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Appendix A: Fire and Forest Ecosystem Health Team Final Report

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EXECUTIVE SUMMARY

The 2004 Amendment to the Sierra Nevada Forest Plan identified a coordinated system of fuel treatments distributed across the landscape as the preferred management alternative. The goals of this approach, defined as strategically placed land area treatments (SPLATs), were to modify dangerous fire behavior and improve forest health in the National Forests in the Sierra Nevada region of California. The 2004 amendment also introduced the concept of fireshed management. In concept, firesheds are analogous to watersheds, but are topographic units based on the behavior of a problem fire – a fire that has the greatest potential impact based on the local topography, weather, and fire history. We tested the performance of SPLATs as designed and implemented by US Forest Service in two firesheds, Last Chance in the Tahoe National Forest and Sugar Pine in the Sierra National Forest. We conducted detailed field measurements before and after treatments in order to quantify changes in forest structure and fuel loads resulting from SPLATs. To account for potential changes unrelated to forest management, a control fireshed was paired with the treated fireshed at each site. Data from the field measurements were used to parameterize fire and forest growth models. These models were then used to simulate wildfire effects on fire behavior and to explore the responses of tree growth efficiency (a measure of tree vigor) to the treatments. At Last Chance, fuel treatments distributed across 18% of the landscape reduced the percentage of the forest exposed to damaging flame lengths from 33% (no SPLATs) to 22% (with SPLATs). The impact of SPLATs on fire behavior was less at Sugar Pine. Fire simulations for Sugar Pine showed that SPLATs completed on 29% of the area, reduced exposure to damaging flame lengths from 29% of the landscape to 25% – a minimal decline of 4 percentage points. In contrast, trees in the treated fireshed at Sugar Pine nearly doubled their growth efficiency in the ten years following SPLATs while there were only minor improvements in growth efficiency following treatments at Last Chance. This dichotomy in the response to SPLATs was related to differences in the extent and intensity of the treatments applied at the two sites as well as ecological and land use variations. The treated fireshed at Sugar Pine supported a mixed conifer forest that was more crowded with bigger trees but exposed to a lower initial fire hazard. Nevertheless, in aggregate our results support the promise of SPLATs. Coordinated treatments across part of the landscape can help minimize the hazards posed by severe fires and at the same time meet forest health objectives.

INTRODUCTION

Overview

A century of forest and fire management in the Sierra Nevada has resulted in a sharp decrease in species richness and a dramatic change in the structure of the Sierran forest (Collins et al. 2011, Knapp et al. 2013, Taylor et al. 2014). Abundances of shade-tolerant white fir (*Abies concolor),* Douglas-fir (*Pseudotsuga menziesii* var. *menziesii)* and incense-cedar (*Calocedrus decurrens)* have increased at the expense of the shade-intolerant ponderosa pine *(Pinus ponderosa)* and sugar pine (*Pinus lambertiana*) which require canopy gaps to regenerate successfully (York et al. 2011). Under an intact disturbance regime these canopy gaps would have been created by small patches of tree mortality resulting from fire, insects, and disease; these gaps are largely absent in contemporary fire-suppressed forests (Larson and Churchill 2012, Lydersen et al. 2014, Fry et al. 2014). Dense stands of young white fir, Douglas-fir, and incense-cedar are characterized by increased numbers of small diameter trees and increased canopy cover (Scholl and Taylor 2010, McIntyre et al. 2015). In some particularly vulnerable communities, these changes may have already increased the likelihood of uncharacteristic impacts from fire and insects Knapp et al. 2013, Taylor et al. 2014).

The regional assessment of current forest conditions in the 2004 Sierra Nevada Forest Plan Amendment (USFS 2004) acknowledged how these changes in forest structure and composition associated with past land management practices have exacerbated the risk of severe fire (Biswell 1989, van Wagtendonk 1998) and made modifying wildland fire behavior the management priority. The preferred alternative identified in the 2004 Plan amendment (USFS 2004) was to apply strategically placed area treatments (SPLATs). SPLATs consist of discrete treatment units arranged in a strategic pattern across a landscape, which collectively slow fire spread and moderate fire effects across the landscape (Finney 2001). Simulations have shown that with as little as 30% of the area in SPLATs, fire risk can be decreased for the entire landscape at a disproportionate rate. For example, model results demonstrated that a realistic SPLAT design that treated 33% of a landscape in the Tahoe National Forest reduced the mean flame length by 46% and the mean fire-line intensity by 48% (Vaillant 2008). The landscape unit of management is defined as a fireshed. In concept, firesheds are analogous to watersheds in concept, but are topographic units based on the behavior of a problem fire – a fire that has the greatest potential impact based on the local topography, weather, and fire history. The size of firesheds can vary but they need to be sufficiently large to assess the effectiveness of fuel treatments and encompass characteristic fire sizes for a given area (Bahro et al. 2007).

Despite the promise of SPLATs, there are only a few spatially relevant, fully implemented landscape treatment projects in mixed conifer forests in the Sierra Nevada from which to evaluate and guide management decisions (Moghaddas et al. 2010). The 2004 Amendment (USFS 2004) recognizes this uncertainty as well as the concern for how SPLATs might affect other forest resources. On one hand, SPLATs may provide important co-benefits. For example, the preferred alternative noted the specific objectives of improving tree vigor and overall forest health that might accrue from reducing tree density. This concern over the health of the Sierran forests due to increased competition in crowded stands is shared by the state (FRAP 2003). More recent evidence has linked rising tree morbidity and mortality in Sierran forests with worsening climatic water deficits (van Mantgem and Stephenson 2007), continued exposure to chronic air pollution (Panek et al. 2013), and greater susceptibility to beetle kill (Hicke et al. 2013). On the other hand, SPLATs may degrade habitat for wildlife species dependent on attributes in late-seral forests (Stephens et al. 2014a) or increase sediment yields to streams.

The Sierra Nevada Adaptive Management Project (SNAMP) was formed to address the uncertainty regarding the efficacy of SPLATs in modifying fire behavior and concern regarding potential impacts on wildlife and water resources. Moreover, given the history of debate over land and resource management in the Sierra Nevada, SNAMP followed a specific mandate not only to engage stakeholders and promote active public participation but also to study the adaptive management process itself (Chapter 1). In this report, we address two objectives at the heart of the 2004 Amendment (USFS 2004):

1) What is the effect of SPLATS on wildland fire behavior?
2) Do SPLATs improve forest ecosystem health?

Background

Fire

Recent research has demonstrated an increased proportion of high-severity fire in yellow pine and mixed-conifer forests of the Sierra Nevada between 1984 and 2010 (Miller and Safford 2012, Miller et al. 2009). In addition, these studies demonstrated that fire sizes and annual area burned have also risen during the same period. The authors point out that these increases co-occur with rising regional temperatures and increased long-term precipitation. Westerling et al. (2006) also demonstrated increased area burned over a similar time period, which they attributed to regional increases in temperature and earlier spring snow melts. Despite these documented increases over the last few decades, California and the western United States as a whole are in what Marlon et al. (2012) described as a large "fire deficit." This is based on reconstructed fire occurrence over the last 1,500 years using sedimentary charcoal records. Marlon et al. (2012) argue that the current divergence between climate (mainly temperature) and burning rates is unprecedented throughout their historical record. In other words, with temperatures warming as they have been over the last several decades, we would expect to see much higher fire activity, based on historical fire-climate associations. This divergence is due to fire management practices, which, as the authors point out, may not remain effective over the long term if warming trends continue. It is likely, given increasing temperature and the precipitation patterns since the onset of fire suppression, that fire activity would have increased over the 20th century rather than decreased had fire suppression not been implemented (Skinner and Taylor 2006, Stine 1996), further exacerbating the current fire deficit. This departure in current fire activity relative to what would be expected given current climate combined with the departed contemporary fire patterns (greater proportions and patch sizes of stand-replacing fire) suggests more problematic fire occurrence in the future.

The large wildfires that are occurring annually throughout the Sierra Nevada demonstrate the pressing need to scale up restoration efforts to larger landscapes. Yet implementing fuels treatment across an entire landscape may conflict with desired conditions or may be operationally constrained by funding, access, and land designations (e.g., wilderness areas, protected wildlife habitats, archaeological preserves, Collins et al. 2010, North et al. 2015). In response, scientists and managers have developed and refined concepts like SPLATs that do not require saturation coverage of the landscape to achieve meaningful modification of fire behavior (Ager et al. 2007, 2010; Finney 2001, 2004; Finney et al. 2007). Owing to the complexity of modeling fire and fuels treatment across landscapes (e.g., data acquisition, data processing, and model execution), fuels treatment project design is often based on local knowledge of both the project area and past fire patterns. Recent studies in the northern Sierra Nevada and southern Cascade Range suggests that these types of landscape-level fuels treatment projects (where treatment arrangement is based more on local knowledge and fairly simple fire behavior modeling rather than intensive modeling associated with an optimization approach) can be quite effective at reducing potential fire behavior at the landscape scale (Collins et al. 2011, 2013, Moghaddas et al. 2010).

Although only a few studies have explicitly modeled effectiveness of landscape fuels treatments using different proportions of treated area, there are some common findings: (1) noticeable reductions in modeled fire size, flame length, and spread rate across the landscape relative to untreated scenarios occurred with 10 percent of the landscape treated, but the 20-percent treatment level appears to have the most consistent reductions in modeled fire size and behavior across multiple landscapes and scenarios (Ager et al. 2007, 2010; Finney et al. 2007; Schmidt et al. 2008); (2) increasing the proportion of area treated generally results in further reductions in fire size and behavior; however, the rate of reduction diminishes more rapidly when more than 20 percent of the landscape is treated (Ager et al. 2007, Finney et al. 2007); (3) random placement of treatments requires substantially greater proportions of the landscape to be treated compared to optimized or regular treatment placement (Finney et al. 2007, Schmidt et al. 2008); however, Finney et al. (2007) noted that the relative improvement of optimized treatment placement breaks down when larger proportions of the landscape (about 40 to 50 percent) are excluded from treatment because of land management constraints that limit treatment activities. It should be emphasized that this is not to preclude treating more than 20 percent of a landscape to achieve restoration, resilience, or other resource objectives. These studies suggest that when beginning to deal with fire hazard in a landscape, the initial objective would be to strategically reduce fire hazard on between 10 and 20 percent of the area to effectively limit the ability of uncharacteristically high-intensity fire to easily move across the landscape. This would buy time to allow restoration activities to progress in the greater landscape (North et al. 2015).

Forest health

The terms “healthy forest” and “forest health” are used often in natural resources, yet rarely are they qualified or standardized. The confusion surrounding the term forest health is understandable, as there is no single, universally accepted definition. However, there are some recurring themes in the literature that create a basis for understanding.

