, which is the height of the rainy season in California. These differences affect herbaceous vegetation much more profoundly than woody vegetation, and the general paucity of rainfall during the growing season in the assessment area means that grass and forb production is usually severely water limited in upland sites.

Norman and Taylor (2003) carried out a study of fire history and fire-climate interactions in pine forests found along meadow edges on the Lassen National Forest in an area of relatively subdued topography. They found that the historical occurrence of widespread fires was partly dependent on moisture conditions 1 to 3 years prior, which suggested that grass production in and around the meadow systems was important to fire spread. It is difficult to extrapolate this study to the broader landscape, as most assessment-area YPMC forests are not located adjacent to extensive meadow complexes, and grass cover in upland forests is generally not sufficient to carry fire on its own (Fites 1993, Oliver 2000, Smith 1994).

In summary, there appears to be little basis for the idea that presettlement assessment-area YPMC forests supported abundant swards of grass in their understory, except possibly in areas of high soil moisture and relatively open canopy conditions, and at lower elevations in yellow pine-dominant stands, especially where these interfinger with oak woodland. Except in these places, surface fires may have been primarily fed by tree litter, dried forbs, and shrubs, with a variable component of grass. Variability in precipitation, especially in the spring and summer, certainly played a role in driving interannual differences in herbaceous and graminoid biomass, however.

Although grass cover in presettlement YPMC forests may not have been particularly high, many forbs are more shade tolerant, and overall herbaceous cover and local species richness has probably dropped as tree cover has increased with fire suppression. Parks (2009) noted that stem densities of understory herbaceous species in the Stanislaus-Tuolumne Experimental Forest have been reduced by around 80 percent over the past eight decades as a result of increases in forest stand density and canopy cover.

Another wildcard is the increased presence of cheatgrass (*Bromus tectorum* L.) in assessment-area YPMC forests. In east-side and lower elevation west-side forests, this invasive grass can take advantage of disturbance to invade forest stands (Keeley and McGinnis 2007). Wet, warm years can increase cheatgrass cover substantially, and in recent wet years, we have seen yellow pine stands with substantial cheatgrass cover in their understories where little understory existed before.

Future—As with shrubs, it seems two trends are likely. On the landscape scale, it seems inevitable that current and projected future trends will lead to increased importance of (early seral) herbaceous vegetation on the YPMC landscape. On the other hand, in undisturbed forest stands, forest cover and density will continue to increase and herbaceous diversity and abundance will continue to be suppressed.

Litter—

NRV and comparison to current—There are no measurements of litter depth or cover that we know of from YPMC forests in the late 19th or early 20th centuries. However, many early observers remarked on the common occurrence of bare soil and the prevalence of thin layers of needle litter on the soil surface (e.g., Fitch 1900, Leiberg 1902, Sudworth 1900).

Modern litter + duff depth measurements from contemporary reference sites tend to average between 1.5 and 2 cm (e.g., Lydersen and North [2012]: 2.1 cm [±1.8 SD]; Stephens [2004], Sierra de San Pedro Mártir: 1.6 cm [no standard deviation given]; Safford, unpublished data, Sierra Juarez: 2.1 cm [± 1.6 SD][16]).

The FIA data compilation (USDA FS 2013a) for YPMC forests gives an average of 3.4 cm (±4.5 SD), with mixed-conifer plots averaging 3.9 cm and yellow pine plots averaging 2.8. These estimates are consistent with measured data from modern fire-suppressed YPMC forests from Stevens et al. (2014), who found an average litter + duff depth of 3.47 cm (±2.17 SD). Van Wagtendonk et al. (1998b) found that modern litter + duff layers ranged between an average of approximately 4 and 6 cm depending on the age of the stand, but there were strong differences in depth among different conifer species.

These are very few data points on which to base an ecosystem-wide conclusion. See the "Forest fuels" section below for more evidence relating to forest floor accumulations of dead plant matter. Van Wagtendonk et al. (1998b) found that modern litter + duff layers ranged from approximately 4 to 6 cm depending on the age of the stand, but there were strong differences in depth among different conifer species.

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[16] Unpublished data. On file with: Hugh Safford, USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592.

Forest fuels—

***NRV and comparison to current*—**Stephens (2004), working in reference YPMC forests in the SSPM in Baja, California, found average surface fuel loads (1- to 1,000-hr summed) of 15.8 tons/ha (±3.9 SE; the 1-hr to 100-hr sum was 2.16 tons/ha) and ground (litter + duff) fuels of 8.7 tons/ha (±0.83 SE). Duff is almost nonexistent in this system (Stephens 2004). Fuel loadings were extremely variable. For example, surface fuel loads were below average on 73 percent of the plots, and above 36.8 tons/ha on 8 percent of plots. Thirty-seven percent of the plots sampled had no 1,000-hr fuels (branches and logs >7.6 cm diameter), and 20 percent of the plots supported 75 percent of the 1,000-hr fuels. Dunbar-Irwin and Safford (2016) sampled a broader area of the SSPM 16 years after Stephens and found that fuel loadings had increased, probably largely because of the strict fire suppression that has been instituted in the area since the 1980s. The 1- to 100-hr sum was 4.7 tons/ha, and the overall sum (including 1,000-hr fuels) was 33.6 tons/ha.

Lydersen and North (2012), in their study of old-growth stands in the assessment area that had experienced at least two fires over the previous 65 years, found an average of 40.2 tons/ha for all surface fuels (1- to 1,000-hr summed; 1- to 100-hr sum was 7.9 tons/ha). Variability was high, with the standard deviations for all of the component fuel types about equal to or greater than the mean. Fuel loadings were lowest on ridgetops and southwest-facing slopes.

Taylor et al. (2014) used three methods to estimate prefire exclusion fuel loads in reconstruction plots in YPMC forests in the Lake Tahoe basin. Average estimated fuel loads from the three techniques ranged from 4.2 to 6.1 tons/ha (1- to 100-hr summed) for Jeffrey pine forest and 4.4 to 8.3 tons/ha for mixed-conifer forest. This compared to contemporary ranges of 4.2 to 7.5 tons/ha for Jeffrey pine forest and 8.5 to 12.9 tons/ha for mixed-conifer forest.

Studies of prescribed fire in modern, fire-suppressed forest can provide insight into fuel loadings that may have characterized presettlement YPMC forests in the assessment area. Kauffman and Martin (1989) report results from 60 prescribed fires from three sites in the northern Sierra Nevada. We report only their early fall and late spring results (30 burns), as those fires are most likely to represent conditions like those during the natural fire season. After fire, Kauffman and Martin (1989) found an average of 1.5 tons/ha (range of site means 0.6 to 2.2) for 1- to 100-hr fuels, and an average of 12.8 tons/ha (5.8 to 18.7) for 1- to 1,000-hr summed fuels; ground fuels (litter + duff) averaged 11.6 tons/ha (fig. 21). Unburned forest supported over eight times more ground fuels by mass, more than five times more fuel in the 1- to 100-hr classes, and 2.8 times more fuel when the 1- to 1,000-hr classes are summed (fig. 21). Other studies of prescribed-fire effects on fuels provide remarkably similar results. The means of postfire 1- to 100-hr fuels, 1- to

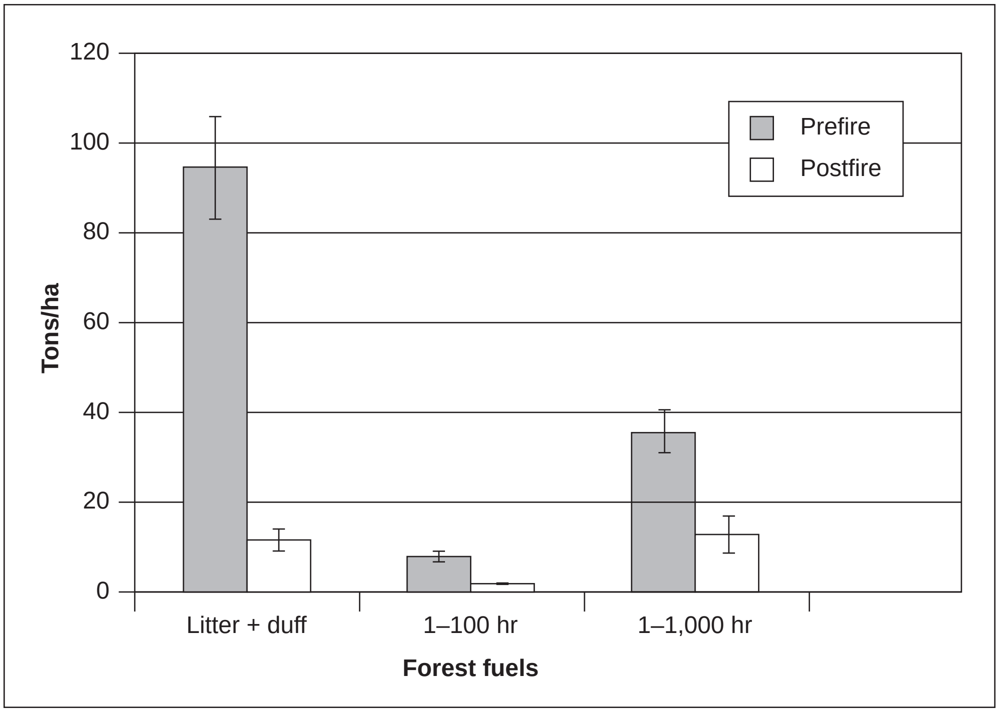

Figure 21—Forest fuels, before and after prescribed fire. Means are from 30 late spring and early fall burns studied by Kauffman and Martin (1989) in the northern Sierra Nevada. Error bars represent standard errors, based on n = 6 (each sample representing five fires).

1,000-hr fuels and ground fuels from Kilgore and Sando (1975), Knapp et al. (2005; fall burn), and Stephens and Finney (2002) are 1.4 tons/ha, 10.7 tons/ha, and 12.5 tons/ha, respectively. Average prefire fuels in these studies were higher than in the Kauffman and Martin study sites. We would expect average presettlement fuel loadings to be less than the postfire loadings reported here, as these modern prescribed fires were one-time events after many decades of fire exclusion, whereas presettlement YPMC forests were experiencing burns every 10 to 20 years on average.

The FIA plot data compilation (USDA FS 2013a) showed that fuel loadings in contemporary YPMC forest plots average 7.3 tons/ha for 1- to 100-hr summed fuels, and 30.3 tons/ha (±24.9 SD) for 1- to 1,000-hr fuels. Mixed-conifer forests support much heavier fuels (1- to 1,000-hr summed = 36.7 tons/ha) than yellow pine forests (1- to 1,000-hr summed = 20 tons/ha). This gives a good idea of the kind of transformation that occurs in the fuel profile of YPMC forests as they transition from pine-dominant stands to mixed-conifer stands under fire suppression. The average of the reference studies detailed above is about 3.6 tons/ha for 1- to 100-hr fuels, and 17.7 tons/ha for 1- to 1,000-hr fuels (the latter including the very high value from Lydersen and North [2012]). We conclude that modern-day fuel loadings in assessment-area YPMC forests are substantially higher than loadings under presettlement conditions.

Future—We know of no scientific attempt to project fuel levels in assessment-area YPMC forests into the future. It seems most likely that the same sorts of trends that have characterized YPMC forests for the past 50 to 100 years will continue into the future, perhaps at an accelerated pace, as climate warming and rising carbon dioxide levels increase plant growth and fuels accumulation.

Composition

Forest landscape composition

***NRV and comparison to current*—**

Here, we refer to the distribution of forest types (rather than specific species) across the landscape. There are not many data available, as mapping or extensive plot networks are necessary to assess this indicator.

Many early observers noted how yellow pine-dominant forests (yellow pine and dry mixed conifer) were more common at lower elevations, on warm aspects (south and west), and in areas of thin or otherwise low-productivity soils. Forests with a notable shade-tolerant component (moist mixed conifer) were mostly in moist microsites, along streams, on north slopes, and at high elevations (e.g., Leiberg 1902, Sudworth 1900). These general trends are also apparent today, although the absolute area supporting yellow pine-dominant forest has dropped and the area supporting shade-tolerant-dominant forest types has increased (Barbour et al. 1993, 2007; Fites-Kaufman 1997; Sugihara et al. 2006; Vankat and Major 1978).

Fites-Kaufman (1997) developed environmental models of presettlement forest types in two watersheds on the western slope of the central assessment area. She concluded that 64 percent of the areas modeled would be dominated by Douglas-fir and white fir forest types in the absence of fire (i.e., on cool and moderate slopes, watered draws on warm slopes, and higher elevations), but 28 percent of that area was in intermediate areas likely historically dominated by ponderosa and sugar pine because of frequent fire. Overall, according to Fites-Kaufman (1997), about two-thirds of the area modeled was probably dominated by pine-dominant forest before Euro-American settlement.

Dolanc et al. (2014a), compared the vegetation types represented by 4,371 VTM forest plots (Wieslander 1935) from the 1930s and 1,000 FIA forest plots from the 2000s in the central assessment area. They found that 19.9 percent of the 1930s plots classified as ponderosa pine, versus 8.9 percent of the plots from the 2000s; 27.3 percent of the plots were classified as mixed conifer in the 1930s dataset, versus 37.1 percent in the 2000s dataset. Both east-side and west-side Jeffrey pine also declined as a proportion of the sampled vegetation between the 1930s and 2000s.

Dolanc et al. (2014a) suggested that much of the ponderosa pine sampled in the 1930s and subsequently lost probably succeeded to mixed-conifer (through infilling of fir, Douglas-fir, and incense cedar) or to montane hardwood forest, through expansion of oaks after disturbance.

Thorne et al. (2008) compared the 1930s Forest Service vegetation maps (Wieslander 1935) of the Placerville Quadrangle, in the center west of the assessment area, with the Forest Service vegetation map from 1996, to compare the extent of different vegetation types in the two periods. The vegetation type with the largest loss of area was ponderosa pine, which declined by 64 percent over the six decades between maps. In their study area, Thorne et al. (2008) documented that ponderosa pine forest had primarily transitioned to forests dominated by hardwoods (where disturbance had reduced or removed the dominant pines) or by Douglas-fir (where lack of disturbance allowed succession of shade-tolerant species). Thorne et al. (2008) did not find much change in their mixed-conifer forest type, but their classification (California Wildlife Habitat Relations types) splits a number of forest types we include in our general definition of YPMC forests.

Thorne et al. (2008) compared the 1930s Forest Service vegetation maps (Wieslander 1935) of the Placerville Quadrangle, in the center west of the assessment area, with the Forest Service vegetation map from 1996, to compare the extent of different vegetation types in the two periods. The vegetation type with the largest loss of area was ponderosa pine, which declined by 64 percent over the 6 decades between maps.

Current Forest Service vegetation maps can also be compared to Show and Kotok's (1929) summary of forest cover types in northern California in the late 1920s. The major changes are in yellow pine and mixed conifer. The former comprised 33.7 percent of Show and Kotok's analysis area in the 1920s (Modoc National Forest south to the Sequoia National Forest, excluding the Inyo National Forest), but only 17 percent of the area in the most recent Forest Service mapping. Mixed-conifer forests covered 19.8 percent of the area in the 1920s, versus about 30 percent today. Other forest types were similar between the two periods.[17]

Future—See the following section.

Forest composition and species diversity—

Trees–A number of excellent summaries of the species composition of assessment-area YPMC forests have been published (e.g., Barbour and Billings 1999, Fites 1993, Fites-Kaufman et al. 2007, Smith 1994, Sugihara et al. 2006, USDA FS 2001). We direct the reader to these and other sources for information on modern forest conditions. In this section, we both qualitatively and quantitatively describe the patterns of tree composition that characterized YPMC forests before significant Euro-American impact.

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[17] Data provided by Jay Miller, remote sensing specialist, USDA Forest Service, Pacific Southwest Region, 3237 Peacekeeper Way, Suite 101, McClellan, CA 95652.

NRV—The U.S. Geological Survey (USGS) carried out general surveys of Sierra Nevada forests at the turn of the 19th century, primarily to assess the status of the timber resource. Leiberg (1902) surveyed forest lands on what is today the Plumas and Tahoe National Forests and the northern Lake Tahoe basin. Sudworth (1900) surveyed the southern Lake Tahoe basin, the Eldorado National Forest, and northern portions of the Toiyabe and Stanislaus National Forests. Fitch (1900) and Marshall (1900) provided brief descriptions of forest conditions in and around Yosemite National Park. McKelvey and Johnston (1992) evaluated the USGS reports and provided a summary of their results. Stephens and Elliot-Fisk (1998) and Stephens (2000) summarized unpublished plot data from Sudworth that were entered into his field notebooks, including data from the southern Sierra Nevada in what is today Sequoia & Kings Canyon National Parks and the Sierra and Sequoia National Forests.

McKelvey and Johnston (1992) note that the composition of forest trees in these early surveys included all the same species we encounter today, but the order of their dominance in assessment area forest stands has changed. Leiberg (1902) divided his survey area into three predominant forest types: his “yellow pine” forest type includes what we call today “mixed conifer” and corresponds to the YPMC forest types covered in this chapter. According to Leiberg, yellow pine was the “most conspicuous and important” species in this forest type, but although it may have once been the dominant species of tree, owing to heavy selective logging throughout his survey area, it was no longer dominant by the turn of the end of the 19th century. Sugar pine was not a dominant species in YPMC forests, but like the yellow pine species, it was selectively harvested and its densities and overall volume had decreased greatly by the time the USGS surveys were made. Leiberg’s (1902) opinions are qualitatively supported by the forest observations of Joseph Bruff, who walked the same northern Sierra Nevada forests a half century earlier. Bruff occasionally made journal notes of forest structure and composition in his 1849–1851 travels, and almost all his observations of conifer trees refer to forests dominated by pines (Read and Gaines 1949).

Sudworth (1900) stated that pine species dominated lower elevation YPMC forests, but incense cedar and fir were mixed with the pine in approximately equal proportions at higher elevations. Sudworth (1900) rarely referred to hardwood species, but he did note that “a few small, unimportant broad-leafed trees” were common along canyon-bottom streams and also grew at times in with the upland coniferous forest. According to Sudworth, yellow pine was the most abundant tree in the YPMC belt, followed by white fir, then incense cedar, sugar pine, and Jeffrey pine. The amount of yellow pine varied considerably from place to place and along the altitudinal gradient, it was most common on south, west, and east aspects, with some sites containing 80 to 90 percent yellow pine. Most forest stands included different mixes of the above species, with Sudworth estimating the typical ranges as being 45 to 50 percent yellow pine, 30 to 45 percent white fir, 20 to 30 percent incense cedar, 5 to 20 percent sugar pine, and 0 to 5 percent Jeffrey pine on the west slope (but a local dominant on the east slope); Douglas-fir, 2 to 5 percent; black oak, 5 to 10 percent of stands at lower elevations. Black oak was a close associate of yellow pine and incense cedar and could account for more than 50 percent of a stand in dry, thinly soiled locations on south and west slopes.

Sudworth and the other USGS surveyors were visiting forests that already had nearly a half century of Euro-American presence. Many of the stands they surveyed had been cut, usually selectively for pine. This had an impact on their estimates of species importance. For example, Sudworth (1900) noted that the best sugar pine had already been removed from much of the forest he surveyed, and the same had happened with the larger specimens of Douglas-fir. Leiberg (1902) described the effects of heavy logging on forests in the Lake Tahoe basin and noted that sugar pine, which had comprised 20 to 25 percent of the virgin stand, was likely to contribute only 2 to 3 percent of the secondary forest. Greeley (1907) lamented that many stands had been so thoroughly high-graded (valuable species and large trees selectively cut) that yellow pine averaged only 15 to 20 percent of the trees in much of the western Sierra. Leiberg and other early surveyors also noted that the contribution of incense cedar to the stands they visited was artificially high, as it had no commercial value and was left standing far more often than the other species.

Leiberg (1902) estimated that YPMC forests in his survey area at the time of his work were on average 25 percent yellow pine, 1 percent sugar pine, 25 percent Douglas-fir, 44 percent white fir, and 5 percent incense cedar. The relative proportions of the pines and fir had been markedly changed by logging, which focused heavily on the former. At the time of the USGS surveys, Leiberg’s survey area had been (much) more heavily cut than the area assessed by Sudworth. (Miller and Safford 2017). Leiberg (1902) also estimated the standing volume of trees species in as yet uncut forests. Proportionally, yellow pine species (both ponderosa and Jeffrey) were dominant and comprised about twice the volume of Douglas-fir, sugar pine, or white fir (see McKelvey and Johnston 1992); incense cedar had no economic value at the time and was not listed. White fir regenerated strongly on formerly pine-dominant lands, and Leiberg estimated that it would amount to 60 to 75 percent of the secondary forest, up from 25 to 40 percent of the uncut stands. Sudworth (1900) also referred to the “thickets of seedlings and saplings” of white fir that covered many acres and often excluded all other species. Other observers made similar observations.

Volume estimates from the Plumas National Forest in 1913 are very similar to Leiberg's earlier volume estimates for the northern Sierra Nevada as a whole. As above, yellow pine species dominated, with 1.6 times the volume of white fir, 2.4 times the volume of sugar pine, and 2.8 times the Douglas-fir volume; other species like red fir and incense cedar comprised the remaining 7 percent of volume (McKelvey and Johnston 1992, Moore 1913).

Greeley (1907) described the forests of the western Sierra Nevada from the viewpoint of a traditional forester. Like the other early observers, he noted that the original forest had varied from pure yellow pine at the lower elevations and on dry exposures to nearly pure fir toward the upper limit of merchantable timber. Greeley outlined "three bad features of the virgin stand (that) quickly impress the forester." Two of these three features pertain to structure ("the widespread over-maturity of the timber," and "the large area on which the stand is open or has disappeared entirely") and are discussed above. The third feature was the "large and apparently increasing proportion of inferior species." Except at lower elevations, cutting had been sufficient to reduce the pines to where white fir comprised a third of merchantable timber, and it was a much higher proportion of the younger growth. Together with incense cedar, white fir outnumbered both of the pines in small size classes. Both white fir and incense cedar produce high volumes of seed, and their seedlings are much more tolerant of shade than the pines. Greeley (1907) noted that except at lower elevations and on very warm exposures, dense thickets of fir and cedar were already crowding the pine to "one-fifth or less of reproduction."

Early GLO land surveying of the assessment area produced useful data on the composition of late 19th century forests. General Land Office crews sampled up to four trees at each section corner and two trees at quarter-section corners (see above). Because of the gridded sampling scheme, GLO samples of forest structure and composition are relatively robust, statistically speaking, although they did not restrict their activities to uncut ground, and they tended to prefer smaller mature trees when they were available, as they were assumed to have the greatest longevity (Hyde 2002). The very low density of GLO data (a maximum of eight points per square mile) means that spatial interpretation of these data is nearly impossible (which is not to say that people have not tried) (e.g., Baker 2012, 2014), but they are very valuable as tabular summaries from larger landscapes. GLO tree data have been summarized for the Lake Tahoe basin (Manley et al. 2000), the Eldorado National Forest (Fites-Kaufman 1997), and for the Stanislaus, Sierra, and Sequoia National Forests (Hyde 2002).

GLO data from Lake Tahoe suggest that yellow pine and fir were present in nearly equal numbers in lower montane forests, with the balance shifting from fir on the wetter west shore to pine on the drier east shore (Manley et al. 2000). Many of the GLO surveys in the basin were conducted after the mid-1870s, however, and in the lower montane zone their section lines, especially on the east shore, crossed stands where selective logging of Jeffrey and sugar pine had already commenced (Lindström 2000). In addition, the data summarized in Manley et al. (2000) are missing many survey points. It seems likely that the GLO counts in the Lake Tahoe basin in lower montane forests may underestimate the presence of pine before logging, at least on the east shore. Data from Taylor's studies in the basin support this viewpoint (Taylor 2004, Taylor et al. 2014). For example, the modern Jeffrey pine stands sampled by Taylor and colleagues on the east shore of the lake support an order of magnitude more Jeffrey pine than white fir, even a century after the institution of fire suppression and 130 years or more after the removal of all merchantable Jeffrey pine. Taylor et al.'s (2014) results from west shore mixed-conifer forest agree more closely with the GLO data, with white fir in the 1873 forest outnumbering Jeffrey pine by 1.5:1 (versus 5:4 in the GLO surveys). Almost half of all the white fir measured were smaller than 25 cm d.b.h., and Jeffrey pine was the dominant tree in the larger size classes (Taylor et al. 2014).

Hyde (2002) summarized compositional patterns in GLO data sampled in the middle and late 1800s from areas on the Stanislaus (37 300 ha sampled), Sierra (46 600 ha), and Sequoia National Forests (18 600 ha). Her study areas were chosen to represent elevational transects of approximately 2000 m, along a latitudinal gradient from the central to southern Sierra Nevada. Below 1000 m elevation, forest vegetation was dominated by oak species (more than three-fourths of stems sampled), with only about 8.5 percent of the trees measured being pines (although these contributed about one-fourth of the basal area). Between 1000- and 1500-m elevation, pine (45 percent of sampled stems) and oak (37 percent of sampled stems, mostly black oak) shared in dominance, with fir species contributing 8 percent of stems. Pines comprised about 60 percent of the basal area, and oaks about 24 percent (Hyde 2002). Between 1500- and 2000-m elevation, pines (mostly yellow pines and sugar pine) accounted for 58 percent of stems, fir about 26 percent, and oaks about 11 percent. Basal area was dominated by pines (49 percent), giant sequoia (29 percent), and white fir (16 percent). Above 2000 m, the fir component increased to 42 percent of stems sampled, with pines comprising about 57 percent; yellow pine, lodgepole pine, and sugar pine were the dominant pine species, in that order. Fir (probably mostly red fir at these elevations) contributed slightly more basal area to the stand than the pines (Hyde 2002). Pines dominated slopes of all aspects except northeast, which was dominated by oak species; fir species were surprisingly constant in their contribution to stem densities, comprising in all cases about 20 percent of stems (Hyde 2002).

Baker (2014) reported results from four large areas of GLO surveys in the northern and southern Sierra Nevada (total area sampled equals about 330 000 ha). Baker does not report results by species, but does report percentage of stems encountered by GLO surveyors that were pines, fir plus incense cedar plus Douglas-fir ("shade tolerant"), and oaks. In his northern sites, the proportions of stems in these three classes were 30:38:29; in the southern Sierra Nevada the proportions were 46:28:22.

Fites-Kaufman (1997) summarized the GLO data for two watersheds on the Eldorado National Forest. She found that GLO sites recorded "fir" (Douglas-fir or white fir) on only 26 percent of the surveyed sites. Although Fites-Kaufman (1997) did not report the overall results of the GLO data, her figure 2.11 gives the proportion of stems by species for GLO sites that contained "fir" and for sites that her modeling had identified as being within the Douglas-fir/mixed-conifer potential forest type (i.e., on cool slopes, higher elevations, etc.). The pines (ponderosa and sugar) accounted for 24 and 31 percent of the stems in the two subsamples, respectively; black oak accounted for 26 and 30 percent in the two subsamples. These fire-tolerant species accounted for much more of the stands sampled by the GLO across the rest of the landscape, but Fites-Kaufman (1997) did not provide a summary of those data.