Forest health is not exclusively a scientific concept (Kimmins 1997, Patel 1999, Sulak and Huntsinger 2012). Forest health is often defined by the social, cultural or economic values of a specific audience. For example, those with an interest in forest products and sustained local economies may define forest health as a sustainable, actively managed forest that is free of disease, with a diversity of tree species for future product markets (Lankford and Craig 1994). Indeed forest pathologists typically consider health to mean the extent and virulence of tree disease present in a forest whether it is timberlands or wildlands (Pautasso et al. 2014). This definition is focused exclusively on trees. However, an audience interested in maintaining vigorous wildlife populations may insist that the definition be expanded beyond tree health to include the capacity of a forest to maintain viable populations of native species and retain biodiversity of flora *and* fauna (Dellasalla et al. 1995). The first definition measures disease and species diversity of trees, and the second measures wildlife populations. Both definitions of “forest health” may mean opposite management regimes. Ultimately, forest health becomes a social construct, defined not by an inherent, “scientifically correct” state (Warren 2007) but by variables society considers most important (Sulak and Huntsinger 2012).

Many definitions of forest health fall under the general term “utilitarian”: a forest is healthy if its condition does not threaten management objectives, current or future (Kolb et al. 1994). While it is easy to diagnose an unhealthy forest under this definition (i.e., a forest is threatening management objectives), the concept can suffer from its own circular logic, where “forest health” is defined by meeting management objectives, yet “forest health” *is* the management objective.

In contrast with anthropocentric utilitarian definitions, forest health has also been defined by specific types and rates of ecological processes (e.g., Tierney et al. 2009) or by the presence of specific indicators (Woodall et al. 2011). Unfortunately, these definitions come with their own set of management problems; quantitative rates and data are not widely available for many ecosystems (Kolb et al. 1994), and there is no gold standard for all rates and processes. Indicators are multifaceted and can provide conflicting information. The challenge then becomes how to integrate multiple lines of information to assess health. Using historical rates and patterns is also tricky. Changing climate and land uses by humans make the selection of the desired parameters difficult, and even if parameters were chosen, it is unlikely that our knowledge of past ecosystem processes is sufficient to design a management regime (Wagner et al. 2000).

Often in the literature, a forest is considered healthy if is resilient or sustainable. Under this guise, a healthy forest is "one that is resilient to change" (Joseph et al. 1991, EPA 2015); "resistant to catastrophic change and/or ability to recover after catastrophe" (Kolb et al. 1994) and has "sustained ecosystem functioning" (Wagner et al. 2000). This definition is also troublesome because resilience is very difficult to measure. The resilience of a forest remains a relative unknown until exposure to disturbance or stress.

The concept of "forest health" is difficult to apply to landscape-level processes because its origins lie at the individual level. Ecosystem health is a metaphor borrowed from human health (Kimmins 1997) and is problematic when applied to whole ecosystems, just as human health is difficult to apply to whole populations (Raffa et al. 2009). A dead or dying single tree is inherently unhealthy, but a dead or dying stand is more difficult to diagnose. Kolb et al. (1994) define an unhealthy stand as only unhealthy if the rate of mortality exceeds the capacity for stand replacement, but this may not necessarily apply at a forest or landscape level.

For SNAMP, we have built on the idea that individual tree growth and survivorship are fundamental components of forest health. While this focus on tree vigor recognizes the foundational role of trees in forests (Ellison et al. 2005), it does not encompass the term's broader usage (Sulak and Huntsinger 2012). Thus in addition to measuring tree vigor we also assessed the impact of SPLATs on forest structure and species composition.

Adaptive Management Experiment

SNAMP was structured as a deliberate experiment in adaptive management (Chapter 1). Thus, the design and implementation of the SPLATs on the landscape was left entirely to the US Forest Service. We measured forest and fuel characteristics before and after treatments. These data serve as the basis for both direct comparisons as well as input for the necessary simulation experiments of fire behavior.

METHODS

Site Description

Last Chance, the northern study area (Figure A1) is defined by the boundaries of four adjoining watersheds. The treatment fireshed consists of the two central watersheds: Deep Canyon and Grouse Creek. We used the two immediately adjacent watersheds as the control (Screwauger Canyon and Peavine Creek). In total, the study site encompasses an area 38.4 mi^2 (99.5 km2), with elevation ranging from 2,625 ft (800 m) in the southwest to almost 7,218 ft (2,200 m) in the northeast portion of the study area. Soils are moderately deep, well-drained Inceptisols with a gravely loam texture. The Crozier and Hurlbut soil series that are most common at Last Chance are derived from andesite and metasedimentary parent material (NRCS 2015). The climate is Mediterranean with a predominance of winter precipitation, a majority of which is snow. Total precipitation averages 46.5 in/yr (1,182 mm/year). Mean monthly temperatures are 37.4 °F (3°C) in January and 69.8 °F (21°C) in July (1990–2008; Hell Hole Remote Automated Weather Station).

Sugar Pine, the southern study area (Figure A2) is located in central Sierra Nevada, approximately 124 mi (200 km) south of Last Chance. Encompassing approximately 12.9 mi^2 (33.6 km^2), elevation at Sugar Pine ranges from 3.936 ft (1,200 m) in the southwest to almost 7,216 ft (2,200 m) in the northeast portion of the study area at Speckerman Mountain. The deep, well-drained soils at Sugar Pine developed from weathered granodiorite. Holland family soils (Inceptisols) with a sandy loam texture are most common (NRSC 2015). The climate is also Mediterranean with snow dominating the 42.9 in/yr of precipitation (1,091 mm/year). Mean monthly temperatures are 35.6 °F (2 °C) in January and 64.4 °F (18°C) in July (1941-2002; Yosemite National Park).

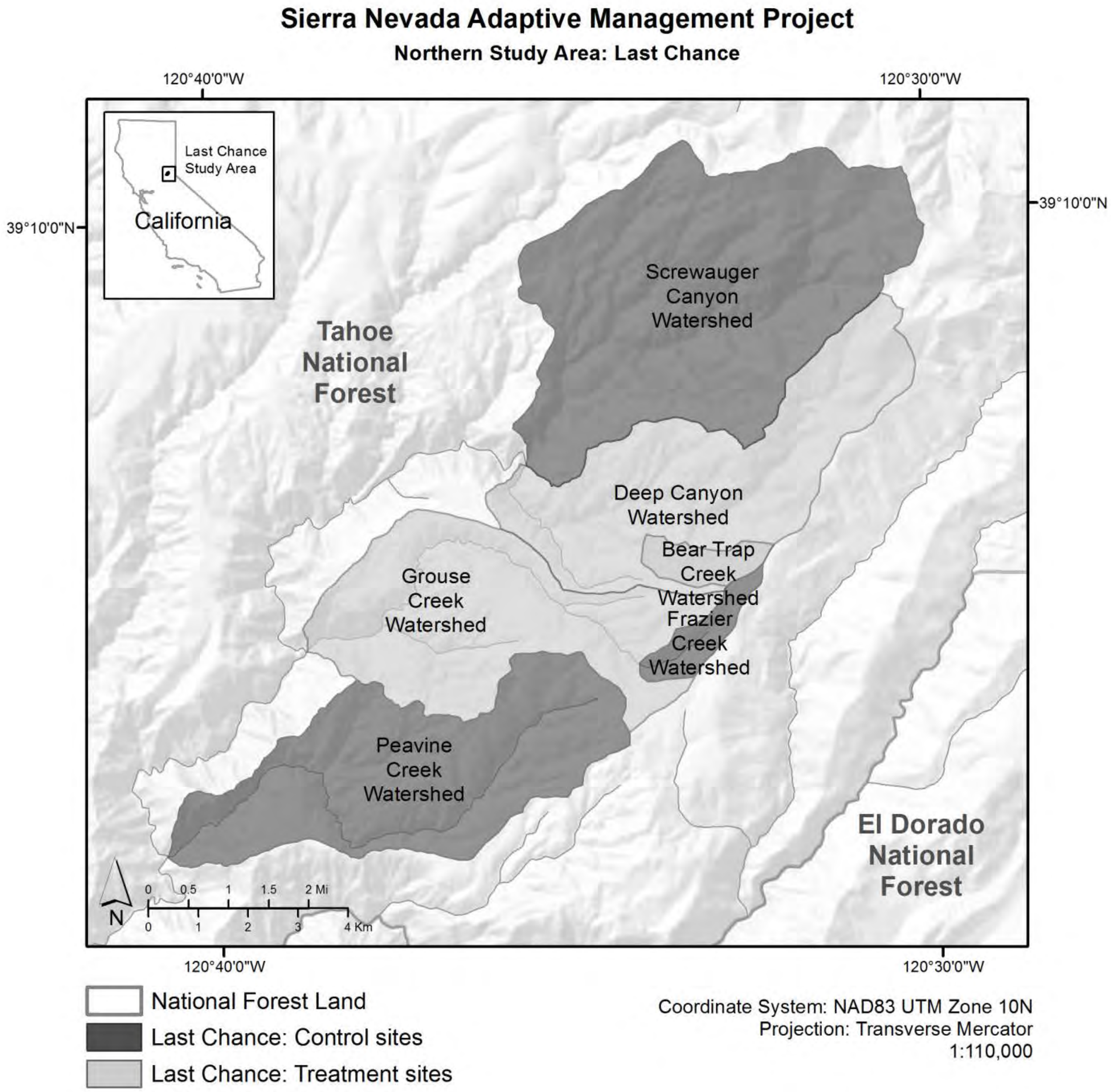


Figure A1: Control (dark grey) and treatment (light grey) areas at Last Chance, the Sierra Nevada Adaptive Management Project's northern study site in the Sierra Nevada, California. Bear Trap and Frazier Creek were the headwater catchments evaluated by the Water Team.

Vegetation at Last Chance is dominated by the Sierra Nevada mixed conifer forest. White fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) are the two most abundant species but incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*) appear as codominants at variable densities. Stands of montane chaparral dominated by manzanita (*Arctostaphylos* spp) are interspersed throughout.

The mixed conifer forest is also the most common vegetation type at Sugar Pine but species composition differs from Last Chance in that there is no Douglas-fir, and the Nelder Grove watershed contains a small grove of giant sequoia (*Sequoiadendron giganteum*). In addition to black oak and interior live oak (*Quercus wislizeni*), typical hardwood and shrub species include white alder (*Alnus rhombifolia*), Pacific dogwood (*Cornus nuttallii*), mountain whitethorn (*Ceanothus cordulatus*), deerbrush (*Ceanothus integerrimus*), and greenleaf manzanita (*Arctostaphylos patula*).

Fire history, inferred from fire scars recorded in tree rings, suggests the fire regime prior to systematic fire suppression and widespread timber harvesting in Sierra Nevada west-side pine-mixed conifer forests was dominated by frequent, low-severity fires occurring at regular intervals (Stephens and Collins 2004, Scholl and Taylor 2010). Based on fire scars collected on site, the median fire interval for Last Chance was 15.0 years and 11.0 years for Sugar Pine (Krasnow 2012). Native American activity in the study areas was likely high before European settlement. The Nisenan Native American community once inhabited the forests of north-central Sierra Nevada. Up until 1901, the area that is now Bass Lake (approximately 5.5 mi [9 km] from the Sugar Pine watershed) was a large, lush meadow inhabited by Chuckchansi and Mono tribes. Fire was used extensively to keep the forest open, encourage herbaceous growth for game animals, and produce vegetative growth conducive to basket weaving and arrow construction (Krasnow 2012).

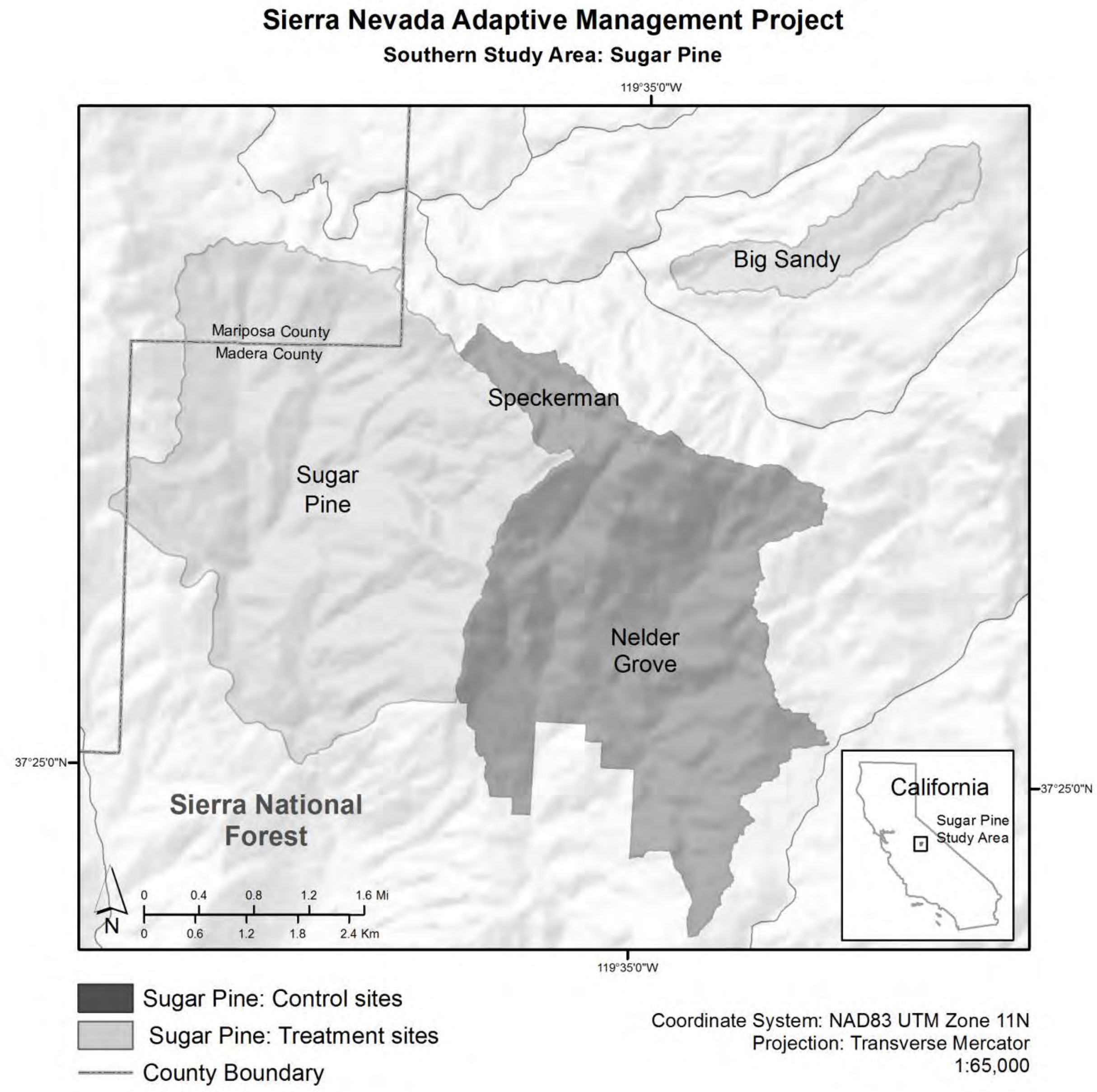


Figure A2: Control (dark grey) and treatment (light grey) areas at Sugar Pine, the Sierra Nevada Adaptive Management Project's southern study site in the Sierra Nevada, California. Big Sandy and Speckerman were the headwater catchments evaluated by the Water Team.

Field Measurements

From a random starting point, we established forest inventory plots at 1640 ft (500 m) spacing across both study areas to characterize stand structure and record changes in conditions due to treatments (Figure A3). This core grid resulted in 328 plots in Last Chance (LC) and 127 plots in Sugar Pine (SP). In the small instrumented catchments used to measure hydrological responses, we increased the sampling effort by reducing the spacing to 820 ft (250 m) or 410 ft (125 m) between plots. To better characterize fire effects, we doubled the number of plots in a recently burned area in LC (Peavine fire) by adding plots at every 820 ft and extended the core plot network to a site with recent fuel treatments just south of SP (Cedar Valley). As a result we have a total of 408 and 284 pre-treatment plots in LC and SP, respectively. Pre-treatment plot measurements were collected during the summer in 2007-08. In order to maximize the time since treatment, we completed the post-treatment sampling in one field season -- 2013. The consolidated field season coupled with limited access due to wildfire (the American Fire began burning on August 10, 2015 just west of LC) forced us to prioritize our sampling efforts. Thus we first re-measured the plots on the core grid followed by plots in treated areas. Our total plot sample size with both pre and post-measurements is 369 at LC and 257 at SP. For vegetation mapping and the development of fire models, we used all available plots. For quantifying forest composition and structure differences between the reference and treated firesheds, we used only the plots on the core grid.

Plots were circular with an area of 0.12 ac (0.05 ha) and located with either a Trimble GeoXH or Garmin handheld global positioning systems (GPS). We used a nested sampling methods based on tree diameter (measured at breast height (dbh 4.5 ft or 1.37 m above the ground): Overstory trees with dbh ≥ 7.67 in (19.5 cm) were sampled on the entire plot (0.12 ac or 0.05 ha); understory trees with dbh between 2.0 – 7.67 in (5- 19.5 cm) were sampled on a random one-third "pie-slice" of the plot (0.04 ac or 167 m^2); small trees with dbh < 2 in dbh (5.0 cm) were sampled with 6.6 ft (2 m) wide radial transect (0.018 ac or 76 m^2). We recorded

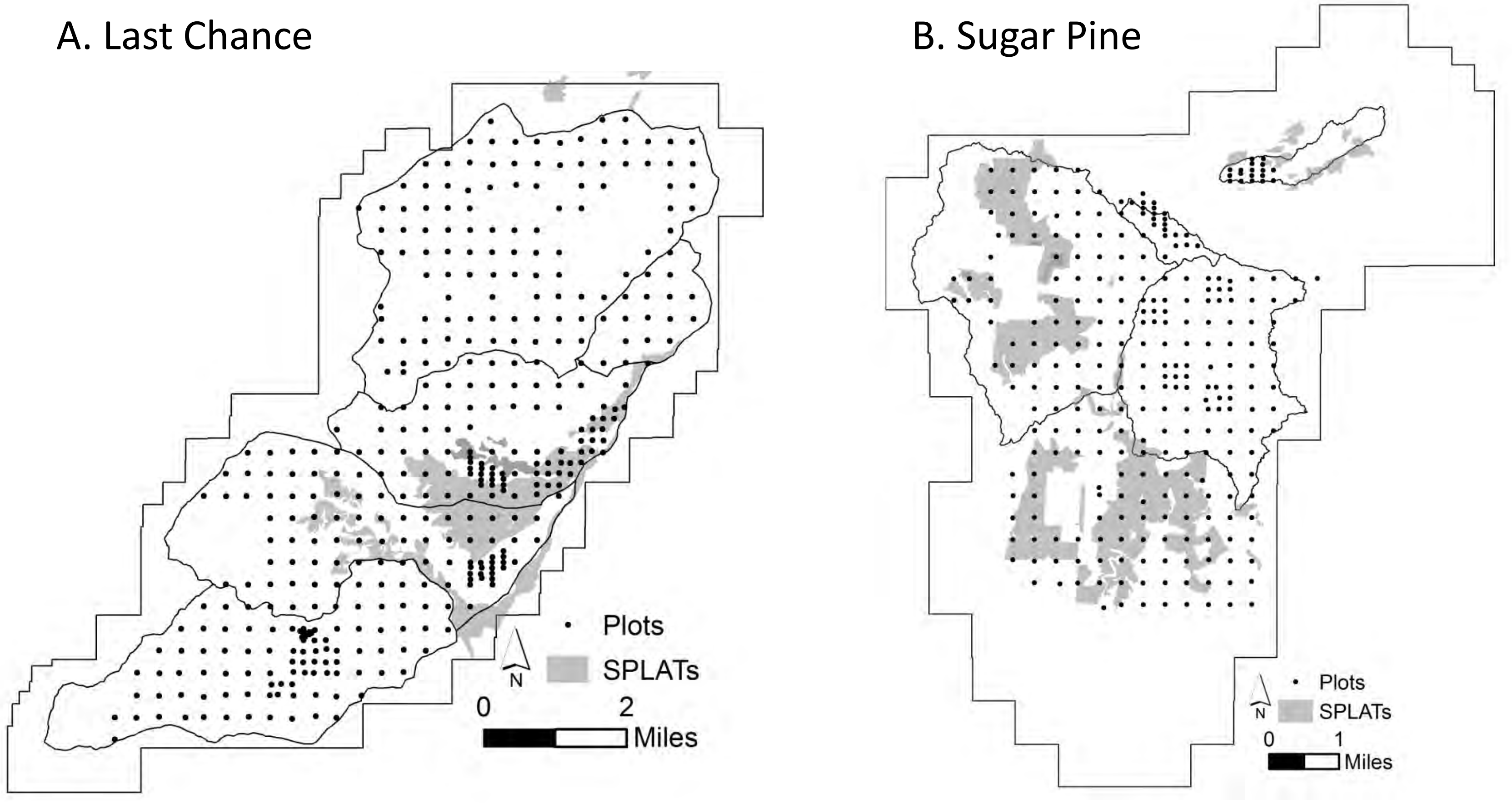


Figure A3: Location of plot network and SPLATs at Last Chance (A) and Sugar Pine (B).

species, vigor, crown position, dbh, total height, and height to live crown base (live trees only) for overstory and understory trees. For small trees, we recorded species and dbh in 0.4 in-classes (1 cm). We tagged all live overstory trees in the plots and tracked the fate of these trees between surveys.