In the VTM project, the Forest Service inventoried and mapped vegetation on much of the land under its jurisdiction in the early 1930s (Wieslander 1935). In the assessment area, thousands of 0.2-ac (809-m^2) vegetation plots were sampled in YPMC forest types (ponderosa pine, mixed-conifer, and east-side Jeffrey pine forests). Figure 22 gives the relative densities of tree species in YPMC forests sampled by the VTM project in forest stands that had not experienced intensive logging (n = 2250) and compares them to the most recent available FIA inventory of assessment area forests (n = 510) (see Dolanc et al. 2014b). The VTM protocol sampled only trees 10 cm d.b.h. and above, so the relative densities of species sampled are biased away from the youngest cohorts of trees, which were dominated by white fir and incense cedar that were beginning to benefit from 2 to 3 decades of fire exclusion. Because of this, relative tree densities represented in the VTM dataset provide an at least approximate idea of dominance patterns among tree species before fire suppression (with the caveat that large- and medium-size sugar pine and yellow pine had been selectively logged through much of the assessment area by the time of VTM sampling). The values given in figure 22 are overall averages, and obviously patterns varied from west-side to east-side forests (e.g., Jeffrey pine strongly dominated east-side stands, and Douglas-fir and black oak

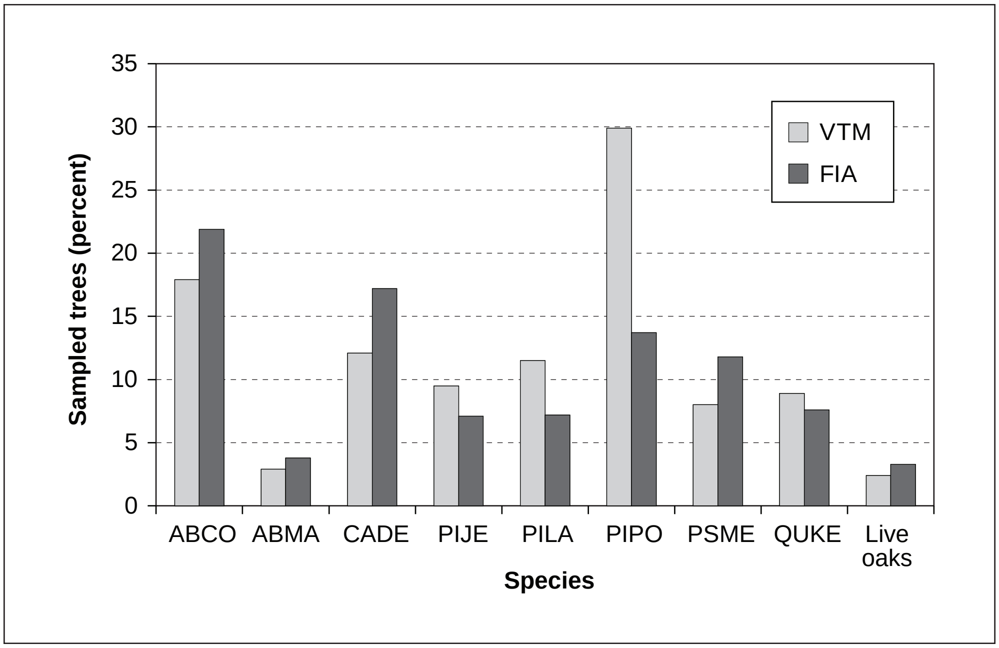

Figure 22—Relative densities of tree species in yellow pine–mixed-conifer forests, comparing vegetation type mapping (VTM) (early 1930s) and Forest Inventory Analysis (FIA) (early 2000s) datasets in the central assessment area (Plumas, Tahoe, Eldorado, Humboldt-Toiyabe, Eldorado, Stanislaus, and Sierra National Forests; Lake Tahoe Basin Management Unit; and Yosemite National Park—VTM data were not collected north or south of this area). Only trees >10 cm diameter at breast height are included. ABCO = *Abies concolor* (white fir); ABMA = *A. magnifica* (red fir); CADE = *Calocedrus decurrens* (incense cedar); PIJE = *Pinus jeffreyi* (Jeffrey pine); PILA = *P. lambertiana* (sugar pine); PIPO = *P. ponderosa* (ponderosa pine); PSME = *Pseudotsuga menziesii* (Douglas-fir); QUKE = *Quercus kelloggii* (black oak); live oaks = canyon live oak and interior live oak. Data are from Dolanc et al. (2014b).

were much more common on the west side), from north to south slopes, and so on. The most obvious pattern in figure 22 is the strong shift in overall dominance from shade-intolerant/fire-tolerant species (ponderosa pine, Jeffrey pine, sugar pine, black oak) in the VTM dataset to shade-tolerant/fire-intolerant species (white and red fir, incense cedar, Douglas-fir) in the FIA dataset. The relative proportions of shade-intolerant versus shade-tolerant species change from 60:40 in the VTM data to 35:55 in the FIA dataset (fig. 22) (Dolanc et al. 2014b).

Figure 23 shows historical stem densities by species for seven sites in the assessment area in which stand reconstruction studies were carried out. Ratios of shade-intolerant to shade-tolerant species range from 92:7 to 16:84 (fig. 23). Collins et al. (2015) analyzed forest inventory data from 1911 in the Tuolumne River drainage at the western border of Yosemite National Park and found that basal areas were divided 58:42 among shade-intolerant and shade-tolerant species (they did not report stem densities). Stephens et al. (2015) conducted an analysis of a similar

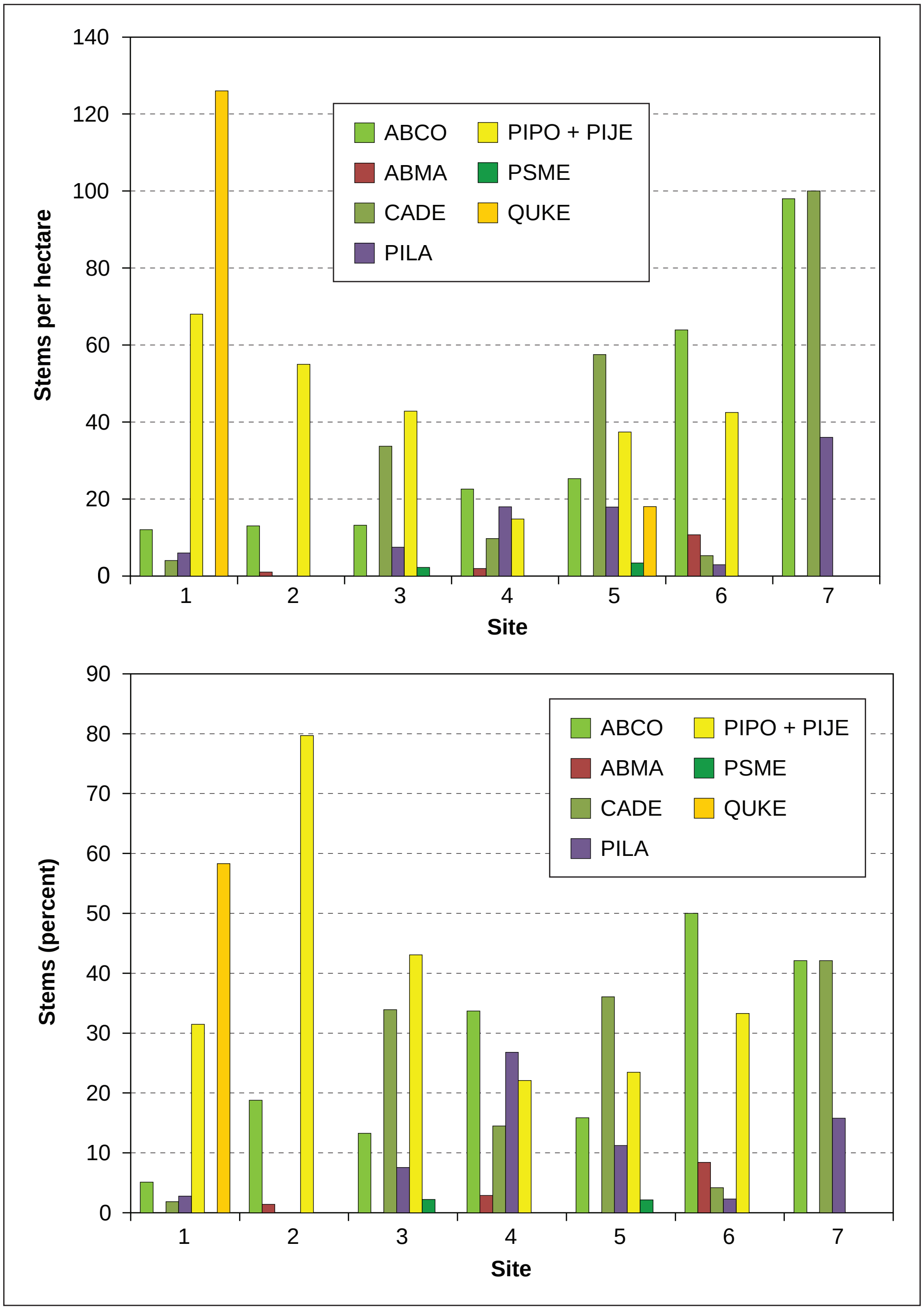

Figure 23—Reconstructions of historical stem densities at seven sites in yellow pine–mixed-conifer forest in the assessment area. Sites are arranged in order of proportional dominance by shade-intolerant species, from high (left) to low (right). (A) absolute densities; (B) relative densities (percentage of stems). 1 = Parsons and Debenedetti (1979) (yellow pine, ≥12 cm diameter at breast height [d.b.h.]); 2 = Taylor (2004) (≥10 cm d.b.h.); 3 = USDA FS (1911) (≥15.2 cm d.b.h.); 4 = North et al. (2007) (≥5 cm d.b.h.); 5 = Scholl and Taylor (2010) (≥10 cm d.b.h.); 6 = Taylor (2014) (≥5 cm d.b.h.); 7 = Parsons and Debenedetti (1979) (mixed conifer). ABCO = *Abies concolor* (white fir); ABMA = *A. magnifica* (red fir); CADE = *Calocedrus decurrens* (incense cedar); PILA = *Pinus lambertiana* (sugar pine); PIJE = *P. jeffreyi* (Jeffrey pine); PIPO = *P. ponderosa* (ponderosa pine); PSME = *Pseudotsuga menziesii* (Douglas-fir); QUKE = *Quercus kelloggii* (black oak).

1911 dataset from the Greenhorn Mountains in the southwestern Sierra Nevada and found that basal areas were split 46:54 between shade-intolerant and shade-tolerant species. It can be appreciated that the relative densities of shade-intolerant and shade-tolerant species were not constant on the landscape, and in some circumstances yellow pines, which dominated much of the general landscape, were entirely absent.

In another forest reconstruction study based on "aggregations" of vegetation, Bonnicksen and Stone (1982) found that a YPMC watershed in Kings Canyon National Park had seen an increase in the area of the watershed covered by white fir-dominant aggregations from 27 to 37 percent between 1890 and 1977. Black oak was reduced from 10 percent of the study area to 6 percent during the same period.

Kercher and Axelrod (1984) developed a Monte Carlo-based model of YPMC forest succession (known as "SILVA") in the Sierra Nevada. This model is further discussed in "Successional processes" above. Kercher and Axelrod (1984) used SILVA to compare forest succession after a simulated clearcut for 500 years at two different elevations, 1520 m and 1830 m. The lower elevation site is at the upper reaches of YPMC forests historically dominated by ponderosa pine; the upper site is nearer the upper limits of YPMC forests in the Sierra Nevada and historically included a significant component of fir species. The time-averaged results of the SILVA lower elevation simulation under frequent fire (mean FRI = 7 years) are given in figure 11. Ponderosa pine strongly dominated the modeled stand throughout the 500-year simulation. The relative proportions of shade-intolerant versus shade-tolerant species in figure 11 are about 66:33. The SILVA model for the higher elevation site projected a forest stand dominated strongly by white fir (which comprised an average of 60 percent of the total basal area over the 500-year simulation), even under frequent fire (Kercher and Axelrod 1984).

In summary, presettlement YPMC forests in the assessment area tended to be dominated by yellow pine and other shade-intolerant species, but shade-tolerant species could be locally dominant, especially at higher elevations, at northern latitudes, and in moist microsites. Most assessments of species densities were carried out after selective logging of yellow pine and sugar pine had already occurred. The actual proportions of shade-tolerant to shade-intolerant species varied across the presettlement landscape, but the data suggest that among mature trees, shade-intolerant species (pine and black oak) typically comprised most of the individuals in the average stand, especially the larger individuals (see below). Then, as now, in the absence of fire, shade-tolerant species dominated the smallest size classes.

Presettlement YPMC forests in the assessment area tended to be dominated by yellow pine and other shade-intolerant species, but shade-tolerant species could be locally dominant, especially at higher elevations, at northern latitudes, and in moist microsites.

***Comparison with current*—**Yellow pine and sugar pine have notably decreased in importance in assessment-area YPMC forests, while shade-tolerant conifers and hardwoods (white fir, incense cedar, Douglas-fir, tanoak, canyon live oak) have increased (fig. 24). This is due to selective logging, increased resource competition under increasing stand densities, the difficulty of regenerating under the denser modern canopy, and—in the case of sugar pine—to the effects of white pine blister rust (*Cronartium ribicola*), an introduced fungal pathogen that is having major effects on five-needled pine populations across the Western United States (Agee 1993; Barbour et al. 1993, 2007; Sugihara et al. 2006; van Mantgem et al. 2004). FIA data show that the component of shade-intolerant species in assessment-area YPMC forests has dropped from an average of maybe two-thirds of the mature forest stand to around one-third of mature trees. The largest decrease has been in ponderosa pine, but all shade-intolerant species have decreased in density.

Geographic, topographic, and successional patterns in tree species composition are driven by ecological differences between species. Table 2 lists the tolerances of common YPMC tree species in the assessment area to shade, frost, temperature, drought, and fire. The dominance of the yellow pine species on south and west aspects, on droughtier soils, and in fire-prone locations is easy to predict from the information in table 2, as is the heightened presence of white fir on north slopes, and in moist and protected topographic locations; incense cedar is somewhat intermediate in most characteristics. White fir is the major successional climax species for most of the YPMC belt in the assessment area, although Douglas-fir plays this role at lower elevations. White fir's shade tolerance and fire intolerance, its ability to survive for very long periods as a suppressed tree, its capacity to respond rapidly to release (increased light availability), and its prolific production of seed are dominant factors in forest succession in the assessment area (Barbour et al. 2007, Burns and Honkala 1990, USDA FS 2013b). In prefire suppression times, very frequent fire limited white fir populations in most of the assessment area, but it could dominate stands in areas where conditions existed (such as high fuel moisture) such that fire frequency was reduced, or where fire intervals were long enough or variable enough to permit adults to develop thick bark. Increasing annual precipitation and lower summer temperatures along the south-to-north axis of the assessment area also result in higher fir densities to the north. The same gradient occurs with elevation, and many early observers noted how YPMC forests were dominated by white fir at higher elevations. With the onset of fire suppression, major increases in white fir and incense cedar began across the assessment area (Vankat and Major 1978). Early observers noted this tendency already in the late 19th and early 20th centuries (Greeley 1907, Leiberg 1902, Sudworth 1900). Today, with the general absence of fire, climate is the principal factor regulating species distributions, and species requiring frequent disturbance to retain their place in the forest canopy—principally species of pine—are in the decline, except in areas of low site productivity such as areas of thin or nutrient-poor soil or extreme microclimates.

Dolanc et al. (2014b) compared forest conditions as documented in the Forest Service forest mapping inventory of the early 1930s (Wieslander 1935) with the most recent compilation of the FIA plot network in the assessment area. Figure 24, using data from table 2 in Dolanc et al. (2014b), is a graphic summary of the relative changes in tree composition that have occurred in the assessment area

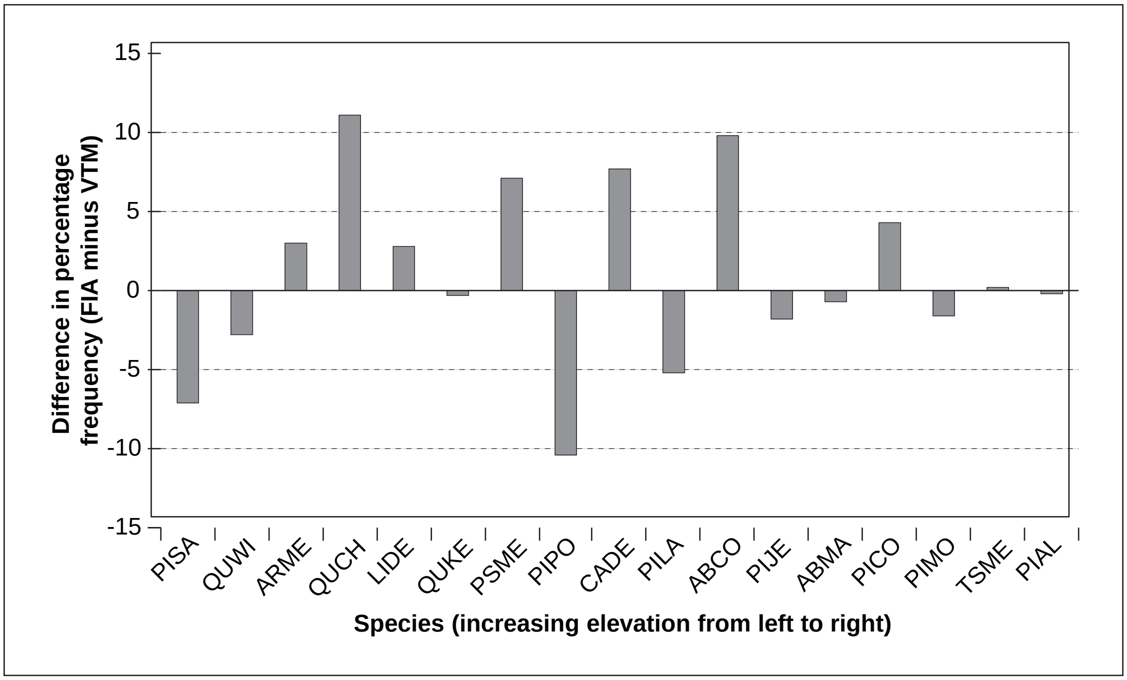

Figure 24—Relative change in species frequencies (measured as the percentage of plots in which a given species is found) between the 1930s Forest Service vegetation mapping inventory (VTM) and the most recent compilation of Forest Inventory and Analysis (FIA) data (USDA FS 2013a). Species below the *x*-axis have dropped in frequency. Codes are from the first two letters of the genus plus the first two letters of the species. PISA = *Pinus sabiniana* (California foothill pine); QUWI = *Quercus wislizenii* (interior live oak); ARME = *Arbutus menziesii* (Pacific madrone); QUCH = *Q. chrysolepis* (canyon live oak); LIDE = *Lithocarpus densiflorus* (tanoak); QUKE = *Q. kelloggii* (black oak); PSME = *Pseudotsuga menziesii* (Douglas-fir); PIPO = *P. ponderosa* (ponderosa pine); CADE = *Calocedrus decurrens* (incense cedar); PILA = *P. lambertiana* (sugar pine); ABMA = *Abies magnifica* (red fir); PICO = *P. contorta* (lodgepole pine); PIMO = *P. monticola* (western white pine); TSME = *Tsuga mertensiana* (mountain hemlock); PIAL = *P. albicaulis* (whitebark pine). Illustration adapted from data in Dolanc et al. (2014b).

since the arrival of Euro-Americans. The YPMC belt begins where QUKE (black oak) is located on the *x*-axis and continues to PIJE (Jeffrey pine). The most obvious pattern in figure 24 is the reduced frequency (calculated as the percentage of plots in which the species in question is found) of shade-intolerant/fire-tolerant species like ponderosa (PIPO), sugar (PILA), and Jeffrey pine; and the increased frequency of shade-tolerant/fire-intolerant species like Douglas-fir (PSME), incense cedar (CADE), and white fir (ABCO). Changes have been driven primarily by fire suppression and timber harvest activities.

Future—

Miller and Urban (1999a) added a soil water routine and a fire model to the forest gap model ZELIG and simulated successional dynamics in Sierra Nevada forests along an elevational gradient in Sequoia & Kings Canyon National Parks under a number of future climate scenarios. Simulations were run for 800 years, with the first 200 years having no fire and the last 600 years under a "natural" fire regime for the elevation in question. In all future climate scenarios except the cool-wet scenario, tree species composition at the two lowest elevation sites (1800 m and 2200 m), which are at elevations currently dominated by YPMC forests, changed markedly. Major changes were not apparent in the models until about a century into the simulations, but fire in Miller and Urban's (1999a) model is entirely surface fire and is internally driven (by fuel load and fuel moisture), not externally forced, and effects of disease or insect outbreak were not modeled, so the results are probably very conservative with respect to the velocity of change. At the lower two elevations, trees either completely or nearly disappeared by the final century of the simulation. Under the less extreme warming and drying scenarios, the forest at 1800 m saw the basal area of tree species change from 15:9:3:1:1 (m^2/ha; ponderosa pine:incense cedar:Jeffrey pine:black oak:white fir) to 1:1:1:1:0. Under more extreme warming, trees disappeared at this elevation. At 2200 m, baseline basal areas of 45:4:2:1:0 (m^2/ha; white fir:sugar pine:incense cedar:Jeffrey pine:ponderosa pine) were changed to an average of 4:0:12:2.5:1 under the less extreme warming/drying scenarios, and the site transitioned to a yellow pine–black oak–incense cedar woodland (total basal area only 8 m^2/ha) under the more extreme scenarios. The 2600 m site, which currently supports a red fir forest, transitioned to a moist mixed-conifer forest dominated by white fir under the less extreme future scenarios, and to a dry mixed-conifer (yellow pine-white fir-incense cedar in almost equal proportions) under the more extreme scenarios (Miller and Urban 1999a).

The Nature Conservancy carried out future climate suitability forecasts for major tree and shrub species of the Sierra Nevada, in support of the northern and southern Sierra Nevada Partnerships. The partnerships are collaborative efforts, organized by The Nature Conservancy, the Sierra Business Council, and a variety of other national, regional, and local conservation organizations, to carry out all-lands conservation planning for important subregions of the Sierra Nevada (see: http://consbio.org/products/projects/southern-sierra-partnership, and http://northernsierrapartnership.org/). Climate suitability forecasts for the period 2045 to 2065 were derived using maximum entropy (MaxEnt) modeling, and based on 11 GCMs run under the IPCC's A2 climate scenario. Models only incorporated climate variables. Three generalized future climate scenarios were developed ("warm-dry," "hot-dry," and "hot-wet") and an ensemble projection was also developed, where the degree of consensus across models was mapped. In the ensemble outputs, areas of projected climate "stress" (possible loss in distribution), climate refugia, and possible expansion were mapped, along with a measure of the degree of model consensus. More information and the data outputs are available at http://app.databasin.org/app/pages/galleryPage.jsp?id=8c5db744f9fe4d3e9375b100dc695c4d. All the projections for California can be viewed at http://www.tnccmaps.org/climate/species/.

Overall, The Nature Conservancy's climate suitability forecasts suggest more climatic stability and less future climate stress in the southern Sierra Nevada than in the north (SSP 2010). This is due largely to much higher elevations and more accentuated topography in the south, which lead to less probability of overall habitat loss as climates warm and snowpack decreases. Nonetheless, the models suggest notable areas of climate stress along the lower, western margins of the YPMC forest belt, as well as the potential for expansion to higher elevations (fig. 25). Both Jeffrey and ponderosa pine are projected to experience increased climate stress in much of the northern and northeastern assessment areas, primarily because of the lower average elevations in those areas. Douglas-fir (not shown) is projected to experience relatively little climate stress, except along the western margins of the central Sierra Nevada, and climate suitability for the species may increase markedly at higher elevations throughout the central and northern Sierra Nevada. In their summary of the top threats to conservation in mixed-conifer forests, the Southern Sierra Partnership (SSP 2010) identified changed fire regimes as the highest threat, followed by climate change and a number of other factors.

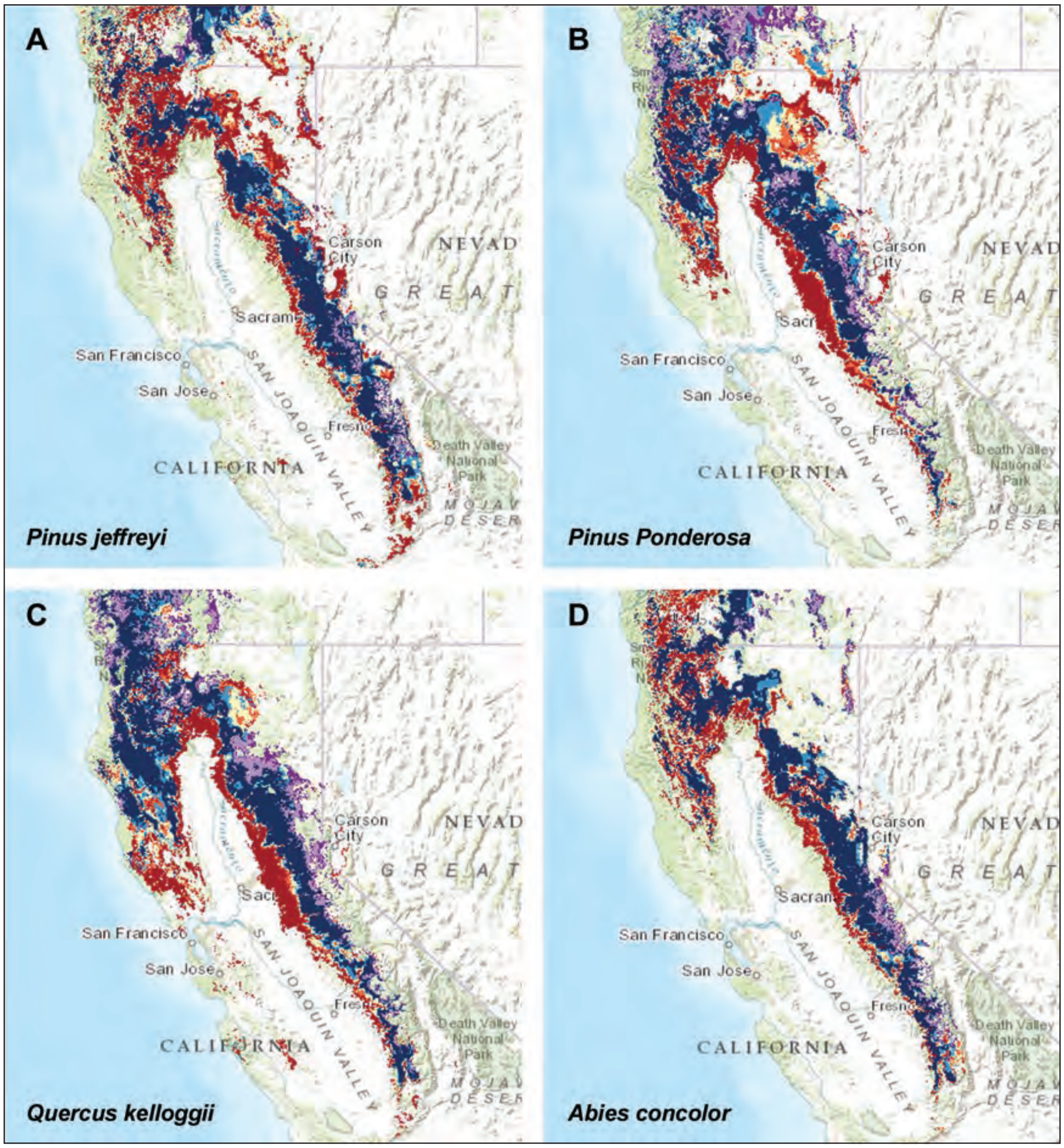

Figure 25—Future climate suitability forecasts for four yellow pine–mixed-conifer tree species for the period 2045 to 2065; ensemble results from 11 GCMs under the A2 IPCC climate scenario. (A) Jeffrey pine; (B) ponderosa pine; (C) white fir; (D) black oak. Red and orange = areas in which climates are currently suitable but will not be in the future (climate "stress"); blue = areas in which current and future climates are suitable (refugia); purple = areas in which climates are not currently suitable but will be in the future (possible expansion). Mapped outputs of MaxEnt species distribution projections are from modeling by The Nature Conservancy. See text for details.