We sampled surface and ground fuels along three radial transects (41.4 ft or 12.62 m) in each plot. We choose the direction of the first transect at random and then placed the remaining two at ±120°angles. Using the line-intercept method (Brown 1974), duff, litter, and surface fuel depths were measured at two points along each transect. Downed woody fuels were tallied along subsets of each transect: 0–1 m (0–0.64 cm and 0.64–2.54 cm branch diameters), 1–3 m (2.54–7.62 cm), and 0–12.62 m (>7.62 cm). Fuel loads were calculated using species-specific coefficients from van Wagtendonk et al. (1996, 1998), weighted by basal area for tree species recorded in the plot (Stephens 2001). On the same three transects we measured shrub species cover via line-intercept and recorded the height of the intercepted shrubs. We used a tube densitometer to estimate canopy cover. We gridded the circular plot into 25 evenly spaced points and recorded if canopy was present directly overhead at each point.

Fuel Treatments

Fuel treatments (Figure A3) were typical of mixed conifer forests (Agee and Skinner 2005). In general, the prescriptions called for treating approximately 25-40% of the treatment firesheds by thinning, mastication, and prescribed fire. Thinning treatments included commercial and biomass thin from below (both sites) and cable harvesting (LC only) followed by mechanical/hand piling and burning. At LC, thinning treatments were designed to retain at least 40% of the existing basal area, reduce ladder fuels by removing trees > 10 in and < 30 in dbh, and maintain a minimum canopy cover of 40%. At SP, residual basal area targets ranged from 55-65% of normal stocking in pine-dominated stands to 80% in the mixed conifer stands. Retention of these higher basal areas ensures minimum canopy cover close to 60%. At both sites, there was an emphasis on increasing vertical and horizontal heterogeneity. Mastication involved the removal of both shrubs and small trees. At LC, mastication occurred primarily within 20- to 30-year-old plantations. At SP, mastication followed some thinning treatments. Prescribed fire focused on understory burning as the primary fuel reduction method (USFS 2009, USFS 2010).

For a host of reasons, treatments were initially delayed and then implemented over several years (2008–2012). During the project planning process some treatments were moderated at SP due to wildlife habitat requirements. At both sites, not all of the planned treatments were completed by 2013 when the final field measurements were obtained. Within the LC study area, the 2008 Peavine Fire (551 ac [223 ha]) burned in August prior to our pre-treatment survey. While not considered a component of our fuel treatment network, post-burn forest structure was measured and incorporated into the landscape forest structure. At SP, fuel treatments in Cedar Valley, the fireshed just south of our paired firesheds (i.e., Sugar Pine and Nelder Grove, Figure A2) started in 2007. Although not part of the experimental design, we extended our plot network into Cedar Valley and obtained pre and post-treatment measurements. Results from Cedar Valley were used to augment our analysis of treatment impacts on forest structure and fuel loads.

We used information from three sources to identify actual treatment area, treatment type, and extent of change. First, changes to forest structure were obtained by repeated measurements of the aforementioned plot network; field observers noted type of treatment. Second, Forest Service District offices supplied GIS-based polygon files identifying treated areas. Lastly, remotely sensed change detection maps, produced by determining areas where differences between pre-treatment and post-treatment maps surpassed threshold values denoting structural change (e.g., > 10% reduction in canopy cover or mean tree height), identified areas that were potentially treated (Su et al. 2015a). Because there can be inconsistencies between agency-generated treatment maps and actual treatment extent, and change detection maps were limited in the ability to identify some treatment types, all three sources were required to ascertain treatment boundaries.

Vegetation Mapping

We developed a vegetation map from our plot and remote sensing data . This map served as the base layer for the development of all landscape map layers required for fire and forest growth simulations. The map consisted of stands, or polygons, classified into vegetation types that captured gradients in tree species composition and forest structure. Classification used both multispectral aerial imagery and lidar-derived metrics (Appendix B-Spatial in this report, Su et al. 2015b). The pre-treatment forest landscape was divided into seven vegetation types at LC and four at SP (Figure A4, Figure A5). We then used the field-plot data to impute detailed vegetation attributes for each polygon (LC, n=1363; SP, n=1100), thereby obtaining the pre-treatment and post-treatment forest structure maps used in the fire and forest-growth modeling. We developed an imputation procedure to assign three field plots to each map polygon based on their similarity in "gradient space" (Ohmann and Gregory, 2002). We performed a multivariate analysis of the plot data to define the gradient space. Variables used in the imputation included treatment type, vegetation type, canopy cover, relative density of big trees, and a suite of topographic metrics. To recreate the fine-scale heterogeneity observed in the field, we identified all plots ranked in the 95th percentile in terms of similarity and then randomly assigned three of those plots to the stand. Some plots were used to populate multiple stands. Each plot contributed data to an average of 12.6 stands (range: 1-77) for LC, and 12.8 stands (range: 1-109) for SP.

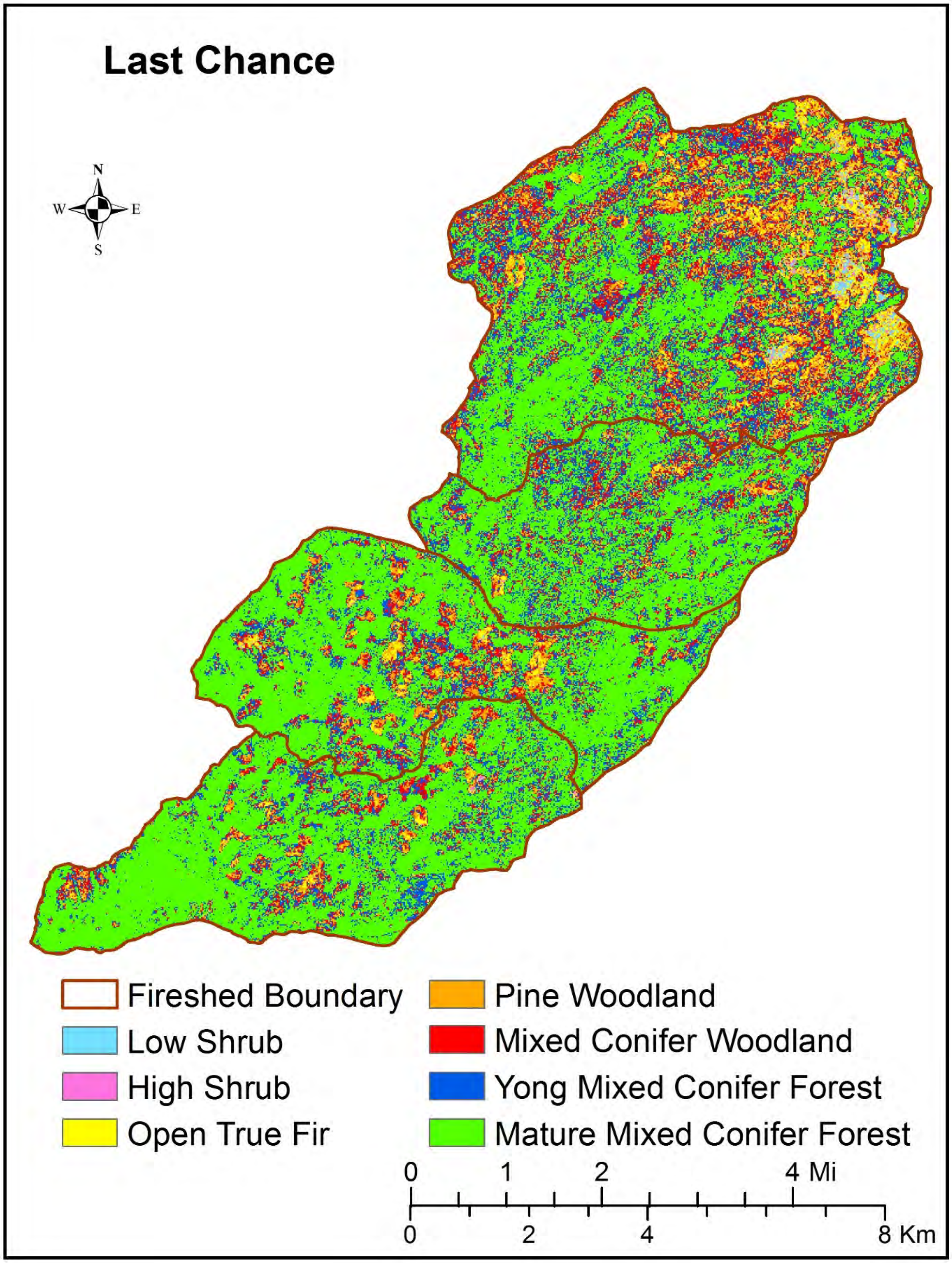


Figure A4: Vegetation map of firesheds at the Last Chance site.

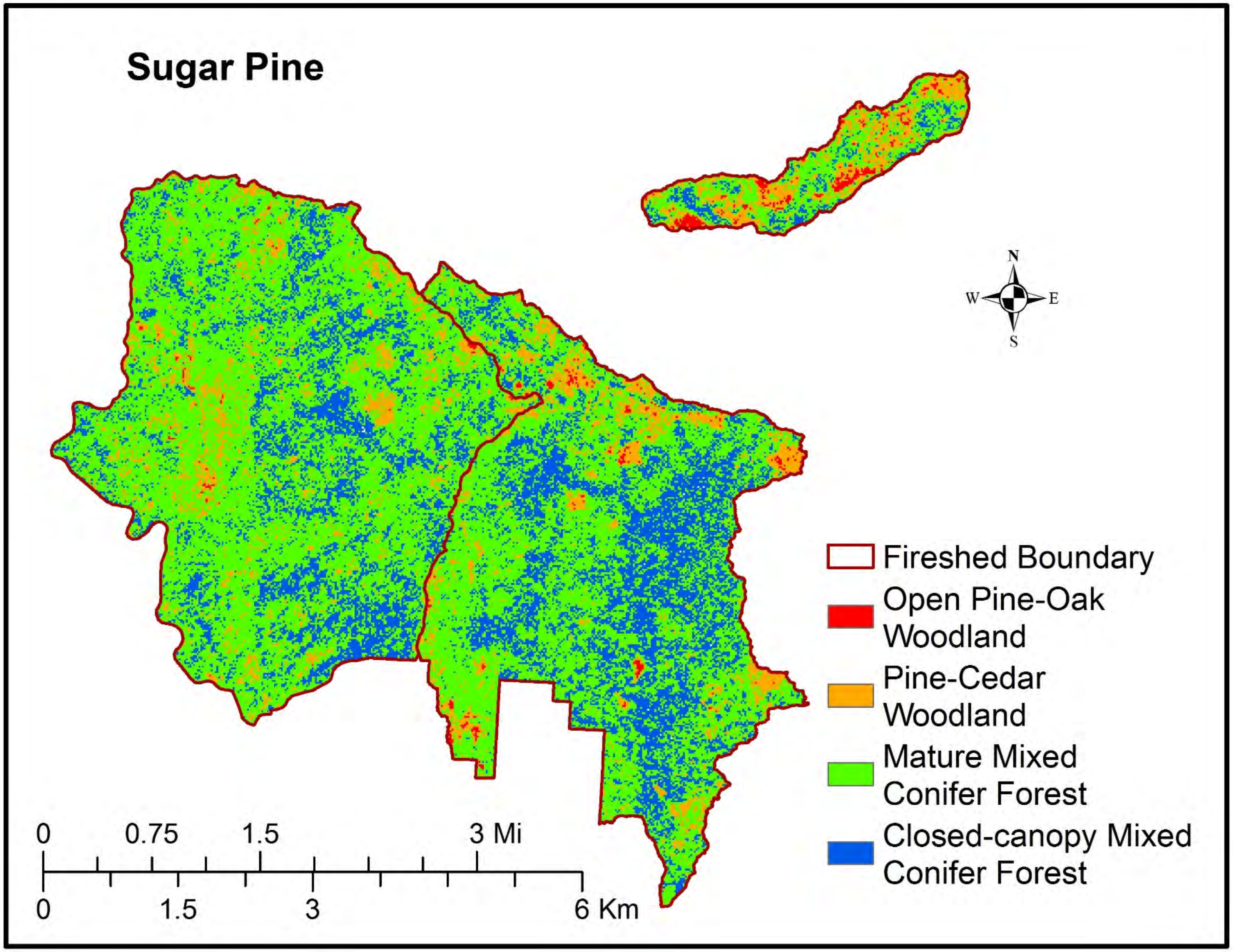


Figure A5: Vegetation map of firesheds at the Sugar Pine site.