Forest understory and nonforest vegetation

NRV and comparison to current—

Early observers did not measure richness of diversity of species other than trees, although they made reference to certain shrubs (mostly those that competed with trees), and sometimes referred in passing to herbaceous species as well. For example, Muir (1894) noted how the open canopy of YPMC forests in the assessment area led to many understory species, especially shrubs and forbs, but the growth was "never so dense… as to prevent the traveler from sauntering where he will" (Muir 1894: chapter 3). A general ecological principle is that the diversity of understory species tends to be negatively correlated with overstory canopy cover, and positively correlated with light availability (Barbour et al. 1987). Presettlement YPMC forests were generally more open than modern forests, and the enhanced incidence of light at the forest floor likely led to higher local species richness in understory plants, but we can only theorize based on numerous modern demonstrations of the negative relationship between forest canopy cover and understory species diversity in forests in and around the assessment area (e.g., Agee and Biswell 1970, Battles et al. 2001, Keeley et al. 2003, Wayman and North 2007, Webster and Halpern 2010). These probable local effects notwithstanding, there is no evidence that we know of that demonstrates any notable change in regional richness (overall species richness across the assessment area) of understory plants in the assessment area since presettlement times.

Although many plant species in California have been demonstrated to require fire scarification of their seeds to induce germination (e.g., through heat, presence of certain volatiles, or chemicals contained in charcoal), such plants are rare in assessment-area YPMC forests (Keeley et al. 2003, 2012; Webster and Halpern 2010). This is probably due to the relative rarity of high-intensity fire over evolutionary time in these forests (Denslow 1980, Grubb 1977). As such, the large decrease in fire frequency and overall area burned in assessment-area YPMC forests since presettlement times has probably not had a highly deleterious effect on regional understory diversity, or at least as deleterious an effect as it might theoretically have in an ecosystem characterized by highly intense fire. Several widely distributed shrub species from the genera *Ceanothus* and *Arctostaphylos* do possess fire-promoted seed germination, and although these are typically shaded out by overstory trees over time, their soil seedbanks may persist for hundreds of years and they are not at regional risk of extinction as a result of fire suppression (Keeley et al. 2012, Knapp et al. 2012).

As with the canopy tree species, understory species composition varies across the assessment area, depending on underlying environmental conditions as well as the influence of the tree canopy layer. It seems probable that understory species requiring higher light environments may have become less abundant (if not less species rich) in the assessment area as a result of fire exclusion. At the same time, shade-loving species have probably increased in abundance, at least locally. Whether such changes have led to overall changes in understory species diversity is difficult to say in any general fashion; however, there are a few recent studies that provide some insight. Knapp et al. (2013) took advantage of surveys done in 1929 on the Stanislaus National Forest and resampled the same plots in 2007/2008. They did not find evidence that overall species richness had changed between the surveys, but shrub and herb species more tolerant of shade and litter layers were much more abundant in the modern forest (dense, high canopy cover, after long-term fire suppression) than in the original surveys (e.g., *Chrysolepis sempervirens* (Kellogg) Hjelmqvist, *Pyrola picta* Sm., *Symphoricarpos mollis* Nutt., *Apocynum androsaemifolium* L.), while heliophilic plants were less abundant (e.g., *Arctostaphylos patula* Greene, *Ceanothus* spp., *Chamaebatia foliolosa* Benth., *Epilobium,* and *Hieracium* spp.). Stevens et al. (2015) found that these same heliophilic genera, which have biogeographic affinity to California and xeric regions in southern North America, increased in richness with fire severity, from unburned forest to low-severity wildfire to high-severity wildfire. The increase in these southern-xeric species was accompanied by a loss of the "Arcto-Tertiary" geoflora (Raven and Axelrod 1978) following fire, particularly in more productive mixed-conifer forests that previously had higher canopy cover and stand density. Stevens et al. (2015) also found that within-plot (alpha) diversity was higher in burned forest than in unburned forest 3 years after fire, and that between-plot (beta) diversity was higher in stands that had previously been treated for fuels reduction and burned at low to moderate severity, compared with previously untreated stands nearby that generally burned at high severity. Their estimates for stand-scale diversity, combining alpha and beta diversity estimates, indicated a peak in diversity at the intermediate disturbance level created by low- to moderate-severity wildfire burning through fuel treatments. The number of invasive, nonnative plant species was positively related to disturbance and fire severity.

Future—

The Nature Conservancy forecasted future climate suitability for a number of YPMC forest shrub species using MaxEnt modeling. See "Trees" on page 161 for more detail on the modeling. Outputs are viewable at http://www.tnccmaps.org/climate/species/. These models suggest notable loss of suitable climates for important species like Greenleaf manzanita (*Arctostaphylos patula* E. Greene) and mountain whitethorn (*Ceanothus cordulatus* (Hook.) Nutt.) in the northern and northeastern parts of the assessment area. As noted above, these models include only climate variables, and many other factors interact to drive species distributions.

If current trends in fire severity continue (Mallek et al. 2013, Miller and Safford 2012, Miller et al. 2009b), it seems likely that species of more mesic habitats will decrease in abundance and perhaps richness, while xeric species adapted to higher light and warmer conditions will expand (Stevens et al. 2015). Alien species richness is also likely to increase under this scenario.

See "Forest understory and nonforest vegetation" above for more information on understory vegetation.

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Summary of Probable Deviations From NRV —and Conclusion

Based on our understanding of YPMC ecosystems in the bioregional assessment area, we have attempted to draw conclusions with regard to whether key ecosystem variables are currently within or outside of the NRV. Table 11 summarizes our conclusions and directs the reader to the areas of this report that discuss the ecosystem elements in question.

We finish by making the following general conclusions:

1. With regard to ecosystem composition of assessment-area YPMC forests, although overall plant species diversity across the assessment area has probably not changed much (except for the addition of nonnative species), there has been a major shift over the past century from dominance by shade-intolerant/fire-tolerant species to dominance by shade-tolerant/fire-intolerant species. This has happened in both the forest overstory and understory.
2. With regard to ecosystem structure, assessment-area YPMC forests are greatly changed from the presettlement period, so much so that people from the 18th or 19th centuries would probably not recognize the modern forest. For example:

    A. Mean adult tree densities are an average of two to four times higher today than during the presettlement period.
    B. Tree seedling densities are similarly much higher in the modern forest, and they are dominated by fire-intolerant/shade-tolerant species.
    C. The average tree in today's forest is 40 to 50 percent smaller (in d.b.h.) than in the presettlement forest.
    D. Even though there are fewer large trees in today's forest, the huge number of small trees has resulted in basal areas that are equal to or higher on average than in presettlement forests.
    E. Tree canopy cover averages about 33 percent more today than in the presettlement period.

Table 11—Summary of probable deviations from the natural range of variation (NRV) for yellow pine and mixed-conifer (YPMC) forests in the assessment area[a]

Ecosystem attribute	Indicator group	Indicator	Variable	Within NRV[b]	Confidence	See discussion on page:	Notes
Function	Disturbance	Fire	Fire regime	No	High	31	Shift from Fire Regime I to Fire Regimes III and IV.
Function	Disturbance	Fire	Fire frequency	No	High	34	Current frequency far below presettlement but rising.
Function	Disturbance	Fire	Fire severity	No	Medium to High	38	Current severity higher than presettlement and rising.
Function	Disturbance	Fire	Fire size	No	Medium	52	For fires >4 ha, current mean and mean maximum fire sizes larger than presettlement mean.
Function	Disturbance	Fire	High severity patch size	No	Medium	51	Current high-severity patch sizes higher than presettlement mean and rising.
Function	Disturbance	Fire	Fire rotation	No	High	37	Fire rotations much longer today than presettlement.
Function	Disturbance	Fire	Fire season	No	Medium	56	Fire season is becoming longer, but general seasonal patterns are similar.
Function	Disturbance	Fire	Annual area burned	No	High	55	Current mean annual area burned is much lower than all estimates of presettlement area (but it is rising quickly).
Function	Disturbance	Insect outbreaks	Tree mortality from insects	unknown		69, 84	Little in the way of presettlement estimates. Some conclusions can be drawn from comparisons of range of current conditions.
Structure	Physiognomy	Canopy cover	Percentage of cover	No	Medium	136	Modern mean canopy cover is above presettlement.
Structure	Physiognomy	Coarse woody debris (CWD)	Pieces of CWD per unit area	No	Medium	141	Density of CWD is higher in contemporary forests.
Structure	Physiognomy	Coarse woody debris	Mass of CWD per unit area	No	Medium	141	Average tons/ha of CWD is higher in contemporary forests.
Structure	Physiognomy	Forest fuels	Tons/ha	No	Medium	158	On average, contemporary YPMC forests support much higher fuel loadings than presettlement forests, in both fine-fuel and coarse-fuel classes.
Structure	Physiognomy	Functional groups/ growth forms	Proportion of early/ middle/late seral forest	No	Medium	87	Current lack of old-forest successional stages, perhaps some localized lack of early stages.
Structure	Physiognomy	Gap size distribution	Gap size	No	Medium	139	Gap sizes are generally decreasing (in undisturbed forests), but also increasing in disturbed forests owing to more severe disturbance.

Table 11—Summary of probable deviations from the natural range of variation (NRV) for yellow pine and mixed-conifer (YPMC) forests in the assessment area[a] (continued)

Ecosystem attribute	Indicator group	Indicator	Variable	Within NRV[b]	Confidence	See discussion on page:	Notes
Structure	Physiognomy	Grass and forb cover	Percentage of cover	Maybe	Low	153	Difficult to assess, little presettlement data. Overall herbaceous cover on landscape may be similar; cover within forest stands may be lower owing to fire suppression.
Structure	Physiognomy	Overstory density	Number of trees per unit area	No	High	97	Current density higher on average than presettlement.
Structure	Physiognomy	Overstory density	Number of large trees per unit area	No	High	97	Large tree density is lower in modern forests.
Structure	Physiognomy	Shrub cover	Percentage of cover	Maybe	Low	148	Difficult to assess, little presettlement data. Overall shrub cover on landscape not much changed over time; cover within forest stands may be lower owing to fire suppression.
Structure	Physiognomy	Snag density	Number of snags per unit area	No	Medium	141	Snag density is higher in contemporary forests.
Structure	Physiognomy	Tree size class distribution	Tree size-class distribution	No	High	99	Major increases in small size classes, and general decreases in large size classes. Change in distribution shape from ± flat, hump-shaped, or weakly J-shaped in average presettlement forest to strongly J-shaped in average modern forest.
Structure	Physiognomy	Average tree size	Mean d.b.h. or quadratic mean diameter	No	High	99	Average conifer tree in modern YPMC forests about one-half the diameter of the average tree in presettlement forests.
Structure	Productivity	Tree basal area	Basal area	Yes	Medium	107	Basal area similar if a bit higher in modern forests; major difference is distribution of more biomass in small and medium trees in contemporary forest than in presettlement forest.
Composition	Functional diversity	Functional groups/ growth forms	Proportion of shade tolerant vs. shade intolerant species	No	High	160	Major shift from dominance of shade-intolerant species to dominance of shade-tolerant species.
Composition	Species diversity	Species richness	Plant species richness	Yes	Medium	161	No evidence of major species loss.

d.b.h. = diameter at breast height. TBD = to be determined.

[a] NRV presettlement reference period is assumed to refer to 1500/1600 to 1850, unless otherwise indicated in notes. NRV for most indicators/variables also includes information from contemporary reference sites.

[b] As defined as the range of means from multiple sources.

   F. Forest structure has been greatly homogenized, with the size and number of forest gaps decreasing almost to zero in many modern forest stands. In presettlement forests, many areas supported more canopy gaps than canopy.
   G. Contrary to what many people think, an objective assessment of the evidence suggests that snag densities and coarse woody debris are not depleted in modern forests, and indeed most of the evidence suggests they are **more** abundant today than in the average presettlement forest stand.
   H. Coarse woody debris is also a component of forest fuels, and modern fuel loadings are much higher today than in the presettlement forest. Our estimate is that fuel loadings in assessment-area YPMC forests have risen by an average of 70 to 100 percent over the past century or so.
   I. Shrub cover in modern YPMC forests is probably not very different from presettlement conditions (maybe slightly lower today), but the distribution of shrub cover certainly is. Modern forests are more likely to support large areas of contiguous shrub fields but relatively low shrub cover within forest stands (owing to higher stand canopy cover today), whereas presettlement forests supported higher cover of shrubs within stands, as light incidence at the soil surface was much higher.
3. With regard to ecosystem function, the major change in YPMC forests has been in the role and behavior of fire. Specifically:
   A. Fires have gone from representing a frequently recurring disturbance on the landscape (5 to 10 events per century on average) to an extremely rare event (75 percent of all YPMC forest has not seen a fire in the past 100+ years).
   B. The average area of fire in the assessment area between 1984 and 2010 was only about 10 to 15 percent of the presettlement mean (±150 000 ha per year), but the past 6 years have seen much more area burn, with large areas experiencing nearly complete tree mortality.
   C. When fire occurs today, it behaves very differently on average than in the presettlement forest because of differences in forest structure and fuels, and as a result of changing climate. The proportional area of fires burning at high severity today (severity is a measure of mortality caused by fire or biomass lost to fire) is 5 to 10 times greater than in the average presettlement period fire.

4. As such, the role of fire has changed from one of forest maintenance (of relatively open-canopy, low-fuel-accumulation conditions with dominance primarily by fire-tolerant species) to one of forest transformation, where dense stands of fire-intolerant species and heavy fuel accumulations are more likely to burn at high severity, resulting in major ecosystem changes.

For decades, the major ecological issue in the assessment area was thought to be the loss of dense-canopied, old-growth forest to logging, and threats to wildlife species that depend on such conditions (Duane 1999, Ruth 1996). Today the major threat is clearly the loss of forest—old growth or not—to severe wildfire and insect and direct drought mortality (Keeley and Safford 2016, McKenzie et al. 2004). The irony is that a primary cause of this major threat is the historical widespread focus on fire suppression, which was viewed as a necessary means to prevent forest loss. In light of new scientific information, such as the information presented in this report, these management views have been changing, and we are at a pivotal point in resource management in the assessment area. Current trends in climate, fire, human land use, economics, and federal budgets are not auspicious, but recent collaborative management efforts at large landscape scales, political developments in California, and more progressive national forest planning suggest that there is a broadening understanding of the necessary ecological role of fire in the Sierra Nevada bioregion. We hope that this assessment of past and current conditions in the broader Sierra Nevada bioregion will add to this growing understanding and support effective management that can conserve California's "Range of Light."

Today the major threat is clearly the loss of forest—old growth or not—to severe wildfire and insect and direct drought mortality (Keeley and Safford 2016, McKenzie et al. 2004). The irony is that a primary cause of this major threat is the historical widespread focus on fire suppression, which was viewed as a necessary means to prevent forest loss.

Acknowledgments

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English Equivalents

When you have:	Multiply by:	To get:
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	0.62	Miles
Hectares (ha)	2.47	Acres
Square kilometers (km^2)	0.386	Square miles
Square meters per hectare (m^2/ha)	4.357	Square feet per acre
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

Metric Equivalents

When you have:	Multiply by:	To get:
Inches (in)	2.54	Centimeters
Feet (ft)	0.305	Meters
Miles (mi)	1.609	Kilometers
Acres (ac)	0.405	Hectares
Square miles (mi^2)	2.59	Square kilometers
Square feet per acre (ft^2/ac)	0.229	Square meters per hectare

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Appendix: Pacific Southwest Region Natural Range of Variation Assessments for Forest Planning: A Summary of the Process and the Products

Hugh Safford, regional ecologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, hughsafford@fs.fed.us, 707-562-8934, May 12, 2013

According to the Forest Service 2012 Planning Rule (36 CFR 219):

> Assessments rapidly evaluate existing information about relevant ecological, economic, and social conditions, trends, and sustainability and their relationship to the land management plan within the context of the broader landscape. The responsible official shall consider and evaluate existing and possible future conditions and trends of the plan area, and assess the sustainability of social, economic, and ecological systems within the plan area, in the context of the broader landscape.

The Planning Rule identifies 15 topic areas that must be addressed in the assessment. Among these are (1) terrestrial ecosystems (and aquatic ecosystems and watersheds), and (2) system drivers, including dominant ecological processes, disturbance regimes, and stressors, such as natural succession, wildland fire, invasive species, and climate change; and (3) the ability of terrestrial and aquatic ecosystems on the plan area to adapt to change.

FSH 1909.12 Chapter 10, Section 12.11

Requires that "the responsible official should identify and evaluate the ecological integrity of… ecosystems within the plan area."

Steps include:

1. Identify relevant ecosystems to be evaluated and the appropriate scale for the assessment
2. Rapidly evaluate available information about those ecosystems, including composition, structure, and function, by:
   A. Selecting key ecosystem characteristics for the evaluated ecosystems that will permit evaluation of ecological integrity (sustainability)
   B. Describe the natural range of variation (NRV) for key ecosystem characteristics, when such information is readily available
   C. (describes an alternative to NRV assessment)
   D. Describe current condition and trends of the key ecosystem characteristics
3. Identify and evaluate system drivers and stressors

4. Describe the projected future status of ecosystem integrity, using the key ecosystem characteristics, by:
    A. Describing the status of the key ecosystem characteristics by comparing NRV to current conditions, or
    B. (describes alternative where NRV assessment is not available)
5. Identify status of key ecosystem characteristics and determine whether they are "functioning in a way that contributes to ecosystem integrity and sustainability."

Natural Range of Variation Assessments

These were carried out by Pacific Southwest Region Ecology Program. Each ecologist was assigned one or two chapters. Work began October 2012, and was completed in May 2013 (with some exceptions). Updates were made in 2015 and 2016.

Detailed steps:

1. Identify ecosystems to be addressed
    A. NRV assessments are focused on terrestrial ecosystems
    B. We used Barbour and Billings (2000) Sugihara et al. (2006), Barbour et al. (2007), MCV, Van de Water and Safford (2011), and California WHR classification, and then requested input from about 25 academic, NGO, and agency experts. Ecosystems had to be mappable, relatively well-studied, common in some form to all of the sources above, and represented through much of the bioregional assessment area. Settled on:
        i. Forest types
            a. Yellow pine
            b. Mixed conifer
            c. Red fir
            d. Subalpine
            e. Pinyon-juniper
            f. Hardwoods
                - Oak-dominated forests
                - Aspen
        ii. Shrub types
            a. Chaparral
            b. Sagebrush
        iii. Herbaceous types
            a. Montane meadows
        iv. Combined types
            a. Riparian vegetation

2. Determine appropriate scale
    A. Spatial:
        i. SNEP/SNFPA boundary
        ii. NRV reference data used from outside of area when necessary and reasonable
        iii. Assessments included both stand-level and landscape-level analyses where possible
    B. Temporal:
        i. Holocene (12,000 YBP to today), with period 1500–1850 set as principal historical reference period (this is a general HRV/NRV standard)
        ii. FSH 1902.12 guidance: should be before widespread Euro-American influence
3. Determine key ecosystem characteristics (= ecological indicators)
    A. Guidance from FSH 1902.12 Chapter 10
        i. "Key ecosystem characteristics include the dominant ecological characteristics that describe the composition, structure, function, and connectivity of terrestrial, aquatic, and riparian ecosystems that are relevant to addressing important concerns about the land management plan. Key ecosystem characteristics are identified, selected, and evaluated during the assessment phase, brought forward to inform the development of plan components, and may be useful for monitoring progress towards maintaining or restoring ecological integrity. Key ecosystem characteristics may be added or modified during the planning phase."
        ii. Need to be characteristics that can be measured, are meaningful, and for which we have data both now and in the past, as well as in contemporary reference ecosystems. Also should be something which will respond to Forest Service management, or "indicates something about the limits to Forest Service authority or the inherent capability of the land."
        iii. Some examples provided in FSH 1902.12 Chapter 10 (12.14 exhibit 01)
        iv. Key ecosystem characteristics include ecological processes ("drivers and stressors")

B. Generated list of ecological indicators (= key ecosystem characteristics)
  i. Ecological indicators: “measurable characteristics of the structure (e.g., genetic, population, habitat, and landscape pattern), composition (e.g., genes, species, populations, communities, and landscape types), or function (e.g., genetic, demographic/life history, ecosystem, and landscape disturbance processes) of ecological systems.” (Niemi and McDonald 2004)
  ii. Based on nested hierarchy of:
    a. Ecosystem attribute (highest level)
      - Composition
      - Structure
      - Function
    b. Ecological hierarchy
      - Population/species
      - Community/ecosystem
      - Landscape/region
    c. Indicator group (examples)
      - Species diversity
      - Physiognomy
      - Productivity
      - Biogeography
      - Nutrient cycling
      - Patchiness
      - Connectivity
      - Disturbance
        - ◦ Fire, grazing, logging, wind, floods, etc.
    d. Indicators
      - Examples from fire regime indicator group
        - ◦ Fire frequency, fire rotation, fire size, fire severity, fire season…
      - Examples from physiognomy indicator group
        - ◦ Tree density, basal area/volume, canopy cover…
    e. Variables and their units (lowest level)
      - Example from fire frequency indicator
        - ◦ Fire return interval (mean number of years between fires)
      - Example from tree density indicator
        - ◦ Number of trees per hectare
    f. A spreadsheet of attributes, hierarchy, indicators and variables is available from the Regional Ecologist (but perusal of the chapters will also provide this list)

4. NRV assessments
    - A. 11 Chapters, Introductory chapter to be written; intention is to publish as general technical report in 2013 or 2014
    - B. NRV is based on historical and contemporary reference systems. Direct data used when available, inference used where necessary and justifiable
    - C. Includes comparisons to current conditions and summary of literature re. possible future trends
    - D. Focus is on peer reviewed publications, including papers in press or soon to be in press; government publications; Forest Service and other federal and state agency data; and in some cases academic theses or dissertations. Because information on the historical state of some ecosystems and ecological processes and patterns is scarce, in some cases we also refer to published anecdotal information from the mid-19th to early 20th centuries. We do not refer to anecdotal information from more recent times.
    - E. Used Forest Service Rocky Mountain Region HRV assessments from early 2000s as rough templates (e.g., Dillon et al. 2005, Meyer et al. 2005, Veblen and Donnegan 2005)
    - F. Basic outline
        - i. Introduction
        - ii. Methods
        - iii. NRV descriptions
            - a. Function
            - b. Structure
            - c. Composition
        - iv. Summary of NRV deviations
        - v. Literature cited
        - vi. Tables and figures
    - G. Timeline
        - i. Dec 14, 2012: Preliminary bibliography assembled
        - ii. Feb 11, 2013: Drafts due for internal review
        - iii. Feb 15: Internal reviews due
        - iv. Feb 25: Delivery of draft chapters to planning staff
        - v. Mar 11: Final revised drafts due for external review
        - vi. Apr 1: External reviews due
        - vii. Week of Apr 8: Final draft NRV assessments
        - viii. Week of May 12, 2013: Final NRV assessments posted to web

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Pacific Southwest Research Station
800 Buchanan Street
Albany, CA 94710

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HABITAT SELECTION IN A CHANGING ENVIRONMENT: THE RELATIONSHIP BETWEEN HABITAT ALTERATION AND SPOTTED OWL TERRITORY OCCUPANCY AND BREEDING DISPERSAL

MARK E. SEAMANS AND R. J. GUTIÉRREZ[1]
Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108

Abstract. Understanding the effect of habitat alteration on avian behavior is important for understanding a species' ecology and ensuring its conservation. Therefore, we examined the relationship between Spotted Owl habitat selection and variation in habitat in the Sierra Nevada. We estimated habitat selection by modeling the probability of territory colonization (γ), territory extinction (ε), and breeding dispersal in relation to the amount of mature conifer forest within and among territories. Alteration of $\geq$20 ha of mature conifer forest (coniferous forest with >70% canopy cover dominated by medium [30.4–60.9 cm dbh] and large [>60.9 cm dbh] trees) within individual territories ($n = 66$) was negatively related to territory colonization and positively related to breeding dispersal probability. Although territory extinction was negatively related to the amount of mature conifer forest, it was not clear whether this relationship was due to variation of mature conifer forest within or among territories. Although modeling results for territory colonization and extinction generally supported the hypothesis that individuals are "ideal" when selecting a habitat in the sense that they settle in the highest-quality site available, we did not find a clear benefit in terms of habitat quality for Spotted Owls that exhibited breeding dispersal.

Key words: breeding dispersal, habitat alteration, habitat selection, occupancy, Spotted Owl, Strix occidentalis.

Selección de Hábitat en un Ambiente Cambiante: Relación entre la Alteración del Hábitat y la Ocupación de Territorios y la Dispersión Reproductiva en *Strix occidentalis*

Resumen. Entender el efecto de la alteración del hábitat sobre el comportamiento de las aves es importante para comprender la ecología de una especie y asegurar su conservación. Por lo tanto, examinamos la relación entre la selección de hábitat por parte de *Strix occidentalis* y la variación en el hábitat en la Sierra Nevada. Estimamos la selección de hábitat modelando la probabilidad de colonización de un territorio (γ), de extinción de un territorio (ε) y de dispersarse para reproducirse en relación con la cantidad de bosque de coníferas maduro dentro de y entre los territorios. La alteración de 20 o más hectáreas de bosque de coníferas maduro (bosque de coníferas con más del 70% de la cobertura del dosel dominada por árboles medianos [30.4–60.9 cm de DAP] y grandes [>60.9 cm de DAP]) dentro de territorios individuales ($n = 66$) se relacionó negativamente con la colonización de los territorios y positivamente con la probabilidad de dispersarse para reproducirse. Aunque la extinción de los territorios se relacionó negativamente con la cantidad de bosque de coníferas maduro, no es claro si esta relación se debió a la variación en el bosque de coníferas maduro dentro de los territorios o entre territorios. Aunque los resultados del modelado de colonización y extinción de los territorios en general apoyaron la hipótesis de que los individuos son "ideales" al seleccionar el hábitat en el sentido en que se establecen en los sitios disponibles de mayor calidad, no encontramos un beneficio claro en términos de la calidad de hábitat para los individuos que se dispersaron para reproducirse.

INTRODUCTION

The effect of habitat alteration on avian habitat choice is a key issue for conservation (Stamps 2001). If birds choose habitats to increase their fitness (Fretwell and Lucas 1969), habitat alteration, both before and after habitat selection has occurred, has the potential to affect population dynamics, particularly if the alteration affects a large area. The consequence of habitat alteration is especially relevant for territorial species that exhibit limited breeding dispersal (individuals switching territories be-

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[1] Corresponding author. E-mail: gutie012@umn.edu

tween breeding attempts). Breeding dispersal is likely an adaptive trait although it is thought to occur infrequently in many species (Greenwood and Harvey 1982). Inbreeding avoidance, mate choice, site choice, or social constraints have all been hypothesized to influence breeding dispersal (Greenwood 1980, Greenwood and Harvey 1982, Dobson and Jones 1985, Payne and Payne 1993). Breeding dispersal that is motivated by habitat alteration could be viewed as adaptive in terms of site choice.