Modeling Forest Dynamics

We considered four scenarios: 1) with SPLATs and with fire; 2) without SPLATs and with fire; 3) with SPLATs and without fire; and 4) without SPLAT and without fire. We used the tree list databases associated with the 2008 pre-treatment and 2013 post-treatment field plots when simulating fire and forest growth under the ‘no SPLATs’ and ‘with SPLATs’ scenarios, respectively. The Forest Vegetation Simulator (FVS) (Dixon 2002) with the Fire and Fuels Extension (FFE) (Reinhardt and Crookston 2003) is an integrated system of forest growth models that can simulate a wide range of silvicultural treatments. We used the western Sierra variant of FVS, which does not explicitly simulate establishment of new trees in the absence of disturbance, or ingrowth. To simulate ingrowth users must input the number, species, and frequency of establishment events. We used a random number generator to choose the actual number of seedlings, within species-specific bounds, that established for a given stand in a given FVS cycle (e.g., Collins et al. 2011). This was to done to attempt to represent the variable regeneration conditions observed across the studied landscapes. Additionally, we regulated seedling height growth to simulate more realistic conditions in a mixed conifer forest. FVS generates estimates of forest stand structure and surface fuel loads for all four scenarios, at four time steps: 1a) 2008 pre-treatment (no SPLATs); 1b) 2013 initial post-treatment (with SPLATs); 2) 2018/2023 2nd cycle (10-year); 3) 2028/2033 3rd cycle (20-year); 4) 2038/2043 4th cycle (30-year). The forest and fuel parameter estimates from FVS were then used to create the necessary stand structure/fuel map layers required by the fire behavior models (Finney 2004, 2006).

We retained the tree lists generated by FVS for each scenario in order to estimate leaf area from basic inventory parameters. For each live tree, we applied a robust set of species-specific prediction models for the dominant species at our sites. These equations were based on an extensive sample of trees (n = 105) in the Sierran mixed conifer forests (Jones et al. 2015). Allometric equations using tree basal area as the primary variable to estimate whole tree leaf area (one-sided) produced excellent fits (generalized $R^2 > 0.95$ for all conifers). We combined the data from Jones et al. (2015) with allometric data for black oak from Gersonde (2003) and recalculated the allometric equations using basal area as the primary variable. However our result vary from Jones et al. (2015) in that we restricted the covariables to those that could be calculated from the tree lists produced by FVS. These revised equation predicted leaf area based on species, basal area, height, and crown length. In all cases, the fits had $R^2 \geq 0.87$. Individual tree leaf areas were summed and expressed as leaf area index (LAI), measured as the projected leaf surface area (one-sided) per unit of land surface area covered.

Fire Simulations

We employed a dual approach to model landscape-scale fire behavior (Table A1, Figure A6). For both approaches, we derived the necessary topographic inputs, slope, aspect, and elevation from the lidar data (Appendix B-Spatial in this report). Stand structure layers were derived from the FVS outputs for each stand: canopy cover, canopy base height (CBH), canopy height, and canopy bulk density. First, for the fire scenarios (1. with SPLATs and with fire; 2. without SPLATs and with fire), we used FARSITE v.4.1.005 (Finney 2004) to simulate a 'problem' forest fire based on the weather conditions during a recent wildfire (Table A1). FARSITE is a spatially explicit fire growth model that uses several topographic, forest structure, and fuel model map layers to project fire behavior parameters over a complex landscape. For wildfire weather conditions at LC, we used the 2001 Star Fire, which burned 16,838 ac (6,817 ha), including 776 ac (314 ha) on the northeast edge of the study area. Approximately 39% of this fire burned at high severity (www.mtbs.gov; accessed on 4 February 2015). For SP, we used the 2014 French Fire, which burned 13, 837 ac (5,602 ha) approximately 12.5 mi (20 km) southeast of the study area (fire severity data not available). We obtained weather information from the Duncan Peak and Batterson Automated Weather Stations (RAWS) for LC and SP, respectively. We used 95th percentile fuel moistures, as these are the conditions associated with large fire growth and difficulty in control (Table A2). The simulation duration was set to allow the fire perimeter to expand through the entire study area. Crown fire using the Scott and Reinhardt (2001) method was enabled, as well as spot-fire growth with an ignition frequency of 2% and a two-minute ignition delay. FARSITE fire behavior outputs (i.e., flame lengths and fire type) were used to simulate fire effects (i.e., changes in forest structure through tree mortality and fuel consumption) in FVS-FFE.

Table A1: Overview of the approach for landscape-scale fire behavior simulations.

Fire model	**Purpose**	**Scenarios**	**Outputs**
FARSITE	Model fire behavior during a single 'problem' wildfire	No SPLATs (2008 pre-treatment data), SPLATs (2013 post-treatment data)	Flame lengths, Fire type
FlamMap	Model fire behavior during a 'problem' wildfire spread events	No SPLATs/No Fire: 2008 pre-treatment (0-yr), modeled forest conditions in 2018 (10-yr), 2028 (20-yr), and 2038 (30-yr) No SPLATs/Fire: modeled forest conditions in 2018(10-yr) following modeled wildfire (FARSITE), 2028 (20-yr), and 2038 (30-yr) SPLATs/No Fire: 2013 post-treatment (0-yr), modeled forest conditions in 2023 (10-yr), 2033 (20-yr), and 2043 (30-yr) SPLATs/Fire: modeled forest conditions in 2023 (10-yr) following modeled wildfire (FARSITE), 2033 (20-yr), and 2043 (30-yr)	Conditional burn probability (flame lengths > 6 ft (2 m)), Fire size

This approach of using a single simulated fire for each treatment scenario (with and without treatment) limits inference that can be drawn from these results due to potentially different fire spread and behavior associated with different ignition locations. We used a single fire in order to obtain specific predictions on how fire would impact forest structure via tree mortality, as opposed to probabilistic predictions on fire occurrence at a specific location (e.g., Ager et al. 2007). By having spatially explicit predictions of fire effects on forest structure, we were able to track the impacts of fire on owl habitat and make more direct assessments of owl demography over time.

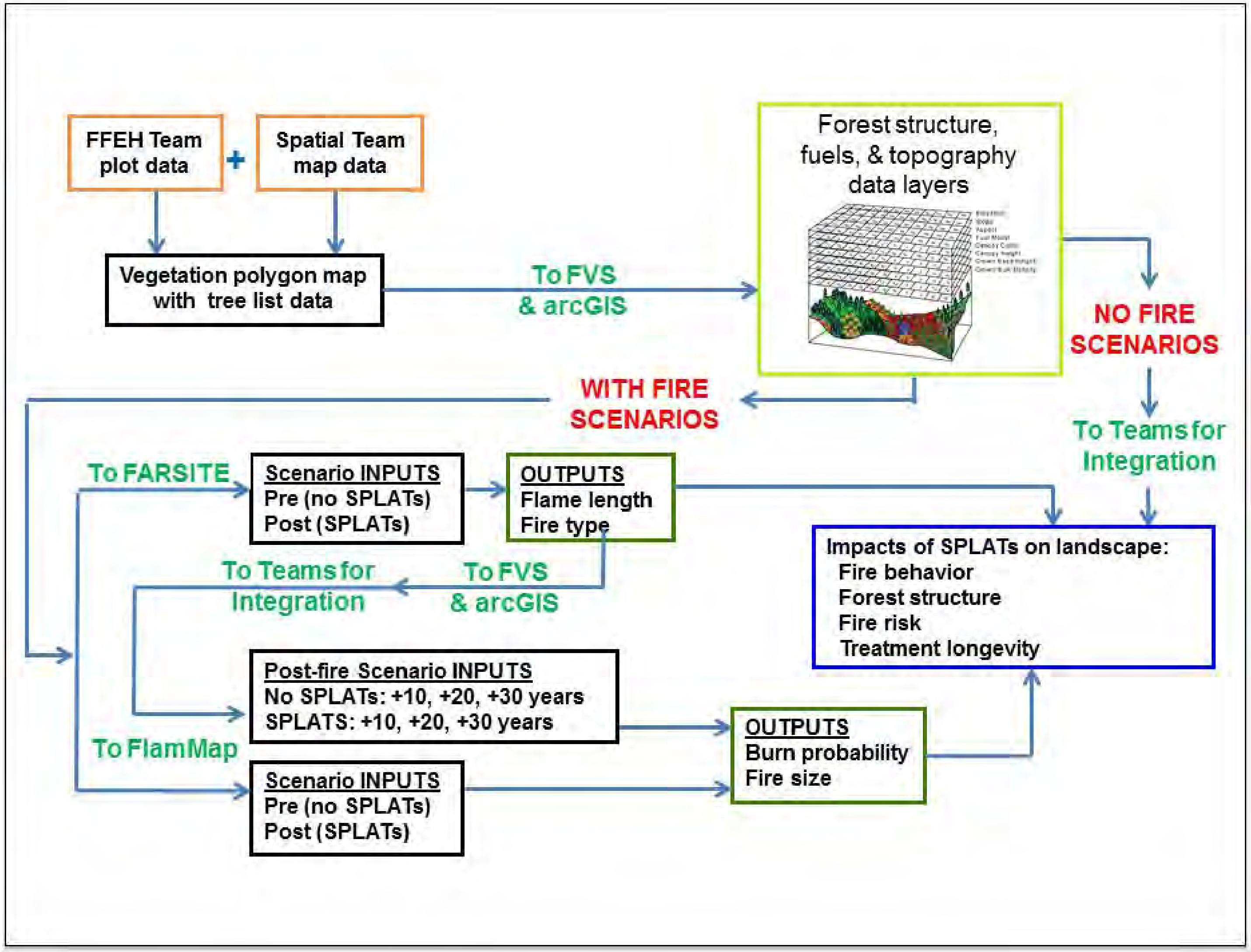


Figure A6: Flowchart of fire behavior and forest dynamics modeling.