The Spotted Owl (*Strix occidentalis*) is a territorial species that has high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006). Most habitat studies have indicated that Spotted Owls preferentially select areas of mature coniferous forest (Forsman et al. 1984, Verner et al. 1992, Chatfield 2005), and that this habitat type influences their population dynamics (Franklin et al. 2000, Olson et al. 2004, Seamans 2005). Because mature coniferous forests in the western United States are prized for lumber production and are also highly susceptible to stand-replacing wildfire, alteration of this habitat type is believed to pose a threat to the owl's long-term viability (U.S. Department of Interior 1990, 1993, Verner et al. 1992). Although the alteration of mature forest is believed to have long-term negative consequences for Spotted Owls, there have been few empirical studies that have attempted to quantify how variation in the amount of mature forest may affect territory occupancy.

In this paper we examine the relationship between the amount of mature conifer forest, alteration of mature conifer forest, and Spotted Owl territory occupancy and breeding dispersal over a 15-year period. We use the term "habitat alteration" because we are not sure that all habitat changes in forest structure can be considered "habitat loss." Thus, habitat alteration represents a change from mature conifer forest to some other forest cover type by logging or wildfire. Ideally, a true experiment (i.e., random allocation of replicated experimental units to treatments) should be used to estimate cause and effect relationships between habitat alteration and Spotted Owl population processes. However, designing and executing true experiments has proven difficult because of constraints involved with endangered species management and because the scale of potential treatments poses significant logistical challenges. Therefore, we used a combination of quasi-experimental (Cook and Campbell 1979) and observational approaches. We accepted treatment units (Spotted Owl territories) as they occurred and recorded observations of forest alteration, territory occupancy, and individual movement among territories over time. Valid inference from this approach required controlling for the confounding effect of variation in the amount of mature conifer forest among Spotted Owl territories. Because of the difficulty in controlling for this confounding effect, and because of the overall study design, we did not infer cause and effect relationships from our results. Rather, our goal was to evaluate whether: (1) alteration of mature conifer forest was correlated with immediate, short-term territory colonization probability (probability of an unoccupied territory becoming occupied), extinction probability (probability of an occupied territory becoming unoccupied), or breeding dispersal probability; (2) alteration of mature conifer forest was correlated with long-term territory colonization or extinction probability; and (3) territory colonization or extinction probability, or breeding dispersal, was related to variation in the amount of mature conifer forest among territories. We sought to increase our knowledge of the relationships between habitat alteration and Spotted Owl habitat choice. Further, our results can be used to identify specific habitat types that should be targeted by experimental studies whose goal is to test the effect of habitat alteration on Spotted Owls.

METHODS

STUDY AREA

Our 925 km^2 study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River (Seamans et al. 2001). Within this area, we surveyed owls in a 355 km^2 "density study area" from 1990 to 2004. We surveyed the density study area completely for Spotted Owls each year regardless of land ownership or past occupancy by owls. In 1997 we established a "regional study area," which surrounded the density study area. The regional study area consisted of previously known owl territories and territories that were located from 1997 to

1999. Areas between owl territories in the regional study area were not completely surveyed.

The Sierra Nevada was the dominant physical feature of the area. The study area was typical of the midelevation Sierra Nevada, with mountainous terrain bisected by steep river canyons. Elevations ranged from 366 to 2401 m. Climate was Mediterranean, with cool wet winters and hot dry summers (Olson and Helms 1996). Sierran mixed conifer forest was the principal vegetation type (Sierra Nevada Ecosystem Project 1996) and was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*) in the canopy and black oak (*Quercus keloggii*), tanoak (*Lithocarpus densiflora*), and big leaf maple (*Acer macrophyllum*) in the understory. Red fir forest was less abundant but common at higher elevations, and montane manzanita chaparral, black oak woodland, and barren rock were less abundant but locally important vegetation or landscape features (Sierra Nevada Ecosystem Project 1996).

DATA COLLECTION

Spotted Owl surveys. We surveyed Spotted Owls from 1 April to 28 August of each year from 1990 to 2004, following methods described by Franklin et al. (1996). We used two types of surveys: (1) nighttime surveys to initially locate owls in an area; and (2) daytime surveys to locate roosts and nests, and to capture, band, and assess the reproductive status of owls. Nighttime surveys consisted of imitating Spotted Owl vocalizations between dusk and dawn at established survey locations and listening for a response. Survey locations were consistent from year to year and were placed to obtain complete survey coverage of the density study area and each Spotted Owl territory in the regional study area. There were 5–12 survey points for each Spotted Owl territory, depending on the topography of the territory. A complete survey for a territory was achieved when we imitated owl territorial calls at all survey points within a territory over a four-day period without receiving a response. We conducted up to six surveys at each Spotted Owl territory to determine owl presence.

If an owl responded during a nighttime survey we conducted a daytime survey within four days of receiving the response. We counted a nighttime survey with a response and the subsequent daytime survey as only one survey for the purpose of modeling occupancy (see below). We attempted to capture and band all Spotted Owls detected using the methods of Franklin et al. (1996). Once captured, we fitted owls with a U.S. Fish and Wildlife Service locking aluminum band on the tarsometatarsus of one leg. On the other leg we marked individuals ≥1 year old with a unique color-band and tab combination. We determined the sex of owls based on the pitch of their calls and their behavior (Forsman et al. 1984). We identified four age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; one-year-old (first-year subadult); two-year-old (second-year subadult); and ≥3 years old (adult).

Habitat metrics. Using a combination of aerial photographs, digital-orthophoto-quarter quadrangles, and extensive ground sampling we created a forest cover map with eight vegetation cover types for the entire density study area and a vegetation cover type map for each regional study area owl territory (Chatfield 2005, Seamans 2005). We defined vegetation cover types based on the dominant vegetation structure (tree diameter at breast height [dbh; measured 1.4 m above the forest floor on the uphill side of the tree] and canopy cover). Because Seamans (2005) estimated that the area of coniferous forest with >70% canopy cover dominated by medium (30.4–60.9 cm dbh) or large (>60.9 cm dbh) trees was the best predictor of demographic parameters for owls in our study population, we chose to examine only the effect of alteration of this vegetation type. Hereafter, we refer to this vegetation type as "mature conifer forest." Minimum polygon size for mapping was 0.1 ha. Map accuracy for mature conifer forest was 91% (Chatfield 2005).

We estimated the total amount of each of the eight cover types within a 400 ha circle in each owl territory using the spatial analyst extension in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). This area was based on a circle with a radius of 1128 m, which was half the mean nearest neighbor distance of occupied territories in the density study area averaged over the years 1990 to 2002. We determined the center of the circle for each territory by estimating the geometric center of all owl locations from each year the territory was occupied. The area encompassed by this circle was approximately one-quarter to one-half of the estimated home range size for Spotted Owls in the central Sierra Nevada (Laymon 1988, Call et al. 1992). Although we did not know if the entire 400 ha area was used by owls, the circles did encompass all nests and >90% of all roosts in each territory. We used the term "territory" to depict the spatial location and area for which we estimated habitat metrics because: (1) owls responded to conspecific calls from these areas during surveys; (2) the 400 ha we used for analyses contained all known nest locations of owls responding in that area; and (3) all areas surrounding the nest were vocally defended by owls during daytime surveys.

We used aerial photographs (a complete set was created approximately every four years of study) to determine the location and extent of habitat alteration. We estimated the year of timber harvest based on: (1) our own field notes; (2) USDA Forest Service harvest records; (3) University of California Berkeley Blodgett Experimental Forest harvest records; and (4) core samples of trees. We used an increment borer to extract complete cores of ≥4 trees immediately adjacent to a clear-cut or within a forest stand that had been thinned. We then estimated the year of harvest by locating a sustained increase in widths of tree rings, indicating reduced competition from other trees.

STATISTICAL ANALYSES

Territory occupancy. For female Spotted Owls, we estimated territory colonization (γ) and extinction (ε) probabilities (vital rates of territory occupancy) following MacKenzie et al. (2003). Territory colonization probability is the probability that a territory unoccupied in year $t - 1$ becomes occupied in year t, and territory extinction probability is the probability that a territory occupied in year $t - 1$ is unoccupied in year t. The probability of occupancy (ψ) in year t can be calculated from γ, ε, and ψ_{t-1} (MacKenzie et al. 2003) by:

$$\psi_t = \psi_{t-1}(1 - \varepsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

We modeled occupancy vital rates for females only because the most appropriate method for coding data of single male versus single female responses from surveys was not clear. Modeling females only was a good indication of pair occupancy of a territory because unpaired females were rare during our study (we located only two females in 15 years that may have been unpaired during a year). Each territory was surveyed up to six times each year for 15 years.

We estimated γ and ε using program MARK (White and Burnham 1999). In addition to γ and ε, the analytical approach we used directly estimated the proportion of territories occupied in the first year of study. We accounted for imperfect detectability of owls while modeling γ and ε. We examined the following temporal structures for detection probability within and among years: constant (means model); linear trend; log-linear trend; and quadratic trend. We fitted a model for each combination of these temporal structures within and among years and ranked models using Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the top-ranked detection probability structure for inference regarding the effect of habitat alteration on γ and ε.

We created three statistical models to examine the relationship between mature conifer forest and γ and ε. For all models we predicted that: (1) increasing amounts of mature conifer forest would be positively related to γ and negatively related to ε; and (2) alteration of mature conifer forest would be negatively related to γ and positively related to ε. The first model included a time-varying individual covariate that depicted the amount of mature conifer forest in each territory each year. For the second model we used a categorical treatment effect with two levels, no alteration of mature conifer forest versus >0 ha mature conifer forest altered, to estimate if alteration of mature conifer forest affected territory extinction or colonization probability the subsequent year. The treatment effect for this model occurred regardless of the amount of mature conifer forest altered. Lastly, we created a third model that hypothesized that the amount of mature conifer forest altered in an individual territory had a long-term effect on colonization and extinction probability. This latter model was essentially an interrupted time series model and included a continuous variable that depicted the total area of mature conifer forest in each territory at the beginning of the study, and a nominal variable with three levels that depicted the size of treatment: no mature forest altered, between 0 and 20 ha altered, or $\geq$20 ha altered. Unlike the second model above, we coded the categorical treatment variable to carry the effect forward in time. For example, if a territory had 30 ha of mature forest altered in 1992, the model was coded to examine a $\geq$20 ha treatment effect on γ and ε for this territory from 1993 to 2004. Our use of a 20 ha cutoff for the treatment level was arbitrary. We also examined variations of this latter model that included the starting amount of mature forest and a nominal variable with two treatment levels (<20 ha versus $\geq$20 ha), and an interaction between the starting area of mature forest and the categorical treatment effect. We ranked the plausibility of these competing models using AIC_c (AIC corrected for small sample size) and examined the 95% confidence intervals around the model coefficients to determine whether γ or ε was related to the area of mature conifer forest or categorical treatment effect. For analysis of γ and ε we divided the covariate depicting the total area of mature conifer forest in a territory by 260 to aid numerical optimization. Model coefficients presented in results are based on this transformation.

Breeding dispersal. Before examining the effect of habitat alteration on breeding dispersal, we first examined the probability of breeding dispersal as a function of owl sex, age, social status, and breeding status with the same approach used by Blakesley et al. (2006) in a study of Spotted Owls in the northern Sierra Nevada. We defined breeding dispersal probability as the probability that an individual moved to a different territory between year t and year $t + 1$. We created a dataset comprised of uniquely marked individuals and their dispersal histories. Each observation in the dataset consisted of a two-year period for one individual, whether the individual dispersed (switched territories) between years, and the U.S. Fish and Wildlife Service band number for the individual. We coded the binomial response as "0" for no dispersal and "1" for dispersal. We considered owl sex, age (first-year subadult, second-year subadult, or adult) during year 1, reproductive status during year 1 (successfully produced young or not), and social status (unpaired, paired, or paired but apparent death of mate during the interval) as factors that might explain variability in dispersal probability. We also considered an interaction term between individual sex and breeding status. We analyzed data using a logistic regression (PROC GENMOD in program SAS release 8.02; SAS Institute Inc., Cary, North Carolina) and considered all possible subsets of factors. We ranked models based on their ability to explain variation in dispersal probability using QAIC (AIC corrected for overdispersion; Burnham and Anderson 1998). We calculated overdispersion of the data as χ^2 divided by the degrees of freedom. We calculated the Pearson χ^2 value using the "AGGREGATE" option of the GENMOD procedure and specified age, sex, social status, and breeding status as subpopulations.

Unlike Blakesley et al. (2006), we did not include a factor depicting territory quality in the all possible subsets modeling of dispersal probability. Instead, we included the variables in the top-ranked model from the all possible subsets regression and constructed two statistical models that were similar to the two treatment models we constructed for γ and ε: (1) a model with a categorical treatment effect with two levels, no alteration of mature conifer forest versus alteration of mature conifer forest; and (2) a model that included a continuous variable that depicted the total area of mature conifer forest in each territory during year 1, and a nominal variable with three levels that depicted the size of treatment (no mature conifer forest altered, between 0 and 20 ha altered, or $\geq$20 ha altered). We also considered variations of this latter model that included only two categorical levels of treatment (<20 ha versus $\geq$20 ha) and an interaction term between the amount of mature conifer forest in year 1 and treatment level. For the two treatment effect models we used a repeated measures approach with generalized estimating equations (Liang and Zeger 1986) to determine if habitat modification was related to dispersal probability. Observations were repeated on individuals (i.e., the blocking factor was the individual owl) and we determined statistical significance using the 95% CI for the regression parameters.

We compared the quality of the original territory with that of the new territory for owls that dispersed. We estimated the quality of individual territories based on their expected survival. We calculated expected survival (E[φ]) following Seamans (2005) using the equation:

$$\begin{aligned} E(\hat{\varphi}) = &\{\exp[1.5886 + 0.0420(\mathrm{SEX}) \\ &+ 1.5938(\mathrm{COR57}) - 1.5602(\mathrm{LAMT1}) \\ &- 1.2481(\mathrm{LAMT23})]\} \\ &\div\{1 + \exp[1.5886 + 0.0420(\mathrm{SEX}) \\ &+ 1.5938(\mathrm{COR57}) - 1.5602(\mathrm{LAMT1}) \\ &- 1.2481(\mathrm{LAMT23})]\}^{-1}, \end{aligned}$$

where SEX was a dummy variable coded 0 for females and 1 for males, COR57 was the amount (ha) of interior mature forest, LAMT1 was the natural log of the amount of hardwood forest, and LAMT23 was the natural log of the amount of pole, sapling, and brush cover types. Habitat covariates were transformed before estimation of the above equation to improve numerical optimization by dividing COR57 and AMT1 by 160, and AMT23 by 350. This model explained 93% of the variability in survival among territories (Seamans 2005). We did not consider reproduction when estimating habitat quality because the relationship between reproductive success and habitat was unclear for this population (Seamans 2005).

RESULTS

TERRITORY OCCUPANCY

We located and monitored Spotted Owls in 66 territories in our study areas from 1990 to 2004. Detection probability was constant among years, followed a log-linear trend within years, and varied between the density and regional study areas (Fig. 1). The area of mature conifer forest in individual territories ranged from 0 to 257 ha among years. Thirty-eight territories (58%) experienced some habitat alteration during our study. Habitat alteration in two territories was the result of stand-replacing wildfire while habitat alteration in all others was the result of timber harvest.

The probability of territory colonization (γ) and extinction (ε) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top three colonization models had essentially the same AIC_c weight (w_i), suggesting a high degree of model selection uncertainty. However, the only model coefficient (β) with a confidence interval that did not include zero was the categorical effect of alteration of ≥20 ha mature conifer forest (gt20). The top model included the amount of mature conifer forest in a territory at the beginning of the study (1990) and the alteration of ≥20 ha of mature conifer forest. Alteration of ≥20 ha of mature conifer forest was negatively related to γ; $\hat{\beta}_{\mathrm{gt20}} = -1.16$ (95% CI = −2.02 to −0.29). The beginning amount of mature conifer forest (BMF) in a territory was positively related to γ, but had a confidence interval that included zero; $\hat{\beta}_{\mathrm{BMF}} = 1.34$ (95% CI = −0.70 to 3.39). The top model, γ(BMF + gt20), indicated that territories in which ≥20 ha of mature conifer forest was altered experienced a 2.5% decline in occupancy probability.

The top territory extinction model (ε[CMF]; Table 1) suggested that ε was negatively related to the amount of mature conifer forest in a territory ($\hat{\beta}_{\mathrm{CMF}} = -2.58$, 95% CI = −4.48 to −0.68). "CMF" was a time-varying individual covariate depicting the amount of mature conifer forest in a territory. Model ε(CMF) was four times as plausible as the second-ranked model; therefore, we chose to use model ε(CMF) for inference. The structure of this model precluded us from separating the confounding effect of habitat alteration within territories versus variation in the amount of mature conifer forest among territories. However, if we assume that differences in mature

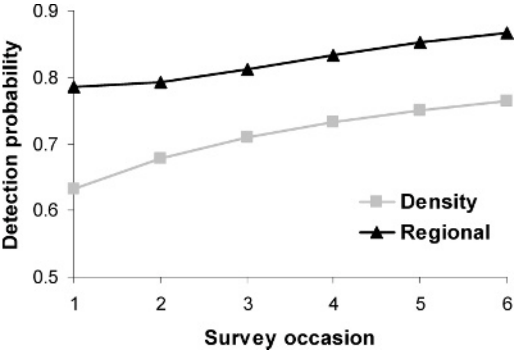

FIGURE 1. Female Spotted Owl within-year detection probability used to model territory colonization and extinction probability in the "density" and "regional" study areas in the central Sierra Nevada, 1990–2004. Each year we surveyed the complete density study area for Spotted Owls, whereas we did not survey areas between owl territories in the regional study area.

TABLE 1. Ranking of models (95% confidence set) depicting the relationship between the amount of mature conifer forest present and altered at individual territories and Spotted Owl territory colonization and extinction probability (n = 66 territories), and Spotted Owl breeding dispersal probability (n = 565), in the central Sierra Nevada, 1990–2004. Ranking of colonization and extinction models based on Akaike's information criterion corrected for small sample size (AIC$_c$), while ranking of breeding dispersal models based on AIC corrected for overdispersion (QAIC). Log($\mathcal{L}$) is the log-likelihood, K is the number of parameters, ΔAIC$_c$ is the difference in Akaike's information criterion from the top model, and w_i is the model weight.

Model[a]	$-2\log(\mathcal{L})$	K	ΔAIC$_c$[b]	w_i
Territory colonization probability (γ)				
γ(BMF + gt20)	3364.84	9	0.00	0.26
γ(BMF + gt20 + BMF*gt20)	3362.79	10	0.01	0.26
γ(BMF + ltgt20)	3362.87	10	0.09	0.25
γ(BMF + ltgt20 + BMF*ltgt20)	3360.53	12	1.87	0.10
γ(CMF)	3369.65	8	2.77	0.07
Territory extinction probability (ε)				
ε(CMF)	3363.84	8	0.00	0.68
ε(BMF + ltgt20)	3362.55	10	2.81	0.17
ε(BMF + gt20)	3366.69	9	4.90	0.06
ε(BMF + ltgt20 + BMF*ltgt20)	3361.39	12	5.77	0.04
Breeding dispersal probability (d)[c]				
d(BMF + gt20 + BMF*gt20)	274.83	9	0.00	0.56
d(BMF + ltgt20 + BMF*ltgt20)	273.69	11	2.86	0.14
d(BMF + gt20)	279.95	8	3.12	0.12
d(gt0)	283.13	7	4.30	0.07
d(.)	285.31	6	4.48	0.06

[a] Abbreviations for model parameters: BMF = individual covariate representing amount of mature conifer forest at beginning of study; CMF = time-varying individual covariate representing amount of mature conifer forest; gt20 = categorical treatment effect for mature conifer forest of <20 ha or ≥20 ha; ltgt20 = categorical treatment effect for mature conifer forest of 0 ha, >0 and <20 ha, or ≥20 ha; gt0 = categorical treatment effect of mature conifer forest of 0 ha or >0 ha.

[b] AIC$_c$ of top colonization model = 3383.07 and of top extinction model = 3385.84; QAIC of top breeding dispersal model = 292.83.

[c] All breeding dispersal models included the variables Age (age of owl: 1, 2, or ≥3 years old); Reproduction (did owl fledge young the previous year); and Social (a combination of pair status and mate loss).

conifer forest among territories caused the variation in territory extinction probability, model ε(CMF) suggested that occupancy probability increased approximately 1.1% for every 20 ha difference in the amount of mature conifer forest among territories.

BREEDING DISPERSAL

We observed 51 incidences of breeding dispersal among 565 owl-years (i.e., total dispersal opportunities of 159 owls in 15 years of study). Overall, 33 females switched territories (of which 12 were single or had lost their mate), while 18 males switched territories (of which 10 were single or had lost their mate). Overdispersion in the dataset was slight ($\hat{c}$ = 1.15). Results from the all possible subsets modeling suggested that owl age, sex, and social status best described variation in the probability of breeding dispersal. The only two competing models (≤4 QAIC$_c$ units from top model) included these same three variables plus: (1) reproductive status (repro) in the previous year; and (2) the interaction of reproductive status in the previous year and owl sex. However, model coefficients for these additional variables had confidence intervals that significantly overlapped zero ($\hat{\beta}_{\text{repro}} = -0.19$, 95% CI = -0.57 to 0.17; $\hat{\beta}_{\text{sex}\times\text{repro}} = 0.10$, 95% CI = -0.28 to 0.53). Therefore, we chose to use a model with owl age, sex, and social status for further inference.

The probability of breeding dispersal (d) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top-ranked model, d(BMF + gt20 + BMF*gt20), suggested that d was negatively related to the area of mature conifer

TABLE 2. Parameter estimates from the top-ranked logistic regression model examining breeding dispersal probability of California Spotted Owls in the central Sierra Nevada, 1990–2004.

Parameter	Estimate	CI
Intercept	6.42	2.55 to 10.30
Age class (S1)	1.08	0.09 to 2.08
Age class (S2)	1.68	0.79 to 2.57
Sex (F)	1.00	0.24 to 1.75
Social status (Pair)	−1.30	−2.04 to −0.57
Social status (Single)	1.85	0.54 to 3.16
BMF[a]	−0.55	−0.90 to −0.20
gt20[b] (0)	−8.61	−12.29 to −4.94
BMF*gt20 (0)	0.53	0.19 to 0.88

[a] BMF = individual covariate representing amount of mature conifer forest in territory in year prior to potential or actual dispersal; transformed for analysis by dividing raw numbers by 10.

[b] Categorical treatment effect for mature conifer forest coded "0" for <20 ha or "1" for ≥20 ha.

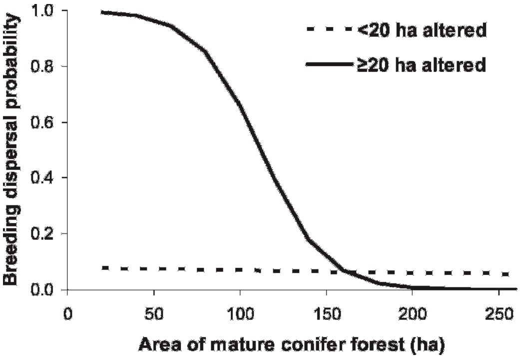

FIGURE 2. The relationship between paired female Spotted Owl breeding dispersal probability and the amount of mature conifer forest in a territory in the central Sierra Nevada, from 1990 to 2004. Dispersal probability increased rapidly at territories with <150 ha of mature conifer forest when ≥20 ha of this habitat type was altered. The *x*-axis represents the amount of mature conifer forest prior to actual or potential dispersal. The dashed and solid lines represent predicted dispersal probability when <20 ha or ≥20 ha of mature conifer forest were altered, respectively.

forest in a territory just prior to actual or potential dispersal, and positively related to alteration of ≥20 ha of mature conifer forest. Confidence intervals for model coefficients representing mature conifer forest and alteration of ≥20 ha of mature conifer forest did not overlap zero (Table 2). The interaction term suggested a steep increase in *d* in territories with <150 ha of mature conifer forest that experienced alteration of ≥20 ha of this forest type (Fig. 2). This steep increase in *d* was disproportional in comparison to territories with lesser amounts of this forest type that did not experience habitat alteration. For example, an individual in a territory with 100 ha of mature conifer forest (median = 99 ha for our study population) in which ≥20 ha were altered was estimated to have a much higher *d* than an individual in a territory that started with 80 ha yet had no mature conifer forest altered. For owl-specific variables in the top model, *d* was: (1) 0.09 times higher for first-year subadults than adults and 0.14 times higher for second-year subadults than adults; (2) 0.08 times higher for females; and (3) 0.11 times less for owls that were paired and did not lose their mates than for owls that were paired but lost their mates, and 0.15 times higher for unpaired owls than for paired owls who lost their mates.

Owls that switched territories apparently did not select new territories based on higher quality; only 53% of owls that switched territories moved to a territory with higher expected survival. We estimated that approximately 6% (three of 51) of owls that dispersed were unpaired after they switched territories, compared to 5% (51 of 1092) of all owls during the study. However, in the year prior to dispersal, 45% (23 of 51) of owls that switched territories were either unpaired or had lost their mate. We observed 14 breeding dispersal events in which one or both pair members switched territories and both formed a pair with a new mate.

DISCUSSION

We found that the amount of mature conifer forest was correlated with Spotted Owl habitat choice. Territories with more mature conifer forest had a higher probability of being colonized and a lower probability of becoming unoccupied. Further, alteration of mature conifer forest appeared to decrease the probability of colonization. Although we estimated that breeding dispersal was more likely when habitat alteration occurred, it was not clear if this increase or changes in other demographic processes were responsible for variability in territory extinction probability. For example, because Spotted Owl survival is correlated with the area of mature conifer forest in individual territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Seamans 2005), it is possible that habitat alteration affected survival, which in turn increased the probability of a territory becoming unoccupied. Conversely, it is possible that habitat alteration did not result in decreased survival but in increased emigration from the study population. In a related study, Olson et al. (2005) estimated that Spotted Owl occupancy declined 5%–15% in three study areas (n = 125 to 146 sites) when Barred Owl (*Strix varia*) presence increased, and noted that these declines could have been the result of either death or emigration.

Our use of a categorical variable to depict the amount of habitat altered allowed us to examine the relationship between alteration of mature conifer forest and Spotted Owl habitat selection. However, our use of broad categories may not have adequately represented the effect of very large or very small changes in mature conifer forest. For example, alteration of 20 ha of mature conifer forest was considered the same as alteration of 80 ha. Although this range within the categorical habitat variables likely made detecting statistical relationships more difficult, creating more detailed categories would have resulted in small sample sizes within categories. Thus, the inference that territory extinction was not related to alteration of mature conifer forest because a categorical treatment variable was not in the top model should be made with caution. In addition, the broad range of values in the categorical variable may be partially responsible for the steep increase in dispersal probability in territories with $<$150 ha of mature conifer forest.

Our estimate of Spotted Owl breeding dispersal probability (9%) is similar to estimates by Forsman et al. (2002; 7%) and Blakesley et al. (2006; 7%) for other Spotted Owl populations. The relationship between breeding dispersal probability and age, sex, and social status appears to be consistent for Spotted Owls. Similar to our study, Forsman et al. (2002) and Blakesley et al. (2006) estimated that younger owls were more likely to disperse than older owls, females were more likely to disperse than males, and unpaired owls were more likely to disperse than paired owls. However, Forsman et al. (2002) and Blakesley et al. (2006) also estimated that owls that nested during the previous year were less likely to disperse than owls that did not nest, whereas the effect of reproductive status in the previous year was poorly supported in our analysis. Prior to our study, the effect of habitat alteration on dispersal probability had not been examined in depth for the Spotted Owl, although Bond et al. (2002) examined Spotted Owl territory fidelity after wildfire and found that 11% (two of 18) of Spotted Owls switched territories the year after wildfire.

Breeding dispersal is an important life history trait that has likely evolved to increase individual fitness (Greenwood and Harvey 1982). Although the mechanisms behind the evolution of breeding dispersal are unclear, it is generally agreed that breeding dispersal can have significant effects on individual fitness and population dynamics (Greenwood and Harvey 1982, Clobert et al. 2001). Most theoretical models either predict or assume that dispersing individuals should be "ideal" when selecting a habitat, in the sense that they should settle in the highest-quality site available (Fretwell and Lucas 1969, Pulliam and Danielson 1991). Our results regarding the effect of habitat alteration on breeding dispersal, territory colonization, and territory extinction support this hypothesis. However, we did not find that Spotted Owls chose sites with more mature conifer forest, i.e., sites of higher quality, following breeding dispersal. This may indicate that the disturbance associated with habitat alteration, regardless of the extent of area altered, was an important factor motivating breeding dispersal, yet owls were either imperfect in their ability to assess habitat quality of new territories or chose a territory in which to settle based on other factors. It did appear that mate acquisition was a primary factor in selecting a territory; 43% of dispersing individuals were unpaired prior to dispersal compared to 6% after dispersal. Thus, it is surprising that we did not find that previous reproductive success was a good predictor of breeding dispersal probability. Prior reproductive success has been suggested as a primary factor determining breeding dispersal of many bird species (Wiklund 1996, Haas 1998, Catlin et al. 2005), including Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006). Further, Ens et al. (1995) viewed site choice for the Oystercatcher (*Haematopus ostralegus*) as a "career decision" because of the long-term consequences for individual fitness. We suspect a similar scenario is possible for the Spotted Owls we studied because they exhibited a relatively low probability of breeding dispersal, and because there appeared to be substantial differences among territories in terms of their quality (Seamans 2005).

Individual Spotted Owls may choose territories for something other than their intrinsic quality. We found evidence that selection of new territories by breeding individuals was not correlated with the amount of mature forest, but may have been associated with the presence of a mate. In addition, Seamans and Gutiérrez (2006) estimated that immigrants (it was unknown if they reflected breeding or natal dispersal events) appeared to use conspecifics as cues for settlement, although conspecifics may not always indicate the highest quality territory available. A further confounding factor for estimating the mechanisms responsible for selection of territories is the unknown effect anthropogenic actions have on the selective pressures responsible for breeding dispersal and habitat selection (Stamps 2001). For example, cues (e.g., the amount of mature conifer forest, the presence of a mate, or the occupancy of neighboring territories) that Spotted Owls once used to evaluate habitat quality may no longer reliably indicate quality (Hildén 1965). Our results for breeding dispersal partially support this hypothesis, while our results for territory colonization and extinction probability suggest that Spotted Owls are occupying higher quality territories.

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Landscape heterogeneity compensates for fuel reduction treatment effects on Northern flying squirrel populations

Sollmann, R.[a,b,1,*], White, A.M.[a], Tarbill, G.L. [a,b], Manley, P.N.[c], Knapp, E.E.[d]
a USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA; rsollmann@ucdavis.edu, angelawhite@fs.fed.us, ginatarbill@fs.fed.us
b Oak Ridge Institute for Science and Education, 1299 Bethel Valley Rd, Oak Ridge, TN 37830, USA
c USDA Forest Service, Pacific Southwest Research Station, 2480 Carson Rd., Placerville, CA 95667, USA; pmanley@fs.fed.us
d USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA; eknapp@fs.fed.us
1 Present address: University of California Davis, Department of Wildlife, Fish and Conservation Biology, 1088 Academic Surge, One Shields Avenue, Davis, CA 95616, USA
*corresponding author

Abstract

In the dry forests of the western United States frequent fires historically maintained a diversity of habitats in multiple seral stages. Over the past century, fire suppression and preferential harvest of large trees has led to a densification and homogenization of forests, making them more prone to larger and more severe wildfires. In response, fuel reduction treatments have become common practice in the management of dry western forests. However, the effect of fuel reduction treatments on late seral forest species, such as the Northern flying squirrels, remains a management concern.

We captured and marked flying squirrels within mixed conifer forest in the Stanislaus-Tuolumne Experimental Forest (California) on a continuous trapping grid (~1400 traps) spanning a 120-ha study landscape in which 24 4-ha units were subject to different fuel reduction treatments (variable thin, even thin, and control, all with or without prescribed burning). The study spanned two pre-thinning and three post-thinning years. We divided the study landscape into three blocks (two with treatments, one control only). For each block we analyzed data with spatial capture-recapture models to estimate density, and tested whether canopy closure before and after thinning and percent area burned were important predictors of squirrel density.

Flying squirrel densities varied from 0.168 (SE 0.086) to 0.808 (SE 0.094) individuals/ha across blocks and years. Densities varied by year, independent of treatments. Percent area burned was not an important predictor of squirrel density. The effect of canopy closure was variable, but more consistently positive after thinning reduced overall canopy closure. When considered by treatment type, squirrel densities were highest in control and burn only units, and lowest in thinned units.

Whereas thinning had negative effects on squirrel density on the scale of a thinning treatment unit, our results suggest that these effects were largely absorbed by the heterogeneous landscape, as squirrels shifted their distribution into un-thinned areas without a decline in overall density. This highlights the need to incorporate the landscape context when evaluating the effects of forest management on wildlife.

Key words: *Glaucomys sabrinus*, variable thinning, even thinning, prescribed burn, distribution, Sierra Nevada

1. Introduction

Heterogeneity is a natural feature of landscapes and has long been recognized as an important factor in supporting diverse communities (Fahrig et al., 2011; Lindenmayer et al., 2006). In the dry forests of the western United States, fire historically maintained a variety of seral stages and forest structures through cycles of frequent disturbance and stand regeneration. Fire severity and extent varied as a function of vegetation/fuels, topography and climatic conditions, resulting in forests that were comprised of patches in multiple seral stages (Agee, 1993). With Euro-American settlement, a combination of fire suppression and preferential harvest of large-diameter trees led to considerable loss in structural and compositional heterogeneity and a predominance of young, dense and relatively homogenous forest (Knapp et al., 2013; Stephens et al., 2015). In addition, the accumulation and continuity of forest fuels have contributed to larger and more severe wildfires, which are projected to become even more common as the climate continues to warm (McKenzie et al., 2004; Westerling et al., 2006).

In response to the increased risks associated with wildfire, mechanical fuel reduction treatments have become common practice in the management of dry western forests, particularly in the wildland-urban interface (Schoennagel et al., 2009). These treatments aim to reduce the risks of high severity wildfire through the mechanical removal of understory vegetation and small trees ("thinning"). Further, these treatments can be used to create heterogeneity in forest structure on the landscape scale, both directly through manipulation of stands, and indirectly, by producing heterogeneous fuel loads so that future wildfires burn with patchy severity (Stephens et al., 2012). More recent silvicultural prescriptions are often designed specifically to promote stand-scale variability in forest structure while reducing fire hazard (North, 2012). A recent meta-analysis supports the notion that the heterogeneity created by fire disturbance (or its surrogates) is needed to maintain the full array of vertebrate species in forests with frequent-fire regimes (Fontaine and Kennedy, 2012).

In spite of this evidence supporting the value of reducing the risk of high severity wildfire, fuel reduction treatments are frequently seen as having a negative impact on habitat quality for species typically associated with late seral forests (i.e. old-growth specialists). A recent publication on California spotted owls (*Strix occidentalis occidentalis*), for example, states that fuel treatments "conflict with conservation of the spotted owl" (Lee and Bond, 2015), and a study on Pacific fishers (*Pekania pennanti*) showed lower persistence at thinned sites (though authors deem this a temporary effect, Sweitzer et al., 2016). Northern flying squirrels (*Glaucomys sabrinus*) are also typically associated with late-seral habitat and play an important ecological role as dispersers of fungal spores and ectomycorrhizal bacteria (Caldwell et al., 2005) as well as the primary prey species for spotted owls and other predators (e.g., Forsman et al., 1984). Forest management activities that include tree removal may be detrimental to the highly arboreal Northern flying squirrel (Carey et al., 1992; Holloway et al., 2012; Lehmkuhl et al., 2006) because of their reliance on canopy for locomotion (Kelly et al., 2013; Scheibe et al., 2007), and because these activities can temporarily disrupt food availability (Carey, 2001). However, other studies found little to no effect of commercial thinning or secondary versus old-growth habitat on the species (Gomez et al., 2005; Ransome and Sullivan, 2002; Rosenberg and Anthony, 1992). Whereas some studies recognize the importance of the landscape context

(Holloway et al., 2012; Lehmkuhl et al., 2006), no study to date has actually measured flying squirrel response to mechanical treatment on a scale larger than the treatment unit.

In this study, we sampled Northern flying squirrel populations across a continuous area that was subject to fuel reduction treatments (mechanical thinning, prescribed burns, and combinations thereof) implemented in discrete patches across the landscape. Our objective was to determine the effects of fuel reduction treatments on flying squirrel density and distribution and tease apart treatment scale from landscape scale effects. Based on the species' association with late seral forest habitat, we expected to find a positive relationship between Northern flying squirrel density and canopy closure, and, consequently, a negative relationship with thinning treatments, which reduce canopy. Our findings have important implications for forest management, providing a more complete picture of the effects of fire and fuel reduction practices on flying squirrels, and wildlife in general.

2. Material and methods

2.1 Study Area

The study was conducted in the Stanislaus-Tuolumne Experimental Forest (STEF), located on the western slopes of the central Sierra Nevada near Pinecrest, CA. Elevation ranges from 1,585 to 1,890 m a.s.l., with about 1,020 mm of annual precipitation falling primarily as snow in the winter months. Temperatures range from -7°C in January to 27°C in July. The mixed-conifer forest on this site was last logged in the late 1920's. Originally, the forest was subject to a frequent low to moderate severity fire regime with fire return intervals between 5 and 8 years (Knapp et al., 2013), but fire has been excluded since the late 19th century. As a result of these changes, the forest today is composed of a greater proportion of shade-tolerant white fir

(*Abies concolor*) and incense cedar (*Calocedrus decurrens*), and a reduced proportion of more shade intolerant sugar pine (*Pinus lambertiana*), and ponderosa pine (*P. ponderosa*). Density of trees > 10cm diameter at breast height (dbh) within the study area was 740/ha, with approximately 45% comprised by small trees (<20 cm dbh, Knapp et al., 2013). Shrub cover has declined dramatically over time, from about 28% pre-logging to about 2% today (Knapp et al., 2012).

2.2 Fuel reduction treatments

Small mammal trapping at STEF was part of a larger study that investigated the effects of two fuel reduction treatments (Even and Variable thinning) with an Unthinned control, combined with prescribed fire, on a variety of ecological, fuels, and hydrological response variables. Twenty-four units (approximately 4 ha each) were arranged in a completely randomized split-plot design (Variable, Even, and Unthinned nested within each burned/unburned split, with four replicates per treatment, Figure 1). In addition, a 24-ha control block was established adjacent to the experimental landscape to serve as wildlife control area.

STEF management completed mechanical thinning between July and October, 2011. The goal of the Variable thinning treatment was to create a highly heterogeneous forest structure similar to what existed historically, with larger trees arranged in distinct clusters, separated in space by small gaps or areas with far fewer and/or smaller trees. The thinning prescription thus created numerous small 0.04 to 0.2-ha gaps (approximately 1 per 0.8 ha) and varied the retained density and basal area within patches at an approximately 0.1 ha scale, similar in degree and scale to what was noted in the historic stands (Knapp et al., 2012; Lydersen et al., 2013). All snags >15” (38 cm) dbh were retained unless they presented a hazard. Because of the current reduced proportion of pine trees compared with historical conditions, removal priority was fir followed by incense cedar, then pines. Details of the prescription are described in Knapp et al. (2012). The Even thinning treatment more closely approximated a standard fuel reduction prescription, retaining the largest, most vigorous trees at a relatively even crown spacing, resulting in a more homogenous stand structure than the Variable thinning treatment. The Even thinning treatment had the same tree species priority, and target basal area of retention trees was similar for both the Even and Variable thinning treatments. Even though thinning increased the percentage of pines in the tree community, white fir remained the most abundant species in both thinning treatments, and contributed a similar proportion to stand basal area as was recorded in nearby stands in 1929 (Knapp et al. 2013). STEF management applied prescribed fire in November 2013, two years after thinning treatments. Units were ignited using strip-head fires, from highest to lowest elevation. In areas where the litter was too moist to carry fire well, pockets of heavy fuels were ignited, with the fire allowed to spread within the burn perimeter as the fine fuels dried.

We collected data on vegetation before thinning, after thinning, and after burning on a 30-m grid set up across the study area. We measured canopy closure at each grid point via 4 convex spherical densiometer readings taken from the grid point in each cardinal direction. To evaluate the impact of fire, we visually estimated the percent area burned at each grid point as the percent of ground cover within a 7.3-m radius (0.017 ha) plot that had evidence of fire (char, bare mineral soil, consumption of litter and duff).

2.3 Northern flying squirrel sampling

We sampled Northern flying squirrels (NFS) as part of a small mammal trapping study, for two years prior to treatment in 2009 and 2010, and again in 2013 (two years after thinning but prior to prescribed burning), and in 2014 and 2015 (after prescribed burning). We used a continuous trapping grid with 1,394 to 1,413 grid points (depending on year) spaced 30 m apart throughout (but not beyond) the 24 fuel treatment units and the untreated wildlife control area (Fig. 1), totaling 120 ha sampled. NFS occupy home ranges between 3.2 (eastern Washington Cascades, Lehmkuhl et al., 2006) and 11 ha (Black Hills, South Dakota, Hough and Dieter, 2009); therefore this setup allows for multiple traps in an average home range, and the exposure of multiple home ranges to sampling. We placed one extra-large Sherman (10 x 11.5 x 38 cm) and one Tomahawk trap (12.5 x 12.5 x 40 cm) at each grid point. We placed Tomahawk traps in trees (within 5 m of the grid point) approximately 1.5 m above the ground on the trunk of a tree at least 50 cm in diameter at breast height (DBH). We placed a cardboard nest box (10 x 10 x 6 cm) at the back of the trap with some polystyrene for warmth. We covered traps with natural materials and/or polystyrene for insulation. As bait we used a mixture of oats, bird seed, and raisins, plus peanut butter and molasses (as per Carey et al., 1991). Trapping occurred between late May and early September, when activity levels are high due to the breeding season but prior to dispersal of young. All traps were set, baited, and locked open for a minimum of three nights before trapping began, then opened for five nights, with traps being opened in the late afternoon prior to the first trap night. We checked traps each morning and afternoon and removed them on the morning of the fifth day, leading to nine consecutive trapping events (i.e., events when traps were checked and captured animals were processed). We marked all captured individuals using both ear and PIT tags and recorded data on sex weight, and age (juvenile, sub-adult, or adult).

Age was determined by examining pelage, breeding status, and size/weight of each individual (Villa et al., 1999).

2.4 Data preparation and analysis

Our objective was to estimate NFS densities across the two years before and up to three years after treatment, and to model how canopy closure (before and after thinning) and the amount of area burned by prescribed fire influenced NFS spatial distribution and density. To do so, we analyzed live trapping data on NFS using spatial capture-recapture (SCR) models (Efford, 2004; Royle et al., 2014). These models estimate density while accounting for imperfect detection and animal movement about the trapping grid and allow for the modeling of NFS density as a function of spatial covariates (Borchers and Efford, 2008). Specifically, SCR models use the location of captures over multiple trapping occasions to estimate the location of an individual's activity center, and assume that the encounter probability of an individual at a given trap is a declining function of the distance of that trap to the activity center. A common detection-by-distance function is the half normal function, which is defined by the baseline detection probability $p0$ (detection probability at a – hypothetical – trap located at an individual's activity center) and a scale parameter, σ, which is related to the average home range radius.

The vast majority of individuals captured were adults and we therefore restricted the present analysis to adults only to avoid having to model age-specific differences in detection parameters. We condensed the nine consecutive trapping events into five daily trapping occasions (occasion representing the temporal dimension of the trapping data for SCR analysis), where occasions one to four consisted of a morning and evening trapping event, and occasion five only consisted of a morning trapping event. We further combined data from traps of both types (Tomahawk and Sherman) at each grid point and treated them as a single trap station. Both procedures aimed to reduce the dimensions of the data set to improve computational feasibility. Live traps can be disturbed or sprung by bears and other non-target species, which renders them unavailable to small mammals. To account for variation in trap station and occasion specific effort (due to disturbed/sprung traps and to the varying number of trapping events) we created an effort metric that is used in the SCR model to adjust the expected trap encounter rate. The metric is described in detail in Appendix A. Effort ranged from 0 (neither trap type was operational in both the morning and evening) to 1 (both trap types were operational both in the morning and evening).

To investigate variation in NFS density with spatial covariates related to fuel treatments, we created 30-m resolution raster layers of canopy closure before and after thinning, and percent area burned. SCR models require spatial covariate information over an area larger than the actual trapping grid, the so-called state-space, which is an area defined by the users that incorporates the activity centers of all individuals that were exposed to trapping (Royle et al., 2014). We defined the state space as the area encompassed by a 500-m buffer around the outermost trap stations. Because we had no information on canopy closure for areas outside of the trapping grid, and these areas were not subject to any kind of fuel reduction treatment, we assigned them the average percent pre-treatment canopy closure and 0 percent area burned, respectively. Spatial covariates were standardized before analysis.

For analysis we split the study landscape into three blocks: the wildlife control (or, short, Control) block (294 - 298 trap stations), which was not subject to any treatment, and two treatment blocks - the Central block (573 - 584 trap stations) and the Western block (527 - 531 trap stations) - both of which consisted of all treatment combinations (Figure 1). Whereas both treatment blocks had equal numbers of Variable thin, Even thin and Unthinned units, blocks differed in the number of burned units (Western and Central block had 3 and 9 burned units, respectively). We separated the Western from the Central treatment block to allow for possible differences in population response to different amounts of burning. This also helped model convergence. The treatment blocks were separated by a road, and even though the species is able to cross considerable canopy gaps (e.g., Kelly et al., 2013), raw trapping data suggested this road was rarely crossed by individuals, indicating that it is appropriate to treat them as independent analytical units. For all three blocks we performed analyses separately for each year of the study.

We implemented SCR models using the package secr version 2.10.0 (Efford, 2015) in the software R version 3.2.2 (R Core Team, 2015). The program fits SCR models in a maximum likelihood framework. We fit the following models to our data: for all years of data from the Control block, and for pre-treatment (2009, 2010) data from the Central and Western block, we fit models with pre-treatment canopy closure as a covariate on NFS density. For the post thinning (2013) data from the two treatment blocks we fit models with post-treatment canopy closure as a covariate on NFS density. For the post burning (2014 and 2015) data from the two treatment blocks we fit models with either post-treatment canopy closure or percent burned as a covariate on NFS density. We were unable to fit models including both canopy closure and percent burned, or models accounting for potentially different effects of Variable versus Even thinning because of sparse data. We fit all models either with or without a behavioral response to trapping (trap aversion or attraction) on baseline detection. Because we were specifically interested in the effect of fuel treatments on NFS, we refrained from fitting additional models without density covariates. We discarded models that did not converge and chose the most parsimonious model out of the candidate model set using AIC adjusted for small sample size (AICc, Burnham and Anderson, 2002).

We also investigated how different treatments affect the distribution of NFS on the landscape by calculating the average NFS density for each treatment type for the Central and Western blocks in post-treatment years. To ensure that differences in density actually reflected treatment effects, rather than spatial variation due to unmeasured factors, we performed the same calculations for pre-treatment years. This analysis was based on output from the secr function fx.total(), which calculates realized density for each 30x30-m pixel of the state space.

3. Results

Over five years of trapping we captured 457 individual NFS (Table B.1) 1,393 times. Three hundred eighty three individuals were caught in one year only, 62 individuals in two years, ten individuals in three years, and two individuals in four years of the study (spanning seven years). Within a year and block, individuals were recaptured, on average, 2.48 (SD 1.87) times, and at 2.38 (SD 1.74) trap stations.

Average pre-treatment canopy closure of the study landscape was 86.69% (SD 11.48%); high canopy closure was consistent across all treatment units (Table 1). Thinning (Variable or Even) reduced canopy closure in treated units to 58.80% – 64.10% and tended to increase its within-unit variability (SD ranging from 11.01% - 18.94%). In units receiving prescribed burning, the percent area burned averaged 65.67 % (SD 30.47 %) in the Western block and 46.15% (SD 28.88%) in the central block. There was no relationship between percent burned and the thinning treatment of a unit, but percent burned was consistently higher in the Western block (Table 1).

For most block and year specific data sets, the most parsimonious model did not include a behavioral response to trapping, with models including a behavioral response consistently having ΔAICc >2 compared to the top model (but note that often, the combination of a density covariate plus a behavioral effect led to non-convergence of the model, Table C.1). For the two treatment blocks in post-burn years (2014 and 2015), models including canopy closure received considerably more support by AICc than models including percent burned (ΔAICc >2, Table C.1). For the Central treatment block in 2014 and 2015, models with density covariates did not converge and we used a null model (no covariates) instead to obtain estimates of NFS density.

NFS densities varied from 0.168 (SE 0.09; Control block 2013) to 0.81 (SE 0.09; Western block 2009) individuals/ha across blocks and years (Figure 2, Tables C.2 – C.4). The relationships of canopy closure with NFS density were mostly positive (Figure 3, Tables C.2 – C.4). Weak negative effects were observed only in the Control block and in pre-treatment years in the treatment blocks. Even though confidence intervals around estimates tended to be wide, the mean effect size of canopy closure on NFS density in the Western treatment block was larger in 2013 (following thinning) and later years, compared to pre-thinning/Control blocks, and confidence intervals of the estimates did not include 0 in 2013 and 2014.

NFS densities in the Central and Western blocks after treatment varied with treatment type: mean NFS density was highest in Unthinned and unburned units, followed by Unthinned, but burned units. Mean NFS densities were lowest in thinned units; differences in density between Even and Variable thinned units were marginal (Figure 4). There was wide overlap in the range of densities observed in different treatments, but particularly in the Western block average density in control units was twice as high as the block average. Pre-treatment unit-level densities (Fig. C.1) showed no systematic pattern, and differences in post-treatment densities among units did not mirror pre-treatment differences. This suggests that post-treatment differences were attributable to treatment effects, rather than unmeasured spatial factors.

In spite of variation in NFS density by treatment type, in any given year, densities were similar across the Western, Central and Control blocks. Variation in density among years was tracked by the entire landscape (i.e., regardless of the block), with highest densities in 2009 and 2014, and lower densities in 2010, 2013 and 2015 (Figure 2).

4. Discussion

Fuel reduction treatments typically are designed for and applied to individual stands imbedded within larger landscapes, leading to a forest with heterogeneous treatment status. Studying the effect of treatments on wildlife at the stand level provides valuable information about immediate impacts, but neglects this larger-scale heterogeneity, i.e., the landscape context. Our results illustrate this important stand-landscape interaction and its implications for understanding wildlife responses to fuel reduction treatments. Within treatment units, thinning had a negative effect on the density of Northern flying squirrels (Figure 3). However, patterns of density across a larger spatial scale showed that NFS shifted their distribution within the landscape in response to thinning, out of thinned units and towards unharvested areas that retained higher percent canopy closure (Figure 4). As a result, average densities in the two treated blocks were very similar to, and tracked the same annual trend as, the wildlife control block (Figure 2). Thus, in spite of the lower NFS densities in thinned units, there was no net loss in density due to treatment at the larger block level, which is only possible with a concurrent increase in density in the unthinned units of the treatment blocks. This provides evidence that immediate negative effects of small-scale thinning on NFS can be buffered if surrounding patches of forest retain high canopy closure.

In the present study, 4-ha treatment units were similar to or smaller than the average NFS home range (3.6-11 ha, Hough and Dieter, 2009; Lehmkuhl et al., 2006). Our analysis was not conducted at the 4-ha treatment unit scale, but modeled the distribution of individuals across each of the three larger blocks. Results suggest that NFS do respond to forest manipulation at the 4-ha scale, even though their home range size suggests that the species would operate on a larger spatial scale. Typical fuel reduction treatment units are variable in size and often larger than the 4 ha used in this study. Our results cannot be extrapolated to such larger disturbances, which could have more pronounced effects on NFS populations (e.g., they may displace individuals where small treatments may only cause them to shift within their home range). Although individual treatment units were small in this study, two thirds of each treatment block was subject to some form of thinning, the extent of which did not appear to affect block level density of NFS.

Density is only one measure of how populations respond to stressors and environmental drivers, and other measures such as physical condition, reproductive success or survival might be more strongly affected by treatments. Increased intraspecific competition resulting from “crowding” of more individuals into remaining suitable habitat patches may also trigger density dependent population regulation mechanisms (Lehmkuhl et al., 2006). Several lines of evidence suggest that the redistribution of individuals in response to thinning had a minimal impact on NFS. First, if crowding resulted in a decrease in reproduction and/or survival, we would have expected densities in the experimental landscape to continue to be depressed. Second, an exploratory analysis of body weight and male:female ratio did not indicate any differences in physical condition or sex ratio across years or treatment types (data not shown). Lastly, post-thinning years occurred during a record-breaking drought in California (Swain et al., 2014), where intraspecific competition for resources was likely at its peak. Under these conditions, we would expect density-dependent effects to manifest particularly severely, lending further support to our interpretation that landscape-level effects of thinning were negligible. However, because our study only extended to four years after thinning treatments, we cannot speak to potential delayed effects on NFS populations. Without longer term studies investigating population dynamics in more detail, the mechanisms underlying our observations of densities in time and space remain speculative.

Thinning affected the relationship of NFS density with canopy closure such that it became a stronger predictor of flying squirrel density after thinning treatments. Pre-treatment canopy closure averaged 85 – 89 % across the Control, Central and Western blocks (Table 1) and effects on density in pre-treatment years were variable and mostly small (Figure 3). After thinning, average canopy closure dropped to 70% in the Central and Western block, and variability increased (Table 1). This indicates that at overall high levels of canopy closure NFS are not sensitive to small fluctuations in that variable, but that it becomes an important determinant of NFS density when forest with high canopy closure is limited (Meyer et al., 2007). Understanding such interactions between overall environmental conditions and relationships with specific habitat characteristics is crucial in making recommendations for desired forest conditions.

Whereas Variable thinning is expected to be favorable compared to Even thinning because it creates within-stand heterogeneity (e.g., Carey, 2001; Lehmkuhl et al., 2006), we found that both thinning strategies had similarly negative effects on Northern flying squirrel densities at the smaller, treatment unit scale (Figure 3). Indeed, thinning has been associated with short-term reduction in truffle production (Colgan III et al., 1999) and increased NFS predation (Wilson and Carey, 2000). Whereas the initial response to both types of thinning may be similar, clusters of trees retained in the Variable thin treatment may in the longer term provide more high canopy-closure refugia for NFS in the treated landscape. In general, the effects of thinning observed here have to be considered as short-term (up to 4 years post-treatment) effects that may be ephemeral. Carey (2001) suggested that NFS populations in variably-thinned units returned to pre-treatment levels as individuals adapted to the disruptions of travel paths and denning availability, and truffle production rebounded (Carey, 2001). Whether these long-term patterns would also hold in even thinned stands remains to be investigated.