Table A2: Weather parameters for fire simulations using FARSITE and RANDIG. We used 90th percentile and above winds (RANDIG only) and the 95th percentile fuel moistures (both simulations) for the predominant fire season in the area (June 1–September 30) based on data from one or more RAWS data near study sites.

	Last Chance	**Sugar Pine**
Temperature (°F)	54-93	59-99
Relative Humidity (%)	11-54	9-68
Wind (mph)	6.3 (3-13.5)	10 (3-20)
Wind direction	S-SW	SE, W
Fuel Moisture (%)		
1-hr	2	3
10-hr	3	4
100-hr	5	6
Live herbaceous	30	35
Live woody	60	65

To address the limitations associated with the single ignition approach, we employed a second fire modelling approach using a command-line version of FlamMap (Finney 2006) called RANDIG to model fires across both study areas to assess temporal changes in fire risk, thereby estimating the effectiveness of the SPLAT network at mitigating simulated fire effects, treatment longevity, and forest recovery. RANDIG uses the minimum travel time method (Finney 2002) to simulate fire spread based on a user-inputs for: number/pattern of ignitions, fire duration, wind speed and direction, fuel moistures, topography, stand structure, and fuels. We used the same stand structure layers as described in the first approach. In the absence of simulated ingrowth in FVS, stand CBH increases over time in untreated stands, which occurs at a rate that is difficult to justify ecologically, and results in an unrealistic decrease in fire risk in fire simulations (Collins et al. 2011, 2013). Instead, we used CBH-adjusted values as follows: initial stand CBH calculated in FVS used in 1st and 2nd cycle fire simulations, and 3rd cycle stand CBH calculated in FVS used in 3rd and 4th cycle. For each scenario and time step we simulated 10,000 randomly placed ignitions, burning for 240 and 360 minutes for LC and SP, respectively. This burn period duration was selected such that simulated fire sizes (for one burn period) approximated large-spread events (daily) observed in actual fires that occurred near the study areas (Ager et al. 2010). Given the limited number of wildfires from which to compare large spread events, especially for Sugar Pine, our burn period calibration represents a reasonable normative for large spread events in Sierra Nevada mixed-conifer forests (Collins et al. 2011).

For the weather information obtained from the Duncan Peak (LC) and the Batterson RAWS (SP), we restricted the analysis period to the dominant fire season for the area (June 1 – September 30). Observations were available from 2002 to 2009. We identified the dominant direction and average speed of all observations at or above the 90th percentile value. This resulted in several different dominant wind directions, each with its own wind speed and relative frequency (based on the proportion of observations recorded at or above the 90th percentile value for each dominant direction). We used 95th percentile fuel moistures, as these are the conditions associated with large fire growth and difficulty in control (Table A2).

Fuel Model Selection

To assign fuel models (Scott and Burgan 2005) to the pre- and post-treatment landscapes we analyzed relationships between fuels, shrub cover, and forest structure data collected from field plots. This approach was used for post-treatment fire simulations in Collins et al. (2011), where a selection logic was developed from regression trees and fuel models were assigned in consideration of the forest characteristics. Regression trees are ideal for such an analysis because they identify break values for predictor variables that can be used to repeatedly assign fuel models to stands. Statistical fits were moderate for each site (R^2=0.2–0.6), but were deemed appropriate for categorizing stands into discrete fuel models (Collins et al. 2011, 2013). The chosen fuel models for each terminal point in the selection logic was based on our familiarity with the study area and fire modeling, and input from local fire/fuel managers. Table A3 summarizes the fuel models used in the pre-treatment landscape.

A different selection logic was used for treated stands based on treatment type and time since treatment , as well as average flame length and fire type (percent of stand crowning) produced through FARSITE (first modeling approach described above) for the fire scenarios. Thinned stands that had reduced surface fuels through pile burning were left in the general selection logic. Stands that were thinned followed by mastication were assigned moderate load timber-litter model. Cable-logged stands (LC only) increased activity fuels and therefore were assigned a slash blowdown model. Masticated stands were assigned a moderate load timber-understory model, increasing to a high load timber-litter model in the second cycle. Stands that were underburned followed a progression of timber-litter fuel models but with slightly lower fuel loads. In the first fire modeling approach where all stands were burned, fuel model succession followed the methods of Davis et al. (2009). Post-burn fuel model assignment would be contingent on pre-burn fuel model, stand average flame length, and percent of the stand crowning.

Table A3: Pre-treatment fuel model assignments (Scott and Burgan 2005) and their proportion throughout both study areas. Fuel model selection logic was based on multiple regression tree analyses using stand-level data for dependent variables (shrub cover and fuel loads by category) and independent forest structure variables summarized using FVS.

Fuel model	**Description of stands with fuel model assigned**	**Last Chance**	**Sugar Pine**
SH3 (143)	Low basal area, low canopy cover, low stature shrub dominated fuels	0.155	-
SH5 (145)	Low basal area, low canopy cover, high stature shrub dominated fuels	0.054	0.044
TU2 (162)	Low basal area, high canopy cover	0.154	0.135
TU5 (165)	Moderate to high basal area, high tree density, moderate fuel load dominated by shrub and forest litter	0.318	0.451
TL3 (183)	Peavine Fire (2008) area	0.014	-
TL5 (185)	Low basal area, low canopy cover, moderate fuel load with coarse fuels present	-	.044
TL9 (189)	Moderate to high basal area, moderate to low tree density, moderate to low site productivity	0.042	.067
SB3 (203)	Moderate to high basal area, moderate to low tree density, high site productivity, moderate fuel load with coarse fuels present	0.263	0.26

Analytical Framework

To evaluate the effects of SPLATs, we used a before-after-control-impact study design (Stewart-Oaten et al. 1986). At each site, a control fireshed was paired with the treated fireshed. Measurements were made before treatments and after treatments. This framework accounts for temporal changes that are unrelated to the treatment and thus any observed differences between firesheds can be attributed to SPLATs. Formally, the impact of the treatment can be quantified as the difference in the response between sites observed over time:

$$\text{Treatment Impact} = (\mu_{ta} - \mu_{tb}) - (\mu_{ca} - \mu_{cb}) \qquad \text{Equation 1}$$

where μ is the mean of the response variable; c represents the control fireshed; a the period after treatments; b the period before treatments; and t the treated fireshed. A key assumption with this approach is that in absence of SPLATs, the differences between the sites would be constant (Stewart-Oaten et al. 1986). Note on usage: To improve clarity, we describe the "before" measurements as "pre-treatment" and the "after" as "post-treatment."

Plot-based summaries of pre- and post-treatment forest structure and surface fuels were produced for both sites, separated by control (untreated) and treatment types. Forest structure variables include canopy cover, tree density, and basal area, and shrub cover. For both fire modeling approaches, outputs of flame length, fire type, and conditional burn probabilities (both overall and proportional for 20 flame length classes [0 –10 m in 0.5 m increments]) were obtained for individual 30 m pixels, spanning the entire study areas. Conditional burn probabilities are computed by dividing the total number of times a pixel burned by the total number of simulated fires (n=10,000). To separate out more problematic simulated fire occurrence, both from a fire effects and a fire suppression standpoint, we only performed analysis on the burn probabilities for which modeled flame lengths were > 6.6 ft (2 m). Flame lengths > 6.6 ft typically correspond with crown fire initiation and present substantial challenges for suppression efforts (NWCG 2004). We imported flame length and conditional burn probability surfaces into ArcGIS software for further data analysis. For each of the four scenarios we computed overall mean flame length, fire type (percent of stand crowning), and conditional burn probability for each stand only using those pixels within the core study areas (i.e., stands within firesheds). We compared these outputs by stand (control vs. treated by type) and fireshed (control vs. treated).

Forest Health Assessment

Mortality was quantified by tracking the status of all tagged trees initially assessed as live in 2007 or 2008 in the re-measured 2013 plots. Harvested and masticated trees in the treated firesheds were noted. We calculated annual mortality (with and without harvested trees) after Sheil et al. (1995). Confidence intervals for mortality by fireshed were determined by profile likelihood (Wyckoff and Clark 2000).

The impact of treatments on forest structure and species composition was also assessed at the scale of the fireshed. Specifically, we used a two-factor analysis of variance (ANOVA) to test for differential changes (Equation 1) in forest structural characteristics (e.g., tree basal area, tree density, canopy cover) between control and treated firesheds. The interaction term in the ANOVA table served as the test of the statistical significance of the treatment effect (Smith 2002).

We developed histograms of tree-size based on dbh to document potential shifts in tree-size distributions (pre- to post-treatment) at each fireshed. Changes in size class were evaluated with a distribution departure index (Menning et al. 2007). This approach uses cumulative histograms to visualize overall trends and shifts in distributions. Specifically

$$M = \left(\frac{2}{k-1}\right)\sum_{i=1}^{k}\left[\left(\widehat{p_i} - \frac{f_i}{n_f}\right)(k+1-i)\right] \qquad \text{Equation 2}$$

Where k is the number of size classes; i designates the size class; f_i is the density of trees in size class i of the test distribution; n_f is the total tree density in the test distribution; and $\widehat{p_i}$ is the relative density in size class i in the reference distribution (Menning et al. 1997). The departure index is typically reported by stating the value and the range endpoints (e.g., –0.10 [-0.4 to 1.6]). The range endpoints refer to the possible changes in distribution depending on the type of reference distribution used. For example, if the reference distribution is symmetrical (e.g., a normal distribution), the possible departure index values will range from –1 to +1. However, if the reference distribution is asymmetrical (e.g., an inverse J-distribution with many smaller trees and fewer larger trees), the possible magnitude of any changes is also asymmetric. For an inverse-J distribution, there is the potential for a greater shift to the right than the left. A test distribution that has shifted to the right of the reference distribution will always have a positive value, while one that has shifted to the left will always display a negative value. The magnitude of the index indicates how far the test distribution has shifted. To statistically evaluate tree-size shifts from pre-measurement to post-measurement, we used a randomization approach with the pre-treatment size distribution serving as the reference (Menning et al. 2007). For each realization, the reference distribution was randomly shifted up to a maximum of 10% in either direction. We obtained 1,000 realizations and the 0.025 and 0.975 percentiles from their respective departure indices. These percentiles served as 95% confidence intervals. Observed changes that fell outside these bounds signified shifts of 10% or more in the tree-size distribution.

Tree species composition was quantified with relative basal area. The value for each species present in the fireshed was calculated as its mean relative basal area in every plot measured. Within-fireshed variance in dominance was expressed as the standard error of this mean.