Contrary to thinning, prescribed burning had little effect on canopy closure because the burns killed only approximately 5% of trees (Knapp et al., unpublished data), mostly ones of smaller size that contribute little to the overstory canopy. Similarly, studies have shown either limited or no effect of prescribed fire on fungal sporocarp abundance and richness (Smith et al., 2004; Trappe et al., 2009). We did not collect data on fungal response to treatment in this study, but prescribed burns did not appear to negatively impact NFS densities. Prescribed burns and thinning also appear to not have affected populations additively - thinned and burned units had higher or similar densities compared to thin-only units (Figure 4). Burning in the present study was implemented two years after thinning, and it is possible that potential additive effects of both treatments did not manifest due to this time lag.

Repeated fuel reduction treatments may also additively affect NFS populations. Prescribed burning would ideally take place at intervals similar to the historic fire regime (e.g., in the study area, every 5 to 8 years; Knapp et al., 2013) in fully restored stands. Return intervals for thinning treatments are likely considerably longer (in the present study, these will not be repeated until the stands once again approach or exceed historic density and/or basal area). Given the large extend of forest in the Sierra Nevada that potentially needs to be treated, it is unlikely that the same area would be subject to frequent (i.e., at intervals below a decade) mechanical fuel reduction. This should limit the potential for compounding effects of repeated mechanical thinning.

Annual variation appeared to drive landscape-level densities of Northern flying squirrels, more so than fuel reduction treatments (Figure 2), which is a common pattern in small mammal populations (e.g., Sollmann et al., 2015). Flying squirrel densities were highest in 2009, then declined for all treatment types in 2010 and 2013. According to snowfall data for a nearby location (Bell Meadow, California Data Exchange Center, http://cdec.water.ca.gov/), the winter of 2008/2009 produced an average snowpack, while the snowpack from the winter of 2009/2010 was somewhat above average, which could possibly have contributed to low NFS densities in 2010, as flying squirrel survival is negatively impacted by snow depth (Lehmkuhl et al., 2006). All subsequent NFS sampling occurred during a drought and followed winters with a much below normal snowpack. During this drought, NFS densities ranged from low (2013) to high (2014, 2015). Clearly, snowpack depth and duration is not the only climatic predictor of NFS populations. It is possible that negative effects of prolonged drought (e.g., on truffle production; Fogel, 1976) may outweigh potential positive effects of milder and dryer winters.

4.1 Conclusion

Many wildlife species in dry forest historically subject to a frequent low-severity fire regime depend on fire-maintained structures and early-seral habitats (Hutto, 2008). Thinning and prescribed fire have been shown to serve as good surrogates for wildfire, with the resulting conditions benefiting many wildlife species (Fontaine and Kennedy, 2012). We showed that such treatments, when implemented on a small scale, only had localized negative effects on NFS that (a) were small relative to annual fluctuations in populations and (b) led to a redistribution in density across space, rather than an actual overall decline. It remains to be tested whether this holds true for other late seral species thought to respond negatively to fuel reduction treatments. Longer-term studies of NFS population dynamics could help elucidate the potential for compounding treatment effects, as well as the mechanisms underlying the patterns in density we observed. Our results highlight the need to incorporate the landscape context when evaluating the effect of forest management on wildlife. They further show that the larger scale heterogeneity of treated versus untreated patches contributes to the maintenance of forest wildlife.

5. Acknowledgments

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Table 1: Canopy closure before and after mechanical fuel reduction treatment (UT = unthinned; ET = even thin, VT = variable thin, Mean = mean across block) and percent area burned following prescribed fires (mean (SD) across 30-m grid) in the Stanislaus-Tuolumne Experimental Forest, California.

Block	Treatment	Canopy closure pre	Canopy closure post	% burned*
Western	ET	88.79 (8.17)	64.10 (14.00)	55.42 (32.71)
	VT	88.12 (9.55)	59.76 (18.94)	62.41 (31.64)
	UT	88.58 (10.35)	86.58 (13.24)	78.52 (22.01)
	Mean	88.50 (9.37)	69.86 (19.50)	65.67 (30.47)
Central	ET	85.53 (11.22)	61.82 (11.01)	54.49 (28.27)
	VT	83.14 (12.38)	58.80 (18.01)	38.26 (26.28)
	UT	85.54 (12.63)	85.47 (12.20)	45.41 (29.79)
	Mean	84.75 (12.13)	68.89 (18.44)	46.15 (28.88)
Control	none	86.67 (11.66)	89.44 (10.71)	0

*Each mechanical fuel reduction treatment includes burned and unburned units; "% burned" gives the average for burned units only (3 and 9 units in Western and Central block, respectively)

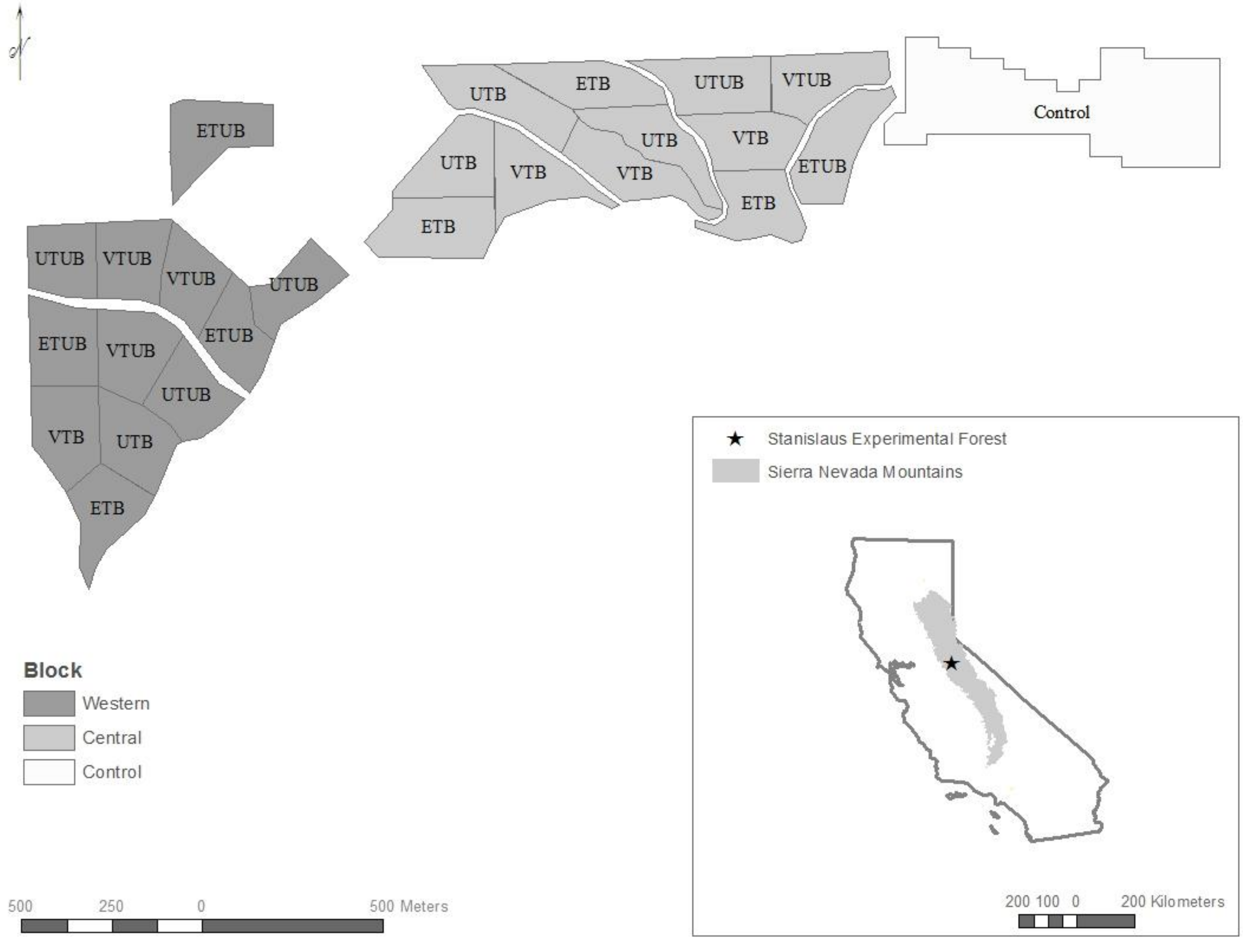

Figure 1: Map of the study landscape in the Stanislaus-Tuolumne Experimental Forest, California, with different fuel reduction treatment units (UTB = unthinned + burned, ETB = even thin + burned, VTB = variable thin + burned, ETUB = even thin + unburned, VTUB = variable thin + unburned, UTUB = unthinned + unburned). Inset shows location of study site in California, USA.

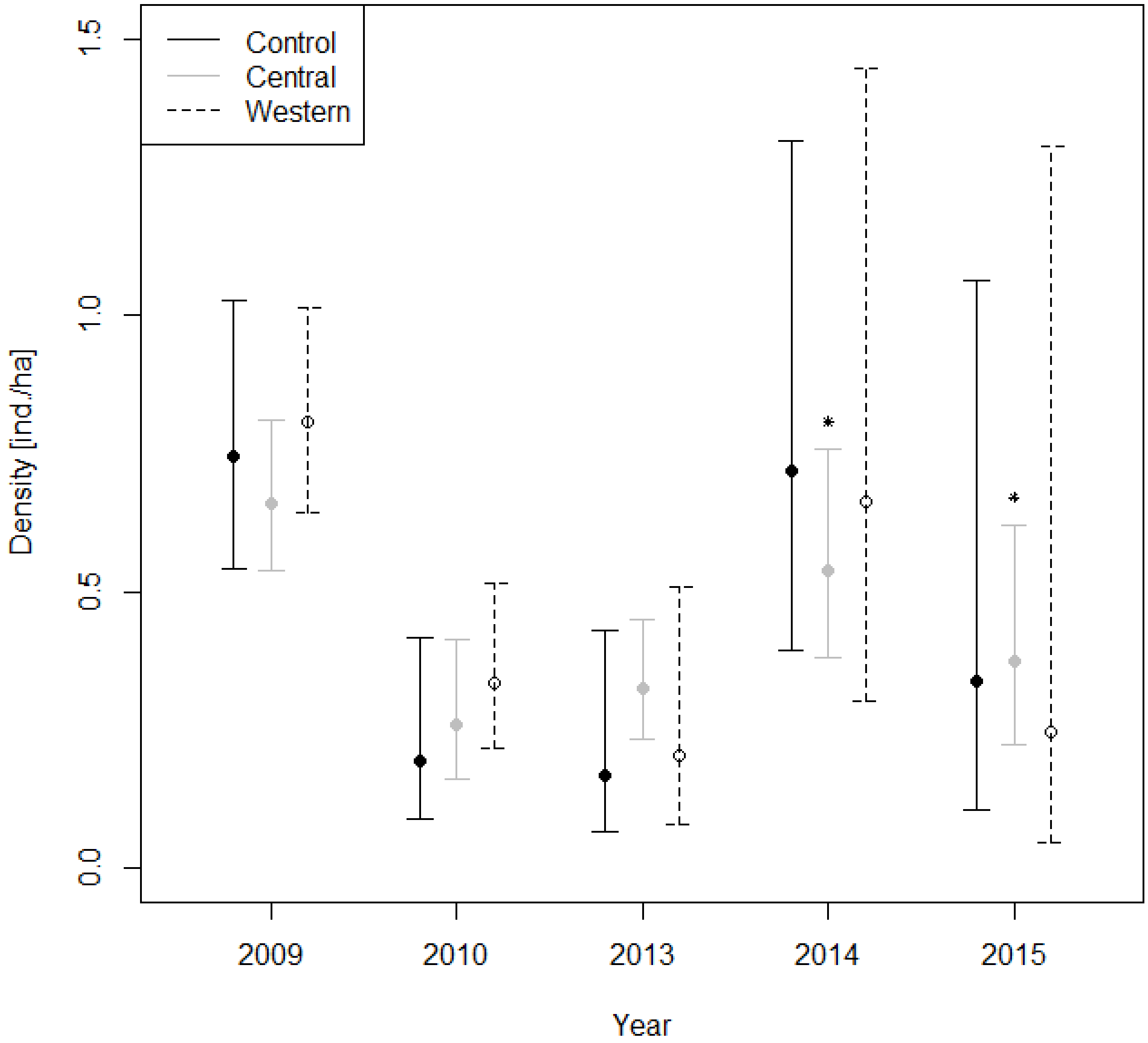

Figure 2: Density (with 95% confidence intervals) of Northern flying squirrels, estimated with spatial capture-recapture models, for three blocks in the Stanislaus-Tuolumne Experimental Forest, California. In the Central and Western block, thinning (Even and Variable, 2011) and prescribed burning (2013, after small mammal sampling) were implemented in 4-ha treatment

units (see main text for study design); no treatments occurred in the control block. *Estimates based on null model (without density covariates).

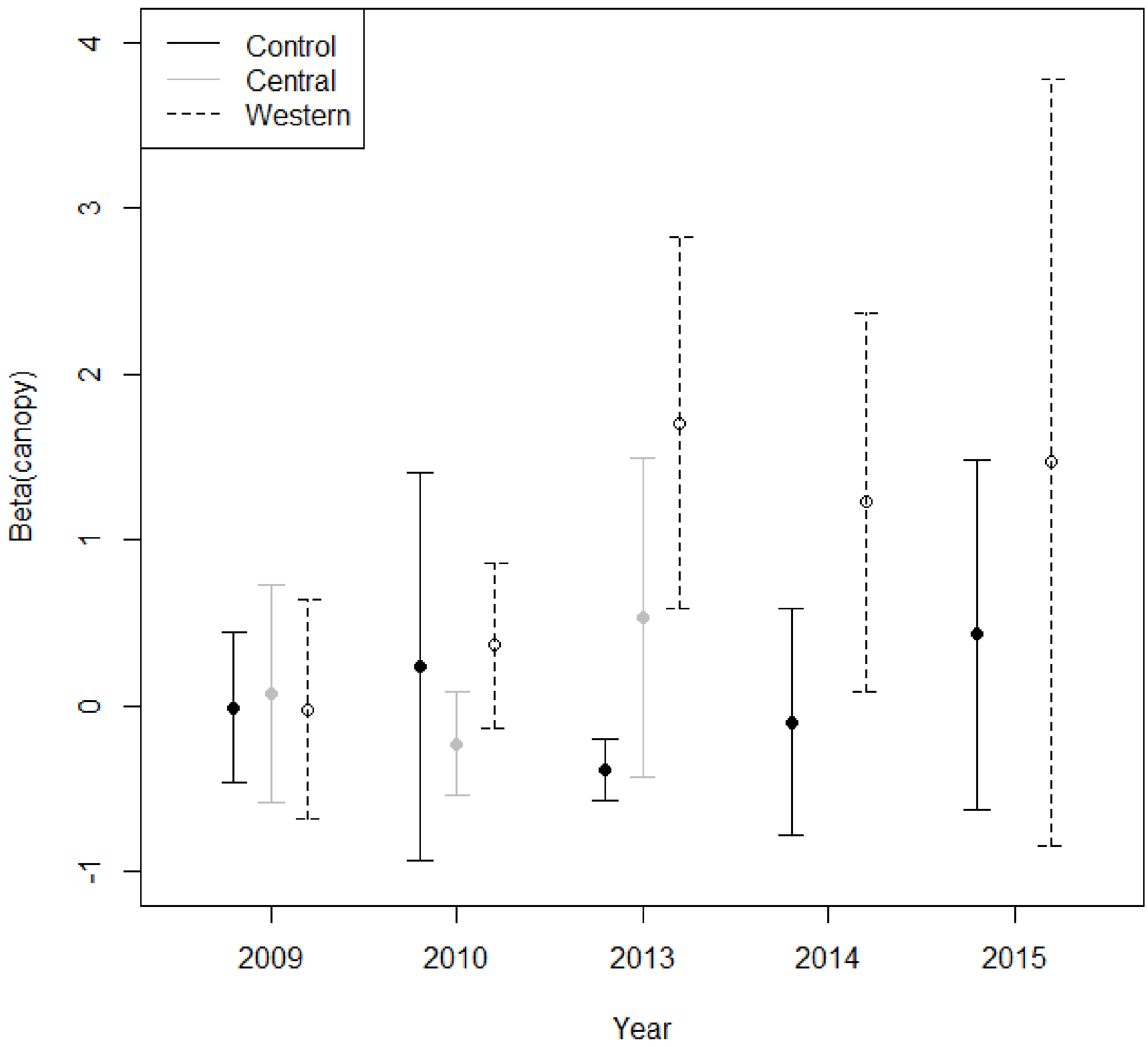

Figure 3: Coefficient describing the effect of canopy closure on northern flying squirrel density (Beta(canopy)) in the Stanislaus-Tuolumne Experimental Forest. Thinning occurred in 2011 and controlled burning in 2013 (after the 2013 small mammal sampling). Estimates for the Central block in 2014 and 2015 are missing because models did not converge.

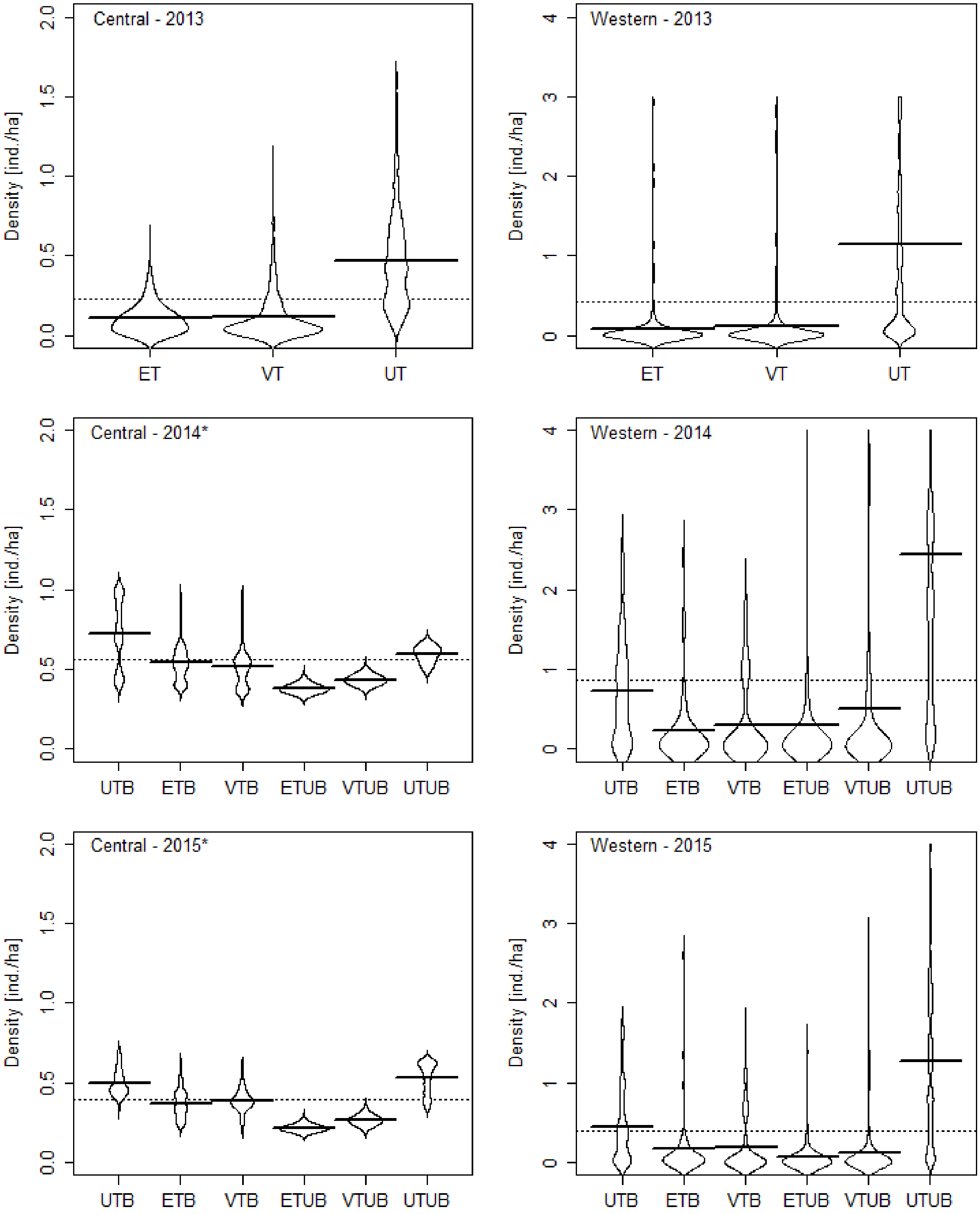

Figure 4: Density of Northern flying squirrels in the Stanislaus-Tuolumne Experimental Forest, California, in different fuel reduction treatments (in 2013, prior to prescribed burns, ET = Even

thin, VT = Variable thin, UT = unthinned; after the Nov. 2013 prescribed burns, UTB = unthinned + burned, ETB = even thin + burned, VTB = variable thin + burned, ETUB = even thin + unburned, VTUB = variable thin + unburned, UTUB = unthinned + unburned), for the Central and Western block of the study landscape. Density was estimated by spatial capture-recapture models for 30x30-m pixels, and violin plots show spread of values across all pixels located in a given treatment type. Dotted line is the block average for that year; black lines show average for treatment type; width of the violin indicates frequency distribution of observations (here, pixel-based densities). *based on null model, as opposed to models with canopy closure as density covariate.

California Spotted Owl, Songbird, and Small Mammal Responses to Landscape Fuel Treatments

SCOTT L. STEPHENS, SETH W. BIGELOW, RYAN D. BURNETT, BRANDON M. COLLINS, CLAIRE V. GALLAGHER, JOHN KEANE, DOUGLAS A. KELT, MALCOLM P. NORTH, LANCE JAY ROBERTS, PETER A. STINE, AND DIRK H. VAN VUREN

A principal challenge of federal forest management has been maintaining and improving habitat for sensitive species in forests adapted to frequent, low- to moderate-intensity fire regimes that have become increasingly vulnerable to uncharacteristically severe wildfires. To enhance forest resilience, a coordinated landscape fuel network was installed in the northern Sierra Nevada, which reduced the potential for hazardous fire, despite constraints for wildlife protection that limited the extent and intensity of treatments. Small mammal and songbird communities were largely unaffected by this landscape strategy, but the number of California spotted owl territories declined. The effects on owls could have been mitigated by increasing the spatial heterogeneity of fuel treatments and by using more prescribed fire or managed wildfire to better mimic historic vegetation patterns and processes. More landscape-scale experimentation with strategies that conserve key wildlife species while also improving forest resiliency is needed, especially in response to continued warming climates.

Keywords: adaptive management, mixed conifer, restoration, Sierra Nevada, wildlife conservation

The role of wildfire in many of the world's forests that are adapted to frequent, low- to moderate-intensity fire regimes has been altered through fire exclusion, timber harvesting, livestock grazing, and urbanization (Agee and Skinner 2005, Collins et al. 2010). In the western United States, these land-use practices have affected forest structure and species composition, increasing surface fuel loads, tree density, the dominance of shade-tolerant tree species, and forest homogeneity (Hessberg et al. 2005, North et al. 2009, Chiono et al. 2012). As a consequence, many forests in the western United States are experiencing higher-severity burns—in some cases, producing large patches of tree mortality that can severely hinder the reestablishment of conifer forests (Roccaforte et al. 2012, Collins and Roller 2013). Consequently, one of the primary focuses of contemporary forest management is the treatment of fuels and vegetation to reduce fire hazards, especially as climate continues to warm (Stephens et al. 2013).

There is increased recognition that forests adapted to low- to moderate-intensity fire regimes experienced some high-severity fire (Perry et al. 2011, Marlon et al. 2012). Patchy, high-severity fire provides opportunities for early-seral habitat development and the production of large pieces of deadwood resources that are important to many wildlife species (Fontaine and Kennedy 2012). As such, forest fuel treatments should not be used to eliminate all high-severity fire. Rather, treatments should allow for patterns of fire effects that approximate those occurring under more natural forest conditions. What little information we have on fire patterns under these conditions suggests that high-severity fire constitutes fairly low proportions of the overall burned area (5%–15%) in these forest types, which is generally aggregated in relatively small patches (smaller than 4 hectares [ha]), as is the case in the upper mixed-conifer forests in Yosemite National Park (Collins and Stephens 2010, Mallek et al. 2013).

Forest management involving habitat used by wildlife species at risk has been one of the principal challenges to US federal land managers for the last 25 years. In the Sierra Nevada, an ongoing debate is focused on several species that use old-growth forest, including the California spotted owl (CSO; *Strix occidentalis occidentalis*) and the Pacific fisher (*Martes pennanti pacifica*). Forest managers need information on appropriate levels of forest manipulations to create the desired balance between habitat conservation for wildlife populations and modifications of forests to improve their resilience to large high-severity fires that could prove more expensive and detrimental than the short-term effects of restoration treatments.

Fuel-reduction treatments reduce the potential impacts of wildfire by reducing the only aspect of the fire behavior

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Figure 1. Fuel treatments implemented in the Meadow Valley project area. (a) Pretreatment mixed-conifer forest. (b) Whole-tree harvester cutting small trees (thinning from below). (c) Small trees, tree tops, and limbs being chipped and shipped by truck to a bioenergy plant to produce electricity. (c) Posttreatment defensible fuel profile zone, taken from the same perspective as in panel (a). Photographs: Keith Perchemlides.

triangle (i.e., topography, weather, fuel) that can be modified by managers: the quantity and continuity of fuel. A number of techniques are employed to reduce fire hazards, and each technique has associated effects on forest structure (Agee and Skinner 2005). Mechanical treatments can reduce stand density, basal area, and ladder and canopy fuel. To reduce accumulated surface fuel and to offset the detritus added from harvest operations, prescribed fire is sometimes used following forest thinning to reduce fire hazards, but whole-tree harvesting (i.e., complete tree removal, with the materials chipped and trucked to a processing facility; figure 1) can also effectively keep much of the harvest detritus from being added to the forest floor. Broadcast burning alone is very effective in elevating canopy base height and in reducing surface fuel (Agee and Skinner 2005).

Recent research confirms the ability of fuel treatments to alter potential fire behavior (Fulé et al. 2012) and actual wildfire effects (Safford et al. 2012). Research has also determined that fuel-reduction treatments achieve their objectives with generally positive or neutral ecological effects (Stephens et al. 2012); however, almost all research on the effects of fuel treatments has been performed at the stand scale (10–25 ha). Given the large home ranges of many key wildlife species commonly at the crux of forest management issues in the western United States (e.g., the CSO, the northern spotted owl [*Strix occidentalis caurina*], the Pacific fisher), it is important to understand fuel-treatment impacts at larger spatial scales. This is particularly relevant because many fuel-treatment projects are being proposed—and, in a few instances, implemented—at landscape scales (15,000–40,000 ha; Ager et al. 2007, Collins et al. 2010).

Fuel treatments directly alter wildlife habitat by removing both aerial (trees) and ground (coarse wood, shrubs) cover. These altered conditions can affect both habitat suitability, which influences the number of individuals that an area can support, and habitat quality, which directly affects the fitness

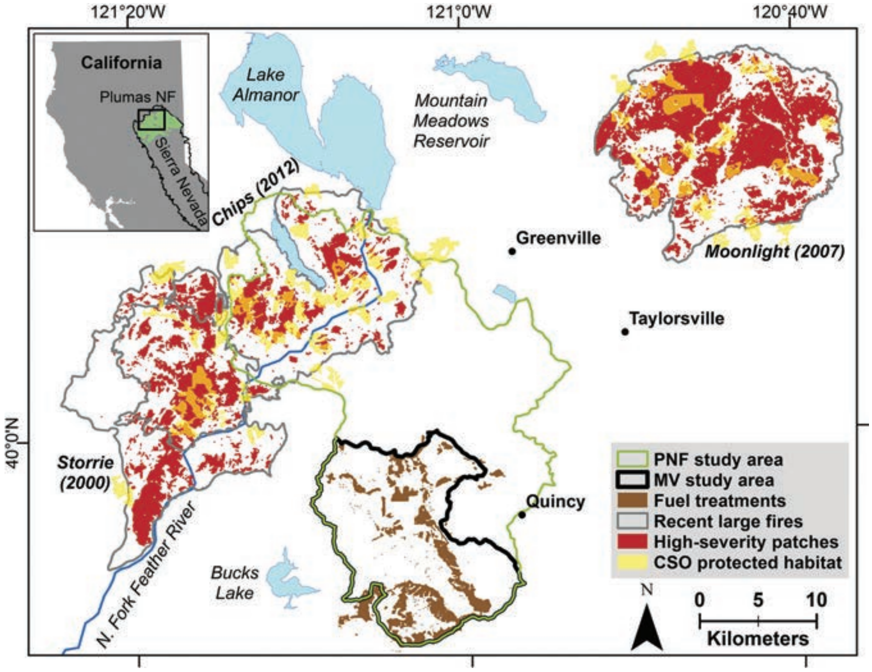

Figure 2. Meadow Valley study area with completed landscape fuel-treatment network. Recent large wildfires and the resulting patches of high-severity fire effects are also indicated. Three wildfires are shown: Storrie (2000), Moonlight (2007), and Chips (2012). These were selected on the basis of the following criteria: proximity to the study area (closer than 25 kilometers), vegetation type (conifer dominated), size (larger than 10,000 hectares), and age (since 2000). Abbreviations: CSO, California spotted owl; MV, Meadow Valley; N, north; NF, national forest; PNF, Plumas National Forest; W, west.

and productivity of individuals. Because more-suitable habitat for certain at-risk wildlife species is associated with greater aerial and ground cover, the effects of fuel treatments are generally perceived as negative. However, large patches of wildfire-caused tree mortality can also negatively affect both habitat suitability and quality (Tempel et al. in press). To the extent that fuel treatments reduce the potential for large patches of tree mortality in wildfire, there may also be an indirect benefit of fuel treatments to certain species' habitat. Finding a balance between these influences is a crucial management need.

Over the past decade, we have studied the ecological effects of one of the few completed landscape-level fuel-treatment networks in western US forests. Here, we distill the results of these efforts. We quantify change in vegetation structure and modeled fire behavior as a result of fuels treatments and assess treatment effects on the CSO, songbirds, and small mammals. Modeling studies have been published in which the trade-offs in these systems have been conceptually examined (Lee DC and Irwin 2005), but this is one of the first studies in which these questions have been empirically examined at landscape scales.

Study area and design

Our study area is located in the Meadow Valley area of the Plumas National Forest, situated in the northern Sierra Nevada, at 39 degrees (°) 56 minutes (′) north, 121°3′ west (figure 2). The climate is Mediterranean, with warm, dry summers and cool, wet winters, which is when most precipitation (1050 millimeters per year; Ansley and Battles 1998) occurs. The core study area is 19,236 ha, with elevations ranging from 850–2100 meters (m). The vegetation is primarily mixed-conifer forest, consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and other less common hardwood species. White fir is the most abundant tree, although large (e.g., larger than 1 m in diameter) stumps of pines encountered frequently in the forest attest to a change in composition and structure in recent history. Red fir (*Abies magnifica*) is common at higher elevations, where it mixes with white fir. In addition, a number of species are found occasionally in or on the edge of the mixed-conifer forest, including western white pine (*Pinus monticola*) at higher elevations, lodgepole pine (*Pinus contorta* var. *murrayana*) in cold air pockets, and western juniper (*Juniperus occidentalis*) on xeric sites. California hazelnut (*Corylus cornuta*), dogwood (*Cornus* spp.), and willow (*Salix* spp.) are found in moister riparian areas. Montane chaparral and some meadows are interspersed in the landscape. Tree density varies as a result of recent fire- and timber-management history, elevation, slope, aspect, and edaphic conditions. Historical fire occurrence, which can be inferred from fire scars recorded in tree rings, suggests that the fire regime was predominantly frequent, low- to moderate-severity fires, at intervals ranging from 7–19 years, with the last widespread fires occurring 85–125 years ago (Moody et al. 2006).

Fire activity in the last 15–20 years has been notably higher in the northern Sierra Nevada than in the rest of the range (Collins 2014). Since 2000, there have been three megafires (covering more than 10,000 ha; Stephens et al. 2014) within 25 kilometers (km) of our study area, burning a total of 73,000 ha (figure 2). These fires burned predominantly in mixed-conifer forests, encompassing approximately 60 CSO protected activity centers (figure 2). Cumulatively, 34% of the area burned in these three fires suffered high-severity fire (more than 95% dominant tree mortality; figure 3a; Miller et al. 2009). More important than the total proportion of area severely burned is the distribution of high-severity patches over the burned area, because this can limit tree seed

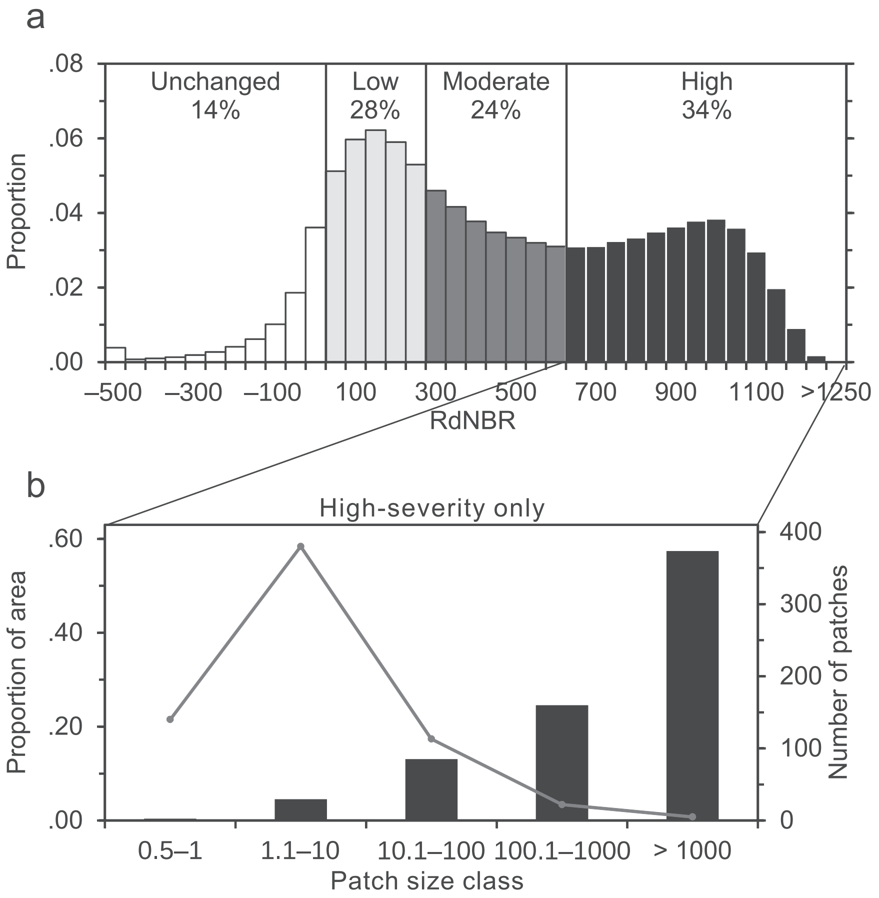

Figure 3. (a) Fire severity distribution for the three recent large fires in the Meadow Valley study area (see figure 2). The fire-severity estimates are based on the relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007). (b) The proportion of total high-severity area (bars) and the number of patches (line) as a function of patch size class.

dispersal from wind and animals (Perry et al. 2011, Collins and Roller 2013). Large patches (defined here as larger than 1000 ha) accounted for a disproportionate amount of the total high-severity-fire area in the recent wildfires near the study area (figure 3b).

The projects that contributed to the fuel-treatment network are part of the larger Herger-Feinstein Quincy Library Group Pilot Project (USHR 1998). This project was directed by the US Congress to involve local communities in forest management. The project objectives included improving forest health, reducing uncharacteristic high-severity fire, conserving wildlife habitats, and stabilizing economic conditions in local communities. The projects in Meadow Valley encompassed a range of treatment types and intensities reflecting changes in regional management directions and differing land-management constraints across a complex landscape (Collins et al. 2010, Moghaddas et al. 2010). The primary fuel treatment used in Meadow Valley was defensible fuel profile zones (DFPZs), which are areas approximately 0.4–0.8 km wide in which surface, ladder, and crown fuel loads are reduced with a combination of moderate thinning from below (Moghaddas et al. 2010) and prescribed fire treatments (figure 1).

The DFPZs were excluded from portions of the landscape set aside as reserves and from designated CSO protected activity centers, which are 121-ha areas of high-suitability nesting habitat designated by forest biologists. In addition, the project predominantly excluded all riparian habitat conservation areas or stream buffers intended to protect riparian and aquatic resources (figure 4). The activities conducted in the DFPZs were chainsaw thinning and pile burning of trees up to 30 centimeters (cm) in diameter at breast height (dbh); mastication: primarily shrubs and small trees were shredded and chipped in place, with the material left on site; prescription burning: stands were burned under conditions of moderate relative humidity and fuel moisture; and a combination of mechanical thinning and prescription burning of trees up to 51 or 76 cm dbh, depending on whether the stands were in the wildland–urban interface, using a whole-tree harvest system (figure 1) to achieve a residual canopy cover of approximately 40%, and some were underburned (Moghaddas et al. 2010). In addition to the DFPZs, group-selection treatments were implemented as part of the project. The group-selection treatments included the removal of all conifers up to 76 cm dbh within an area of 0.8 ha, followed by residue piling and burning, then either natural regeneration or replanting to a density of 270 trees per ha with a mix of sugar pine, ponderosa pine, and Douglas-fir. These treatments collectively covered 3688 ha (3448 ha in the DFPZs, 240 ha in the group-selection treatment), or 19% of our study area, and were implemented between 2003 and 2008.

Forest structure and microclimate

Although they are designed to reduce fire hazards, forest treatments alter stand conditions directly by reducing tree density and canopy cover, and indirectly by altering microclimate conditions affecting the understory community. To assess these changes we measured stand structure, light, understory plant cover, micro-meteorological variables, soil moisture, and fuel moisture in replicated control, thinning, and group-selection treatments plots embedded within the landscape-level treatments (see Bigelow al. 2009, 2011, Bigelow and North 2012 for detailed methods).

The mean forest canopy cover was 69% (standard deviation [SD] = 7%) before treatment; after treatment it was 53%

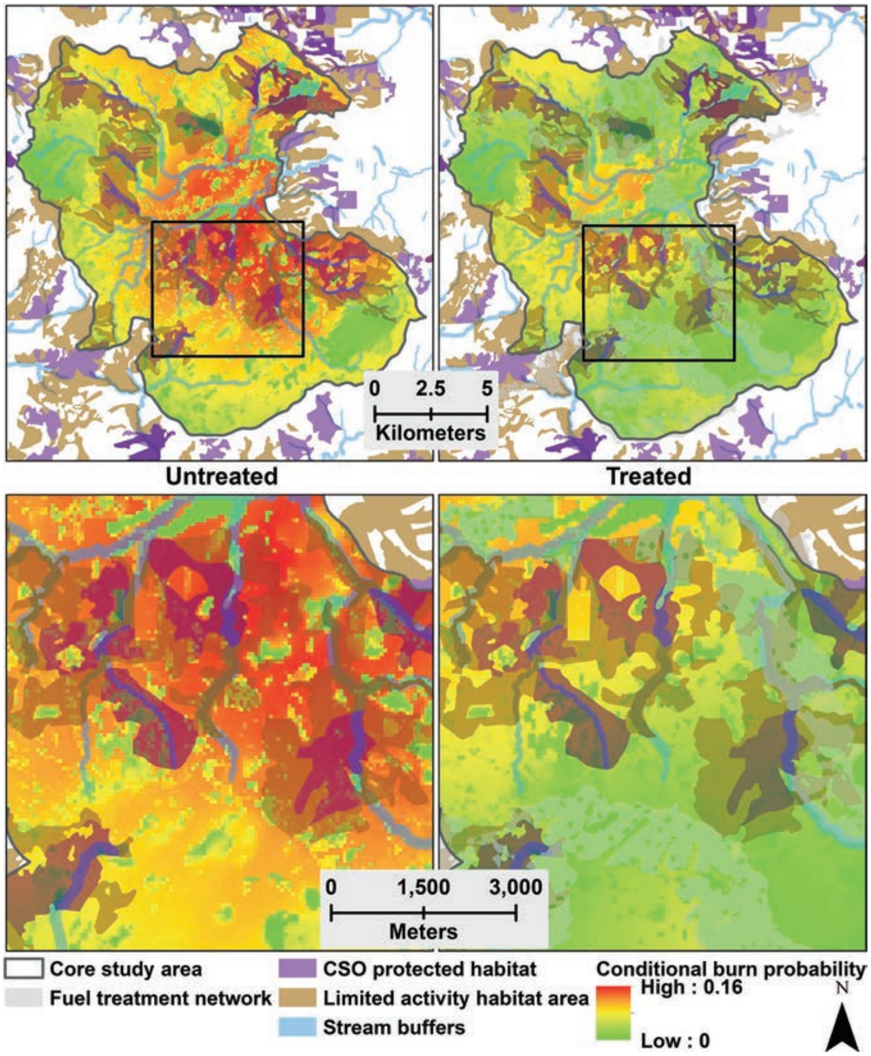

Figure 4. Hazardous fire potential across the Meadow Valley study area for the untreated and treated landscape conditions. This fire potential is based on the conditional burn probability of fire occurring with flame lengths greater than 2 meters, which is consistent with tree torching (see Collins et al. 2013 for specific details). Land designations that often limit or exclude active forest management (e.g., California spotted owl [CSO] protected habitat, stream buffers) are also shown to illustrate off-site effects of the landscape fuel-treatment network. The black square in the upper panels indicates the focal area shown in the bottom panels.

(SD = 7%) in thinned stands and 12% (SD = 6%) in the group-selection openings (Bigelow et al. 2011). These differences were reflected in growing-season understory light, which averaged 17% of full sun before treatment and increased to 26% in thinned stands and 67% in group-selection openings. Models of regenerating tree growth and light availability demonstrated that the height growth rates of shade-intolerant yellow pines (ponderosa and Jeffrey pines) and shade-tolerant white fir were equal at 41% of full sun. Light levels greater than this correlated exponentially with the height growth of the pines. The group-selection treatments provided ample light to recruit shade-intolerant species to the canopy, but only 8% of the sample locations in the thinning treatments had light levels exceeding the 41% crossover point, which suggests that these treatments would not substantially contribute to pine restoration across the landscape. An analysis of hemispherical photographs showed that the treatments decreased canopy closure following thinning. At the plot (1-ha) scale 3 years after treatment, cover of understory plant life-forms only changed under group selection ($p < .05$). Shade-tolerant conifers decreased, and graminoids, forbs, and broad-leaved trees (mainly California black oak and dogwood) increased (figure 5). There was no increase in exotic plant species cover with any of the treatments (Chiono 2012).

Changes in abiotic conditions followed differences in canopy cover for only some of the variables measured (Bigelow and North 2012). Soil moisture increased and duff moisture decreased in the group-selection treatments relative to the thinned and pretreatment conditions. Wind gust speeds (measured 2.5 m above ground) averaged 31% higher in the thinned stands than in the controls, but this was far less than the 128% increase in the group-selection openings. However, there was no difference in air temperature or relative humidity among the treatments, possibly because the increase in understory wind increased air mixing and eliminated any gradients in air temperature and humidity that might have resulted from increased irradiance.

Treatment increased within-stand variability for some vegetation and microclimate conditions but, in general, did not create the landscape-level heterogeneity characteristic of historic forest conditions in the Sierra Nevada (North et al. 2009). Mixed-conifer forests support the highest vertebrate diversity of California forests (Verner and Boss 1980), and studies suggest that this may result from habitat variability associated with the observed range of tree species diversity, canopy cover, microclimate, and deadwood conditions (Rambo and North 2009, Ma et al. 2010, White et al. 2013). This historic forest heterogeneity appears to reflect differences in fire intensity and site productivity associated with local and large-scale changes in slope, aspect, soil, and slope position (North et al. 2009, Lydersen and North 2012). On average, more mesic sites (e.g., drainage bottoms and north-facing slopes) historically supported greater stem density, canopy cover, and tree basal area, whereas drier and

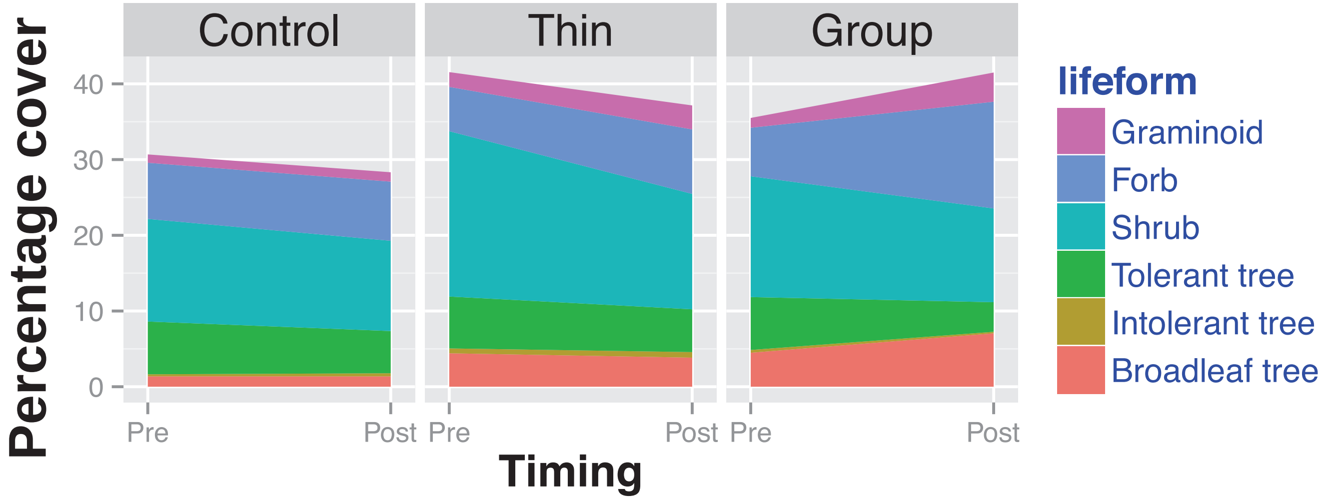

Figure 5. The percentage cover of plant life forms before* (pre) *and 3 years after* (post) *fuel-reduction thinning and group-selection treatments* (n = *300 subplots per treatment) that were implemented in 2007 in Meadow Valley. Changes in understory cover in thinned stands were not significant* ($p > .16$)*. Graminoids, forbs, and broadleaf trees increased and shade-tolerant conifers decreased* ($p < .05$) *in group selection openings.

steeper areas burned more frequently and intensely, creating more-open, pine-dominated forests (North et al. 2009). Although the Meadow Valley treatments did increase within-stand heterogeneity, they were not explicitly designed to vary with site topography or local productivity to produce this historic landscape variability.

Potential fire behavior

We employed a spatially explicit fire behavior model (Finney et al. 2007) to simulate fire spread across the Meadow Valley area. We simulated 10,000 individual fire events, with random ignition locations, and compared patterns of burn probability based on the number of times a particular area burned with the given ignition locations and simulated flame lengths for the study area prior to and following the implementation of landscape fuel treatments. Each fire event simulated burning for 240 minutes (one 4-hour burn period) under 97th percentile fuel moisture and wind conditions. These are the conditions associated with large-fire growth in this region (Collins et al. 2013). The burn period duration was selected such that the simulated fire sizes (for one burn period) approximated large-spread events observed (daily) in nearby recent wildfires (Collins et al. 2013). One of the primary assumptions with this approach is that, during these large-spread events (burn periods), fire suppression operations have limited impact, which is consistent with observed large-fire occurrence throughout the western United States (Finney et al. 2007). We summarized the burn probabilities across the Meadow Valley area into land allocations determined by the US Forest Service (USFS; Moghaddas et al. 2010).

The simulated fire behavior indicated that the landscape-scale network of DFPZs and prior fuel treatments were effective at reducing conditional burn probabilities across all land-allocation types, except the small area of off-base lands (figure 4; Moghaddas et al. 2010). Because burn probabilities are correlated directly and positively to fire size (Finney et al. 2007), it is clear that the pretreatment landscape was more conducive to large-fire growth than the posttreatment landscape was (Moghaddas et al. 2010, Collins et al. 2013). Although the influence of the treatments on the modeled burn probabilities of each land allocation varied, the untreated stands (e.g., those designated for protected CSO habitat, riparian and aquatic resources, and reserve lands) and the remaining private and unclassified lands all experienced reduced burn probabilities from the application of fuel treatments at the landscape scale (figure 4; Moghaddas et al. 2010). A similar reduced burn severity immediately adjacent to treated areas has been reported for actual fires across the western United States (Finney et al. 2005).

The substantial reduction in both the total area and the area burned at higher flame lengths under a posttreatment wildfire scenario was notable, given that only 19% of the study area had been treated (Moghaddas et al. 2010, Collins et al. 2013). Both the orientation of the treatments (approximately orthogonal to the predominant wind direction throughout the duration of the simulated fire), and the long, continuous shape of the DFPZs resulted in potential wildfires' intersecting fuel treatments in multiple places. In addition, the treatments were somewhat concentrated in the southwestern portion of the study area (figure 2), which is the dominant direction of strong winds during the fire season (Collins et al. 2013). In combination, these factors limited the ability of the simulated fire to both circumvent the treated areas and to regain spread and intensity after encountering the treatments. These results are important to managers, because similar installations of fuel and restoration treatments are needed in many Sierra Nevada

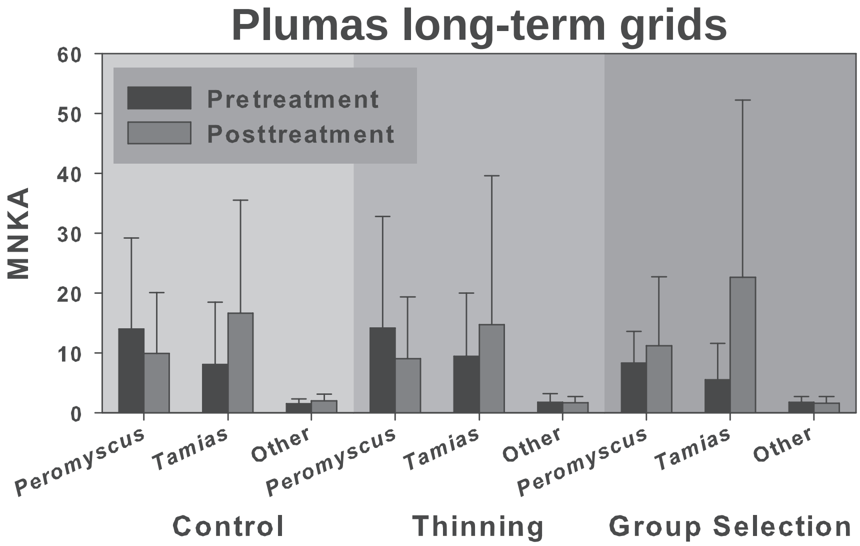

*Figure 6. The mean minimum number of small animals known alive (MNKA), recorded before and after fuel treatments in the Plumas National Forest study area. For ease of presentation, we present three species groups (***Peromyscus boylii** *and* **Peromyscus maniculatus; Tamias quadrimaculatus** *and* **Tamias senex***; all other species; see Kelt et al. 2013 for details). The bars represent the means of the replicate sampling grids. The error bars represent the positive standard deviation.*

mixed-conifer forests, where the present treatment rates are very low (North et al. 2012).

Small mammals

The northern Sierra Nevada supports a diverse fauna of small mammals that play key ecological roles as consumers, seed and fungal dispersers, and prey for both terrestrial and aerial predators (Hallett et al. 2003, Kelt et al. 2013). We studied small mammals in the Meadow Valley study area and the greater Plumas National Forest study area (PNFSA; figure 2), with a particular focus on two species that are key prey of the CSO (Gutiérrez et al. 1995): the dusky-footed woodrat (*Neotoma fuscipes*) and the northern flying squirrel (*Glaucomys sabrinus*). Results on focal species efforts have been reported elsewhere (Innes et al. 2007, Smith et al. 2011), but one finding merits emphasis here. California black oak, the primary hardwood in mixed-conifer forests, is an important habitat element for both the woodrat and the flying squirrel. Woodrat density was positively correlated with black oak density (Innes et al. 2007), and both species strongly preferred black oaks for nest sites (Innes et al. 2008, Smith et al. 2011). California black oak may be important for other wildlife species as well (Zielinski et al. 2004), but its persistence in our study landscape is in doubt. California black oak is shade intolerant, and across our study area, there were few thriving seedlings and many mature trees in decline as adjacent conifers overtopped them. California black oak trees were present in only 133 of 602 plots placed randomly in the PNFSA and were in a codominant canopy position in less than 10% of the plots in which it was present (see supplement S1).

Our broader studies on the management needs of entire small mammal assemblages included two complementary efforts. We sampled small mammals annually for 8 years on replicate trapping grids in treated and untreated mixed-conifer forests dominated by white fir in order to evaluate the responses of the small mammal community to canopy thinning (Kelt et al. 2013). To determine whether the habitat associations of the mammals in these forests were similar to those of mammals in other forest types, we expanded our efforts to include stratified random sampling of the PNFSA that encompassed the Meadow Valley study area (figure 2).

Whereas canopy thinning in white-fir-dominated mixed-conifer forests caused some significant changes in forest structure, small mammal assemblages were similar before and after canopy thinning and group selection (Kelt et al. 2013), which suggests a minimal response in the short-term to these treatments (*contra* Suzuki and Hayes 2003, Gitzen et al. 2007, but see Carey and Wilson 2001). Although each treatment may have elicited somewhat different responses (figure 6), the variance across replicate plots eroded any such differences even in the face of the substantial variation in canopy cover. The lack of a short-term response may not be surprising in a system characterized by high interannual variation in weather and in a system dominated by generalist species; we look forward to resampling these sites after 10–15 years to assess potential longer-term responses. Because our manipulative experiment was focused on white-fir-dominated mixed-conifer forests, we pursued a more general assessment of mammalian responses to habitat and environmental variation across the entire PNFSA, capitalizing on a series of point-count transects established throughout the forest in a stratified (by forest type) random manner (see the "Songbirds" section below). We sampled eight randomly selected points on each of 74 transects to characterize how small mammals respond to broader variation in forest structure.