Integration Analysis

An important goal of SNAMP was to provide an integrated assessment of the impacts of SPLATs not only on fire behavior but also on forest health, populations of spotted owl and Pacific fisher, water quality, and water quantity (Chapter 4). Thus we designed the four modeling scenarios described above: no fire and no SPLATs; fire and no SPLATs; no fire and SPLATs; fire and SPLATs. Initial parameters (pre-treatment and post-treatment) were defined using our field data with models extended for 30 years. In the fire scenarios, one explicit “severe” wildfire was modeled immediately after the field measurements (time = 0.1 yr). To ensure consistency, all results were reported for 10 year time intervals from Year 0 to Year 30 at the spatial scale of the fireshed. To keep the analysis succinct, each team was charged to select one informative "integration metric." For fire behavior, we used the conditional burn probability (described above, see **Fire Simulations**). For forest health, we defined two different metrics: one for scenarios without simulated fire and one with simulated fire.

Tree growth has proven to be a reliable indicator of tree survivorship in these forests (Das et al. 2007, Battles et al. 2008, Collins et al. 2014) and overall a robust indicator of forest health

(Tierney et al. 2009). In this context, forest health is narrowly defined in terms of the growth of canopy-sized trees. It is an admittedly narrow definition, but forest health in all its complexity is difficult to capture. We can measure the performance of trees. Therefore for the integration analysis, our fundamental premise is that "healthy" trees are necessary components, but are not sufficient to comprise a "healthy" forest. However, growth rate by itself is not an ideal measure in the no-fire scenario because of its mutual dependence on individual traits (e.g., tree size, tree age) and community characteristics (e.g., tree density, soil fertility, moisture regime). Waring (1983) argued that a good index of forest health is the efficiency with which a stands grows. Growth efficiency (GE) was defined as the increment in stand basal area produced per unit leaf area. Specifically:

$$\text{Growth efficiency} = \frac{\text{Basal area}_{\text{time 1}} - \text{Basal area}_{\text{time 0}}}{\text{mean}(\text{LAI}_{\text{time 1}}, \text{LAI}_{\text{time 0}})} \qquad \text{Equation 3}$$

where time 0 refers to the starting conditions, time 1 refers to conditions ten years in the future, basal area is the cross-sectional area of trees per unit area, and LAI is the leaf area index. For the fire scenario, we used the rate of return to pre-fire basal area to quantify forest health differences between treatment and no-treatment. Specifically for each post-fire interval, we reported the "fraction retained" of the pre-fire (Year 0) basal area. Since the basal area response was reported on a relative scale, we expressed growth efficiency relative to the maximum efficiency observed for the no-fire scenario.

RESULTS

Fuel Treatments and Changes in Forest Structure

Pre-treatment forest structure varied between the two sites (Table A4). In general, the mixed conifer forests at SP had more late-seral characteristics including high basal area (242 ft^2/ac), dense canopy cover (70%), and tall trees (92 ft). Compared to LC, basal area at SP was 80% greater; the canopy was a third taller; and canopy cover was 46% higher on average. The more open structure at LC supported more trees (i.e., higher tree density) and almost double the shrub cover (Table A4).

Table A4: Pre-treatment forest structure at the two study sites. Results based on pre-treatment measurements were made in 2007 and 2008. Only plots on the core sampling grid were included. Basal area was calculated for all live trees ≥ 2 in in diameter at breast height (dbh); density was calculated for live trees ≥ 2 in dbh; canopy cover was defined as tree cover ≥ 6.6 ft; tree height includes all live trees ≥ 2 in dbh; shrub cover excludes cover from trees < 6.6 ft tall. Means are reported with standard errors in parentheses. Results include plots with no trees present.

Site	**Basal Area** (ft^2/ac)	**Density** (stems/ac)	**Canopy Cover** (%)	**Tree Height** (ft)	**Shrub Cover** (%)
Last Chance	133 (5.9)	252 (12)	48 (1.9)	47 (1.1)	43 (1.5)
Sugar Pine	242 (11.0)	218 (13)	70 (1.8)	63 (1.9)	26 (2.8)

There were three main types of fuel reduction treatments: thinning, mastication, and prescribed fire. In the treated fireshed at Last Chance, SPLATs occurred on 18.4% of the area; considerably more area was treated at Sugar Pine -- 29.3% (Table A5). Thinning at LC was separated into two types, tractor thinning and cable logging, based on harvest prescriptions and subsequent post-treatment fuel conditions. Some tractor thinning units at SP were followed by mastication, which removes small trees and shrubs, converting ladder fuels to surface fuels. At the time of our re-measurement (2013) at SP, no prescribed fire treatments had been implemented.

For all surface fuels categories, pre-treatment plot averages were higher at SP compared to LC (Table A6, Table A7). Although treatment area was more extensive at SP (Table A5), treatments tended to be more intensive at LC. As results, we observed greater changes in fuels and forest structure variables (e.g., litter, woody fuels, canopy cover, tree density, and basal area) for a given treatment type at LC (Table A6, Table A7, Figure A7). Plots in cable logging units had to be relocated, prohibiting direct comparisons of pre- and post-treatment plot measurements. For plots that were in masticated units, shrub cover decreased by 50% at LC and only 10-15% at SP (Figure A7).

Table A5: Cumulative area treated (ac, [% of total watershed area]) for all treatment watersheds, separated by treatment type.

Type	**Last Chance**	**Sugar Pine**
Mastication	348 (3.1)	217 (3.5)
Thinning	915 (8.3)	1298 (20.7)
Cable Logging	193 (1.7)	-
Thinning+Mastication	-	328 (5.2)
Prescribed burn	577 (5.2)	-
Total	2033 (18.4)	1843 (29.3)

Table A6: Average (1 standard error) of surface fuels (tons ac^{-1}) and shrub cover, by treatment type, collected from plots in the Last Chance study area. C-thin, cable logging.

	Control	**Burn**	**Mastication**	**Thinning**	**C-thin**
	Pre-treatment				
Litter	7.7 (0.3)	8.2 (1.4)	3.5 (0.8)	11.0 (0.1)	4.7 (0.3)
Litter + 1-hr	7.9 (0.3)	8.4 (1.4)	3.6 (0.7)	11.2 (0.1)	4.9 (0.3)
1000-hr	10.8 (1.3)	2.8 (0.8)	1.9 (1.7)	13.7 (0.3)	17.7 (15.0)
1–1000-hr	13.1 (1.4)	5.4 (1.2)	3.3 (1.7)	16.9 (0.3)	22.0 (14.9)
Total	37.3 (1.9)	28.7 (4.8)	12.5 (2.9)	49.1 (0.4)	41.9 (13.3)
Fuel depth (in)	1.4 (0.1)	1.2 (0.1)	0.6 (0.2)	1.7 (0.0)	2.2 (0.0)
Shrub cover (%)	45.6 (1.5)	37.0 (9.8)	50.3 (9.8)	24.0 (0.4)	42.5 (4.2)
Shrub height (ft)	2.4 (0.1)	1.6 (0.4)	2.3 (0.4)	1.1 (0.0)	1.6 (0.4)
	Post-treatment				
Litter	6.7 (0.3)	5.3 (1.2)	4.3 (0.6)	6.6 (0.1)	22.0 (17.3)
Litter + 1-hr	7.0 (0.3)	5.5 (1.2)	4.5 (0.6)	6.8 (0.1)	22.2 (17.4)
1000-hr	10.0 (1.2)	3.5 (1.5)	4.4 (3.8)	8.2 (0.2)	3.4 (1.7)
1–1000-hr	14.0 (2.4)	6.1 (1.8)	6.5 (3.9)	12.3 (0.2)	7.4 (1.9)
Total	42.2 (3.1)	32.6 (5.7)	23.2 (4.3)	44.9 (0.4)	94.0 (46.1)
Fuel depth (in)	1.5 (0.1)	1.1 (0.3)	1.1 (0.2)	1.8 (0.0)	4.4 (1.8)
Shrub cover (%)	46.5 (2.5)	42.4 (9.5)	26.9 (8.1)	12.3 (0.3)	0.7 (0.7)
Shrub height (ft)	2.2 (0.1)	1.3 (0.2)	1.8 (0.8)	0.9 (0.0)	0.2 (0.2)

Table A7: Average (1 standard error) of surface fuels (tons ac^{-1}) and shrub cover, by treatment type, collected from plots in the Sugar Pine study area. Thin+Mast, thinning followed by mastication.

	Control	**Mastication**	**Thinning**	**Thin+Mast**
	Pre-treatment			
Litter	12.0 (2.1)	11.2 (2.7)	21.4 (3.0)	15.7 (2.3)
Litter + 1-hr	12.1 (2.2)	11.3 (2.7)	21.5 (3.0)	15.8 (2.2)
1000-hr	13.4 (6.2)	5.3 (1.8)	14.1 (5.4)	9.4 (2.3)
1–1000-hr	25.4 (10.4)	9.0 (2.7)	21.4 (7.2)	17.9 (3.8)
Total	65.7 (14.2)	37.0 (7.0)	72.4 (9.9)	65.8 (6.9)
Fuel depth (in)	2.0 (0.4)	2.3 (0.7)	3.3 (0.5)	2.4 (0.4)
Shrub cover (%)	25.1 (7.4)	39.6 (6.9)	20.1 (6.9)	20.3 (7.1)
Shrub height (ft)	3.0 (0.7)	7.0 (0.8)	2.6 (0.7)	3.9 (0.6)
	Post-treatment			
Litter	11.0 (2.5)	9.6 (1.6)	13.1 (2.1)	12.2 (2.3)
Litter + 1-hr	11.1 (2.5)	9.9 (1.6)	13.4 (2.1)	12.4 (2.3)
1000-hr	12.6 (5.0)	9.1 (4.4)	18.0 (10.2)	16.5 (7.1)
1–1000-hr	19.0 (7.3)	14.5 (4.5)	23.8 (10.3)	21.0 (6.7)
Total	60.9 (11.1)	43.8 (5.7)	72.5 (13.8)	72.1 (14.9)
Fuel depth (in)	2.3 (0.6)	2.4 (0.5)	3.3 (0.8)	4.0 (1.2)
Shrub cover (%)	27.6 (7.4)	24.1 (8.0)	15.8 (5.3)	9.1 (4.2)
Shrub height (ft)	2.3 (0.5)	2.9 (0.9)	1.4 (0.3)	2.7 (0.6)