We assessed assemblage-wide responses to this variation with ordination (canonical correspondence and canonical correlation) and species-specific responses with multiple stepwise regression. All data were standardized (both rows and columns) by centering and normalizing, and the mammal data were log-transformed to prevent domination of the axes by common species. The results from all of the analyses were qualitatively identical to those of the Meadow Valley experimental grids, which indicates minimal responses of small mammal assemblages to variation in forest structure or composition. Although the spatial arrangement of the

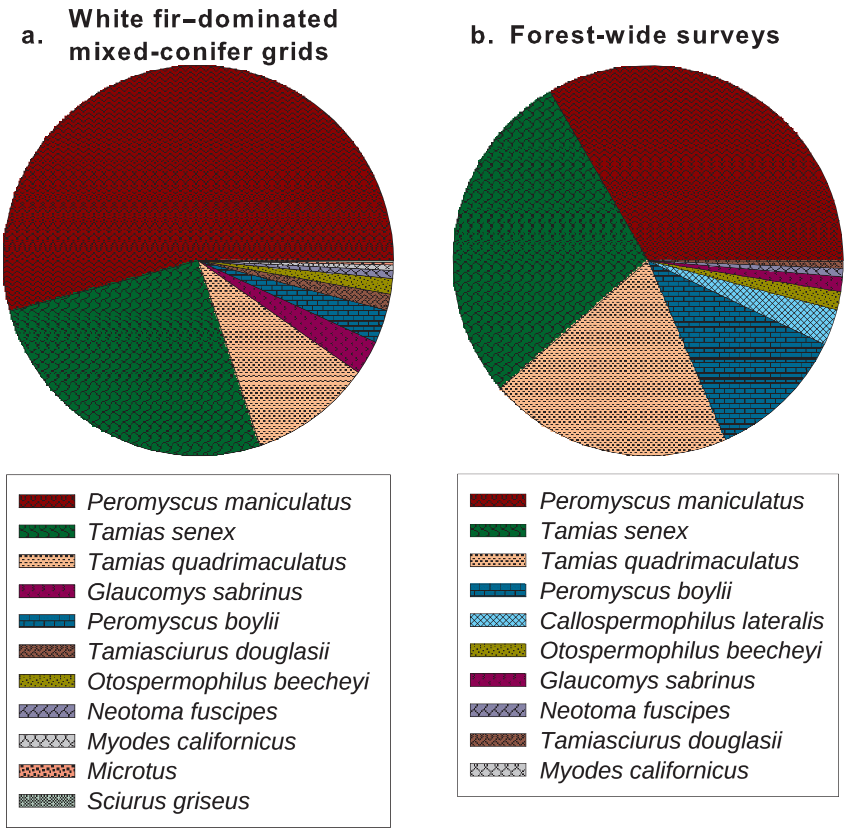

Figure 7. Small mammal composition at two spatial scales in the Plumas National Forest study area. At both scales, captures were dominated by three species. At the forest scale, only one other species was highly represented. All other species at both scales were only minor elements.

small mammal species in the ordination space was ecologically reasonable (e.g., woodrats and brush mice [*Peromyscus boylii*] associated with oaks, and chipmunks [*Tamias*] and Douglas squirrels [*Tamiasciurus douglasii*] associated with conifers and with a high basal area of trees and snags), ordination explained only a small proportion of variance in the distribution of small mammals. Similarly, regression failed to produce compelling associations for any species (or for community metrics such as species richness or diversity). The coefficients for both sets of analyses were universally low (Kelt et al. 2013).

In trapping efforts on the Meadow Valley experimental grids and in the larger PNFSA (figure 2), our captures were overwhelmingly dominated by 3–5 species (figure 7). Deer mice (*Peromyscus maniculatus*) dominated the captures at both spatial scales, comprising a full 55% of the captures on the Meadow Valley experimental grids and just over one-third of the captures in the PNFSA. Two species of chipmunk (*Tamias quadrimaculatus*, *Tamias senex*) represented an additional 40%–44%, and brush mice were an additional 8% in the PNFSA. Therefore, our samples were dominated by ecological generalists known to be tolerant of diverse habitats. What appears to be missing is a reasonable representation of species with more restricted niche requirements. Our sampling was not designed to sample shrews (*Sorex*), but California red-backed voles (*Myodes* [formerly *Clethrionomys*] *californicus*) may have been more common in this region in the 1940s and 1950s (Kelt et al. 2013) and should have been present in our study. This species forages on fungi, however, and requires large downed woody debris and a closed-canopy forest to allow sufficient moisture retention to promote fungal growth (Alexander and Verts 1992). In 177,216 trap nights of effort, we captured only 11 *Myodes* (all but one on Meadow Valley experimental grids). Other species that are mesic habitat specialists were not sampled (e.g., *Zapus trinotatus, Sorex palustris*).

It is not clear whether the taxonomically depauperate assemblage structure documented in our study represents a relatively recent reduction or is more historic for this region. No data on mammal assemblages exist prior to European settlement and the beginning of widespread changes to the Sierra Nevada forest ecosystems (Merchant 2012). However, one implication of this research is that, in spite of nearly a kilometer of vertical elevation relief and diverse forest types from ponderosa pine to red fir, the current forest conditions support a relatively homogeneous small mammal community dominated by ruderal species. It is unclear whether this reflects a legacy of fire exclusion and the resulting accumulation of fine woody debris or, perhaps, a response to a history of logging and fire suppression in this region. In contrast, other recent work in Yosemite (Roberts et al. 2008) confirms that small mammals respond strongly to variation in burn history. Taken together, these results support the fundamental ecological role of fire and broadscale forest heterogeneity in managing mixed-conifer forests in the Sierra Nevada (North et al. 2009).

Songbirds

To evaluate the effects of the Meadow Valley fuel-treatment network on songbirds, we compared avian community diversity before and after treatment. From 2004 to 2011, we surveyed the breeding community in and adjacent to Meadow Valley, using standardized point-count surveys with a 50-m radius (Ralph et al. 1995). Surveys were conducted at 51 stations where DFPZs were implemented (treated) and 201 stations where no treatments were implemented (untreated), proportional to the 19% of the study area treated. An additional 180 stations were surveyed in adjacent untreated PNFSA (figure 2) watersheds (the reference group). We used geographic information systems to establish locations

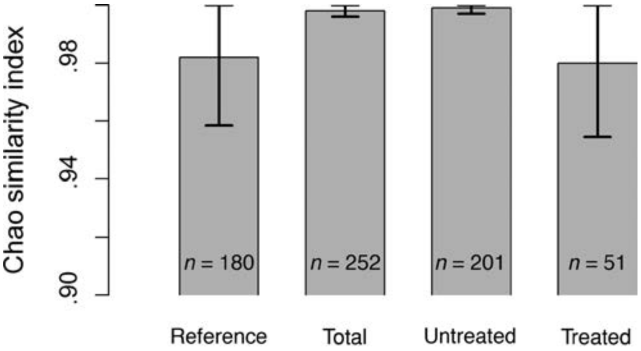

Figure 8. Chao similarity index for the avian community (60 species) before and after treatment at treated and untreated locations in the Meadow Valley study area and reference locations in the adjacent Plumas National Forest study area that also received no treatment. This metric ranges from 0–1, with 1 representing perfect similarity (all species and relative abundances shared among both samples). The error bars are 95% confidence intervals.

for the untreated and reference stations from a randomly selected origin (constrained by slopes lower than 35% and on USFS land) along a random compass bearing in a linear array of 4–12 points. The treated stations were placed within proposed DFPZ treatments across the breadth of treatment types and geography described above. All of the stations were a minimum of 250 m apart.

We surveyed all of the stations in both 2004 and 2005, prior to treatment, and for 2 years after all treatments were implemented (2010–2011). In each year, we surveyed every station twice during the peak of the breeding season (15 May–10 July), with a minimum of 10 days between visits. We limited our analyses to the 60 species breeding in upland habitats that were reliably recorded with point counts (Hutto et al. 1986). The results were summarized at the level of the three treatment groups described above (treated, untreated, reference) and for treated and untreated locations in Meadow Valley combined. For all of the analyses, we summed detections across four surveys (two visits per year over 2 years) for the pre- and posttreatment periods. We compared avian assemblages before and after the treatment with Chao–Jaccard's similarity index (Chao et al. 2005), calculated using EstimateS (version 9.1, University of Connecticut, Storrs). Chao–Jaccard similarity is sensitive to changes in species composition and abundance. Differences in avian diversity were evaluated using the exponent of the Shannon index (Nur et al. 1999). For both analyses, 95% confidence intervals were derived from estimated standard errors from 1000 bootstrap samples.

Our results indicate little change in the Meadow Valley avian communities in response to treatment. The communities were similar across the treated, untreated, and reference samples (figure 8). There was some evidence that the treated areas were less similar to each other than were the untreated areas, but this was not statistically significant ($p > .05$). Avian diversity (the Shannon index) was lowest for the treated sample prior to treatment but increased more in the posttreatment period, such that the Shannon index after treatment was equivalent in the treated and untreated samples (figure 9).

Evaluating the effects of fuel treatments with coarse metrics such as similarity and diversity can cause one to overlook large effects on select species (Hurteau et al. 2008). Numerous studies in seasonally dry fire-prone US forests have shown that fuel treatments can result in at least modest changes in the abundance of a broad range of avian species (Fontaine and Kennedy 2012). We recently reported that mechanical fuel-reduction treatments in the northern Sierra Nevada (including Meadow Valley) resulted in modest decreases in the abundance of a few closed-canopy associates and increases in some edge and open forest associates (Burnett et al. 2013). None of the 15 species evaluated in that study showed a significant decline following the construction of shaded fuel break DFPZ treatments—the primary treatment used in the Meadow Valley study area. With the moderate portion of the landscape treated, small differences in avian community similarity and diversity resulting from treatment, and the results from our previous evaluation of individual species response, we conclude that the effects of the Meadow Valley fuel-treatment network on the songbird community were minimal.

The fuel treatments implemented in Meadow Valley were typically less intense than those shown to result in large changes in avian communities (for a review, see Vanderwel et al. 2007). The treatments were applied to 19% of the landscape, and the prescriptions left relatively high canopy cover. Fire suppression and silvicultural practices over the last century have reduced forest heterogeneity and increased stand density (Scholl and Taylor 2010, Collins et al. 2011). In the Sierra Nevada, most fuel treatments changed the forest structure moderately from historic forest conditions (North et al. 2007). The Meadow Valley mechanical treatments primarily removed ladder fuels, which reduced crown fire potential but did not substantially alter the existing habitat features associated with songbirds, such as shrub cover or large overstory trees.

Our results should be considered in the context of the conditions that existed in the study area prior to the implementation of the landscape treatments. If an objective of these treatments was to maintain the existing avian assemblage and diversity, they appear to have been successful. However, a frequently stated objective for fuel reduction is to act as a surrogate for the natural fire regime (Stephens et al. 2012). Therefore, the maintenance of the pretreatment wildlife community may not always be the most desirable outcome in landscapes such as Meadow Valley and the larger PNFSA, where fire has been excluded for 85–125 years (Moody et al. 2006). Creating or enhancing

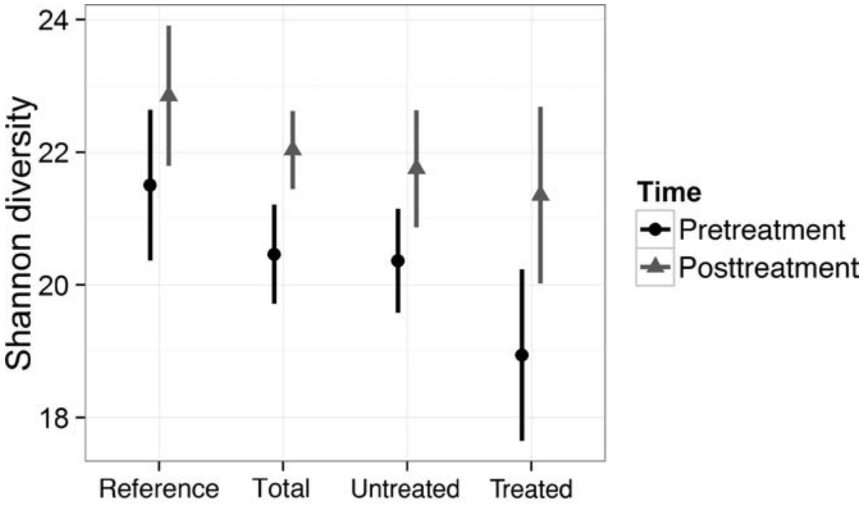

*Figure 9. Shannon diversity index of avian diversity before (*pretreatment*) and after (*posttreatment*) fuel treatments were implemented at treated (*n *= 51) and untreated (*n *= 201) locations and the first two combined (*Total; n *= 252) in the Meadow Valley study area and in reference locations in the adjacent Plumas National Forest study area, which received no treatment (*n *= 181). The error bars are 95% confidence intervals.*

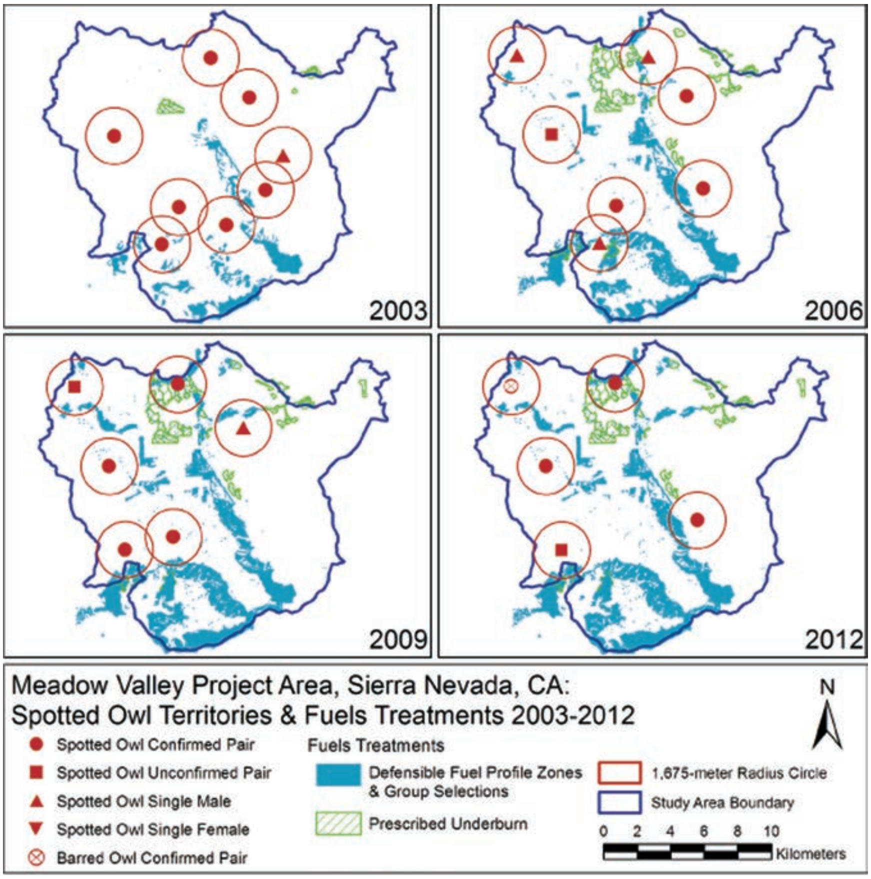

Figure 10. Distribution of territorial California spotted owl sites and landscape forest fuel treatments within the Meadow Valley study area from 2003 to 2012.

conditions for species associated with postdisturbance habitat, some of which have experienced recent declines, may be a prudent approach for achieving some biological diversity objectives (Fontaine and Kennedy 2012). If fuel-reduction treatments are to be a complementary tool to fire in achieving biological objectives, we suggest that they be designed to further increase landscape heterogeneity in fire-excluded forests.

California spotted owls

Modeling studies have projected that fuel treatments on a portion of the landscape (20%–35%) may have minimal effects on owl habitat and that the longer-term benefits of reduced wildfire risk may outweigh the short-term treatment effects on owl habitat (Ager et al. 2007, Roloff et al. 2012). However, no empirical data are available to assess the effects of landscape fuel treatments on the CSO and its habitat.

We used standardized surveys and color banding of individual owls to monitor the distribution, occupancy, survival, and reproduction of CSO sites annually across 1889 square kilometers between 2003 and 2012 in the Plumas and Lassen National Forests. Within this area, four areas were identified for implementation of landscape-scale fuel and restoration treatments. Our initial objectives were to establish baseline values for CSO distribution and abundance and to monitor the owl's response in the treated and untreated landscapes in posttreatment years. However, complete implementation of the fuel-treatment network only occurred on one (Meadow Valley; figure 10) of the four landscapes because of legal challenges to the proposed US Forest Service management strategy.

In the Meadow Valley study area, the number of territorial owl sites declined after treatment. Prior to and throughout the implementation of the treatment, the number of owl sites ranged from seven to nine. Between the final year of the DFPZ and group-selection installations (2008) and 2 years after treatment (2009–2010), the number of owl sites declined by one (six territorial sites), and by 3–4 years after treatment (2011–2012), the number of sites had declined to four—a decline of 43% from the pretreatment numbers (figure 11). These results mirror similar declines of the CSO in the larger Plumas-Lassen CSO study area over the past 20 years (Conner et al. 2013) but suggest a greater magnitude of decline within Meadow Valley (figure 11).

The CSO nests and roosts in dense, multilayered, mature forest patches, and the adult survival and territory occupancy of these owls is positively correlated to the amounts of mature forest in core areas around CSO sites (Dugger et al. 2011). For foraging, however, the CSO uses a broader range of vegetative conditions. Radio-telemetry conducted in Meadow Valley indicates that the CSO avoids foraging in DFPZs in the first 1–2 years after fuel treatments and that the owl's home range size was positively correlated with the amount of treatment within the home range (Gallagher 2010). Barred owls (*Strix varia*) began to colonize the Meadow Valley study area in 2012 and are likely to become a threat to the CSO and a confounding factor to be accounted for in assessments of forest management effects (Keane 2014).

Although inference must be tempered from a single study, the Meadow Valley area is the first large area to receive full the implementation of landscape-scale DFPZ and group-selection treatments in which CSOs were monitored annually both before and after treatment. CSOs are long-lived (up to 20 years) and exhibit high site fidelity as adults, although there is high annual variation in reproduction associated with weather and food (Gutierrez et al. 1995). Given these traits, individual CSOs may exhibit both short- and long-term responses to fuel treatments or wildfire, and understanding both is important to land-use managers. Our results documented a decline in CSO territories as a result of landscape fuel treatments, but the factors driving the decline remain unknown.

Conclusions

This study has shown that coordinated landscape-scale fuel treatments can substantially reduce the potential for hazardous fire across a large montane region, even when a moderate proportion of the area that could not be treated because of management constraints. In many cases, lands with designated management emphasis, such as wildlife habitat reserves and stream buffers, are distributed throughout the landscape. Creating fuel treatments that exclude these lands can result in a patchwork of treated areas heavily dissected by, for example, untreated stream buffers. Hazardous fire potential decreased in untreated areas, but that effect is not stable over time. Even if the existing network was maintained in a "treated" condition (i.e., periodic prescribed fire to keep surface and ladder fuels low) hazards will continue to increase in untreated areas because of stand development (Collins et al. 2013).

Our results indicate negative CSO responses to treatments, supported by the avoidance of DFPZs by foraging owls, larger owl home ranges associated with increasing amounts of treatment within the home ranges, and a 43% decline in the number of territorial CSO sites across the Meadow Valley study area within 3–4 years of the implementation of landscape treatments. In addition to changes in the number of owls, we also observed spatial redistribution of owl sites over time across the landscape (figure 10). The specific mechanisms driving these observations are unclear, but given the region-wide decline in the CSO population (Conner et al. 2013) and the increasing barred owl populations, it is difficult to disentangle fuel treatment effects from background or external pressures. Despite the challenges of working at landscape scales, studies such as this provide opportunities for addressing scale-dependent ecological phenomena, such as population-level species responses and responses to management strategies that cannot be addressed at smaller spatial scales.

To date, little discussion has been focused on what may constitute sustainable, viable CSO populations under various landscape conditions designed to address projected fire and climate scenarios. Furthermore, there is not a clear understanding of the balance between the potential short-term impacts from treatments and the longer-term benefits provided by introducing landscape heterogeneity (North et al. 2009), reducing potential for severe fire (Ager et al. 2007, Collins et al. 2013), increasing the potential for more desirable fire effects (North et al. 2012), and increasing resilience to climate change (Stephens et al. 2010). The Meadow Valley study is an important step in learning about the responses of wildlife species to fuel-reduction treatments.

Recent research in Yosemite National Park suggests that CSOs are not adversely affected by low- to moderate-severity fire (Roberts et al. 2011, Lee et al. 2013). Studies of the CSO both in Yosemite and in Sequoia and Kings Canyon National Parks have not shown population declines that have been found in several national forests in California. There are many differences between the two ownerships: National forest lands generally contain younger forests and lack the large tree structures associated with preferred owl habitat. With continued fire suppression, national forest lands continue to develop dense, small-tree stand conditions, reducing the habitat heterogeneity associated with a variety of small mammals that constitute the CSO's prey base. Because of these differences, it is difficult to determine whether more recent mechanical treatments or existing fire-suppressed conditions might be associated with declining CSO populations. Uncertainty also persists regarding the potential thresholds at which the amounts and patch sizes of high-severity fire reduce the postfire probabilities of CSO occupancy, survival, and reproduction. This is a significant information gap, given the trend for increasing amounts and patch sizes of high-severity fire in many Sierra Nevada forests (Miller et al. 2009). Unfortunately, only one CSO pair in Meadow Valley used an area that received prescribed burn treatments, but unlike those in some of the mechanically treated areas, these owls continued to occupy the burned area through the duration of the study and foraged within the burn-treatment areas (Gallagher 2010). The introduction of barred owls to Meadow Valley adds another important factor that may

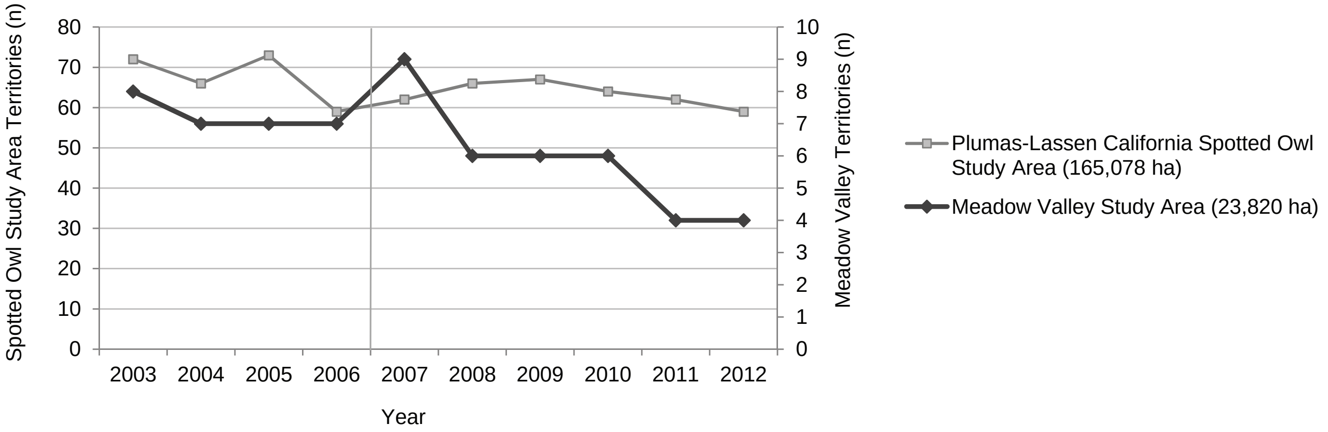

Figure 11. The annual number of territorial California spotted owl sites from 2003 to 2012 within the Meadow Valley study compared with the rest of the Plumas-Lassen study area (in the Plumas and Lassen National Forests). Vertical line represents completion of >80% of treatments.

reduce the population and viability of the CSO, possibly independent of forest structure.

Mechanical treatments can reduce fuels, but, in this study, they also left the largest trees and retained more than 40% canopy cover, two structural characteristics associated with CSO habitat use (Verner et al. 1992). However, although mechanical treatments retain these live features, they often remove snags for operator safety and fuel objectives; reduce tree density and canopy layering; reduce canopy cover to the minimum level (around 40%) considered to function as owl foraging habitat; and simplify the ground structure through a reduction of logs and small trees. Furthermore, DFPZ treatments are often uniformly implemented over large areas along roads, which results in extensive patches of simplified stand structure with regularly spaced trees. Another concern is that treatment size and placement are determined by land-use constraints (gentle slopes, access to roads) and opportunities to affect fire behavior. We have little information about how the location of treatments may affect CSOs' use of areas outside their core nesting locations. Several small mammals appeared to favor sites with steeper slopes (Kelt et al. 2013), possibly reflecting the spatial allocation of treatments in this landscape.

The importance of increasing heterogeneity within stands and across the landscape in mixed-conifer forests is well documented to meet restoration objectives (North et al. 2009, Stephens et al. 2010). Our ability to optimize heterogeneity at large scales may be more effectively achieved with prescribed and managed fires that are allowed to burn under moderate weather conditions. This type of burn often produces variable forest conditions that mimic historic patterns (Collins et al. 2011) to which this fauna, including the CSO, has adapted. Alternatively, mechanical treatments that produce the complex forest structure and composition that more closely mimic the patterns generated under a more active fire regime (North et al. 2009) may provide habitat conditions to support CSOs and a diverse fauna superior to those of the DFPZ and group-selection treatments implemented in Meadow Valley. Although mean stand conditions (e.g., canopy cover) have often been used to infer management impacts on preferred habitat (Tempel et al. in press), the historic heterogeneity of frequent-fire forests suggests we have yet to identify the optimal scales at which to create variable forest conditions.

We encourage further work to examine landscape-level treatments that are intended to emulate the influence of fire in creating spatial heterogeneity in vegetation and fuel conditions. A working hypothesis is that increased habitat heterogeneity, including the retention and development of currently limited but ecologically important forest conditions (areas of large, old trees) and more-open, patchy, early-seral stage conditions, would promote a diverse wildlife community while providing a more fire-resilient landscape. The results from the Meadow Valley study area illustrate the benefits and challenges of working at the landscape scale. Rigorous and controlled experiments are difficult because of the inherent variability across landscapes, sociopolitical constraints, and competing management objectives that can influence planned treatments. However, inferences from these studies can be strengthened by careful replication of management strategies across multiple landscapes.

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Supplemental material

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Scott L. Stephens (sstephens@berkeley.edu) *is affiliated with the Division of Ecosystem Science at the University of California, Berkeley. Seth W. Bigelow, Brandon M. Collins, Claire V. Gallagher, John Keane, Malcolm P. North, and Peter A. Stine are affiliated with the US Department of Agriculture, Forest Service, Pacific Southwest Research Station, in Davis, California. BMC is also affiliated with the University of California Center for Fire Research and Outreach, in the College of Natural Resources at the University of California, Berkeley. Ryan D. Burnett and Lance Jay Roberts are affiliated with Point Blue Conservation Science, in Petaluma, California. Douglas A. Kelt and Dirk H. Van Vuren are affiliated with the Department of Wildlife, Fish, and Conservation Biology at the University of California, Davis.*