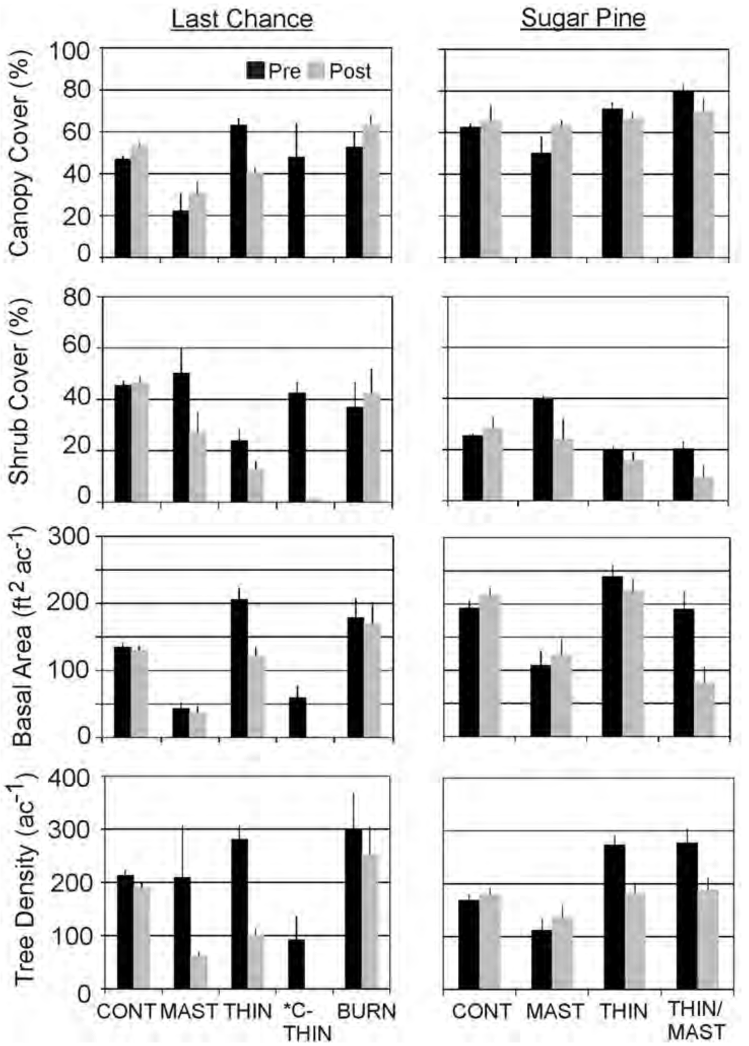


Figure A7: Changes in forest structure by treatment type at both SNAMP study sites. Results based on pre- and post-treatment forest inventory plot measurements. Tree density and basal area are for trees with diameters > 2 in. CONT, control; MAST, mastication; THIN, thinning; C-THIN, cable logging; THIN/MAST, thinning followed by mastication; BURN, prescribed fire. *Only two plots were located in cable logging units and these had to be relocated for post-treatment measurements, prohibiting direct comparisons to pre-treatment measurements.

From 2007-08 to 2013, the mortality rate of overstory trees (dbh ≥ 7.67 in) in the control firesheds ranged from 1.57%/yr (95%CI: 1.2 – 2.0 %/yr) at LC to 1.05%/yr (95%CI: 0.6 to 1.7%/yr) at SP (Figure A8). The implementation of SPLATs significantly increased (based on non-overlap of 95% CI) the death rate in treatment firesheds by about 1.2 percentage points at each site. This increase can be directly attributed to SPLATs and not background differences between control and treatment firesheds. When harvest removals were excluded in the calculation of mortality in the treatment firesheds, we obtained values indistinguishable from controls (Figure A8).

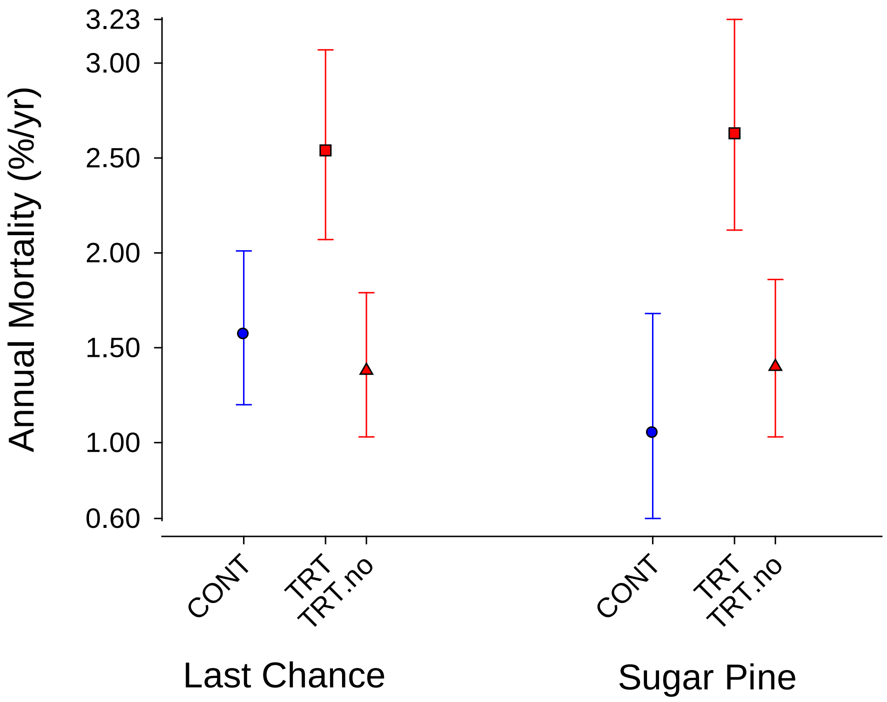


Figure A8: The mean annual mortality rate of overstory trees (dbh ≥ 7.67 in) in the control and treated plots at the SNAMP study sites in the Sierra Nevada, CA. Rates were calculated by tracking the fate of tagged trees between 2007-08 and 2013 inventories. Only trees in the plots from the core grid were included to ensure a representative sample. CONT refers to the control firesheds; TRT refers to the treatment firesheds; TRT-no is the mortality rate in the treatment firesheds if harvested trees are excluded from consideration. Error bars represent 95% confidence intervals.

The higher mortality rate in the treatment firesheds translated into net reductions in tree basal area and tree density in the treatment firesheds (Table A8, Table A9). For both basal area and density, the magnitude of forest structural changes was smaller in the control firesheds than in the treatment firesheds. At Last Chance, the treatments led to an approximate 10% net decrease in tree basal area and an 11% decrease in total (overstory + understory) tree density (Table A8). The emphasis on mastication treatments at SP was evident. The largest changes related to SPLATs at SP were a 15% net reduction in understory tree density and a 35% reduction in shrub cover (Table A9). Canopy cover and big tree density (defined as trees that serve as critical habitat elements for spotted owl and Pacific fisher, Chapter A4) barely changed between control and treatment firesheds at either site (Table A8, Table A9).

It is important to note that despite the documented treatment effects at the plot and fireshed level, none of the treatment impacts (Equation 1) reported in Table A8 and Table A9 were statistically significant ($p \leq 0.05$) based on test of the interaction term in the full-factorial analysis of variance (Smith 2002). In other words, we did not detect a SPLATs effect on forest structure in the treated firesheds compared to the changes with time in the control firesheds. At the standard of $p \leq 0.1$ level, treatment impacts on shrub cover at Sugar Pine were significant.

Forest Health

There were no changes in tree size distribution in pre-to-post treatment greater than 10% in any of the firesheds. At all sites, tree density declined exponentially with size class (Figure A9, Figure A10). The largest shift from this reverse-J shaped distribution was observed in the control fireshed at LC (Figure A9A). The post-treatment size distribution is less concentrated in the small diameter classes that the pre-treatment distribution. Such a shift results in a departure index (M) = 0.30 [min-max: -0.36; 1.64]. However, this move toward a more uniform size distribution was still within the 95% CI of a 10% change: M (95%CI) = -0.14; 0.37.

Table A8: SPLATs treatment impact on forest structure at the Last Chance site. Results based on forest inventories. Pre-treatment measurements were made in 2007 and 2008. Post-treatment measurements were made in 2013. Only plots on the core sampling grid were included. Basal area was calculated for all live trees ≥ 2 in in diameter at breast height (dbh); overstory density was calculated for live trees ≥ 7.67 in dbh; understory density was calculated for live trees trees ≥ 2 in dbh and < 7.67 in dbh; big tree density was calculated for live tree ≥ 28 in in dbh; canopy cover was defined as tree cover ≥ 6.6 ft. Means are reported with standard errors in parentheses. For change over time/treatment (Δ), the 95% confidence interval for the difference in means is reported in brackets. The estimate of treatment impact is the difference of means between control and treatment (Equation 2.1).

	Control Fireshed				**Treatment Fireshed**				**Treatment Impact**
	pre	**post**	**Δ**		**pre**	**post**	**Δ**		
Basal area (ft^2/ac)	138 (8)	134 (9)	-4 [-29; 20]		142 (8)	125 (8)	-18 [-45; 3]		-14 (17)
Overstory density (stems/ac)	76 (4)	73 (4)	-3 [-13; 8]		86 (4)	77 (4)	-9 [-20; 3]		-6 (8)
Understory density (stems/ac)	193 (15)	147 (12)	-46 [-84; -10]		241 (19)	169 (16)	-72 [-122; -23]		-26 (31)
Big tree density (stems/ac)	16 (1)	16 (1)	0 [-3; 4]		16 (1)	16 (1)	0 [-3; 4]		0 (2)
Canopy cover (%)	46 (1.7)	52 (1.9)	6 [-8.5; 1.2]		48 (2.1)	53 (2.2)	5 [-10.5; 1.7]		-1 (3.9)
Shrub cover (%)	46 (2.0)	45 (2.0)	-1 [-5.1; 6.0]		42 (2.1)	45 (4.9)	3 [-14.1; 7.7]		4 (5.8)

Table A9: SPLATs treatment impact on forest structure at the Sugar Pine site. Results based on forest inventories. Pre-treatment measurements were made in 2007 and 2008. Post-treatment measurements were made in 2013. Only plots on the core sampling grid were included. Basal area was calculated for all live trees $\geq$ 2 in in diameter at breast height (dbh); overstory density was calculated for live trees $\geq$ 7.67 in dbh; understory density was calculated for live trees trees $\geq$ 2 in dbh and $<$ 7.67 in dbh; big tree density was calculated for live tree $\geq$ 28 in in dbh; canopy cover was defined as tree cover $\geq$ 6.6 ft. Means are reported with standard errors in parentheses. For change over time/treatment (Δ), the 95% confidence interval for the difference in means is reported in brackets. The estimate of treatment impact is the difference of means between control and treatment (Equation 2.1).

	Control Fireshed				**Treatment Fireshed**				**Treatment Impact**
	pre	**post**	**Δ**		**pre**	**Post**	**Δ**		
Basal area (ft^2/ac)	265 (19)	267 (20)	2 [-53; 57]		231 (13)	223 (14)	-8 [-44; 29]		-10 (32)
Overstory density (stems/ac)	89 (7)	87 (7)	-2 [-22; 19]		125 (7)	114 (7)	-11 [-30; 8]		-9 (14)
Understory density (stems/ac)	100 (14)	103 (15)	3 [-40; 45]		158 (15)	137 (14)	-21 [-62; 19]		-24 (31)
Big tree density (stems/ac)	23 (2)	23 (2)	0 [-4; 6]		17 (1)	18 (2)	1 [-3; 5]		1 (3)
Canopy cover (%)	68 (2.9)	69 (3.1)	1 [-9.1; 7.6]		71 (2.3)	72 (2.7)	1 [-8.1; 6.1]		0 (5.6)
Shrub cover (%)	21 (4.1)	22 (4.4)	1 [-12.8; 10.9]		30 (3.8)	22 (3.4)	-8 [-2.1; 17.8]		-9 (7.9)

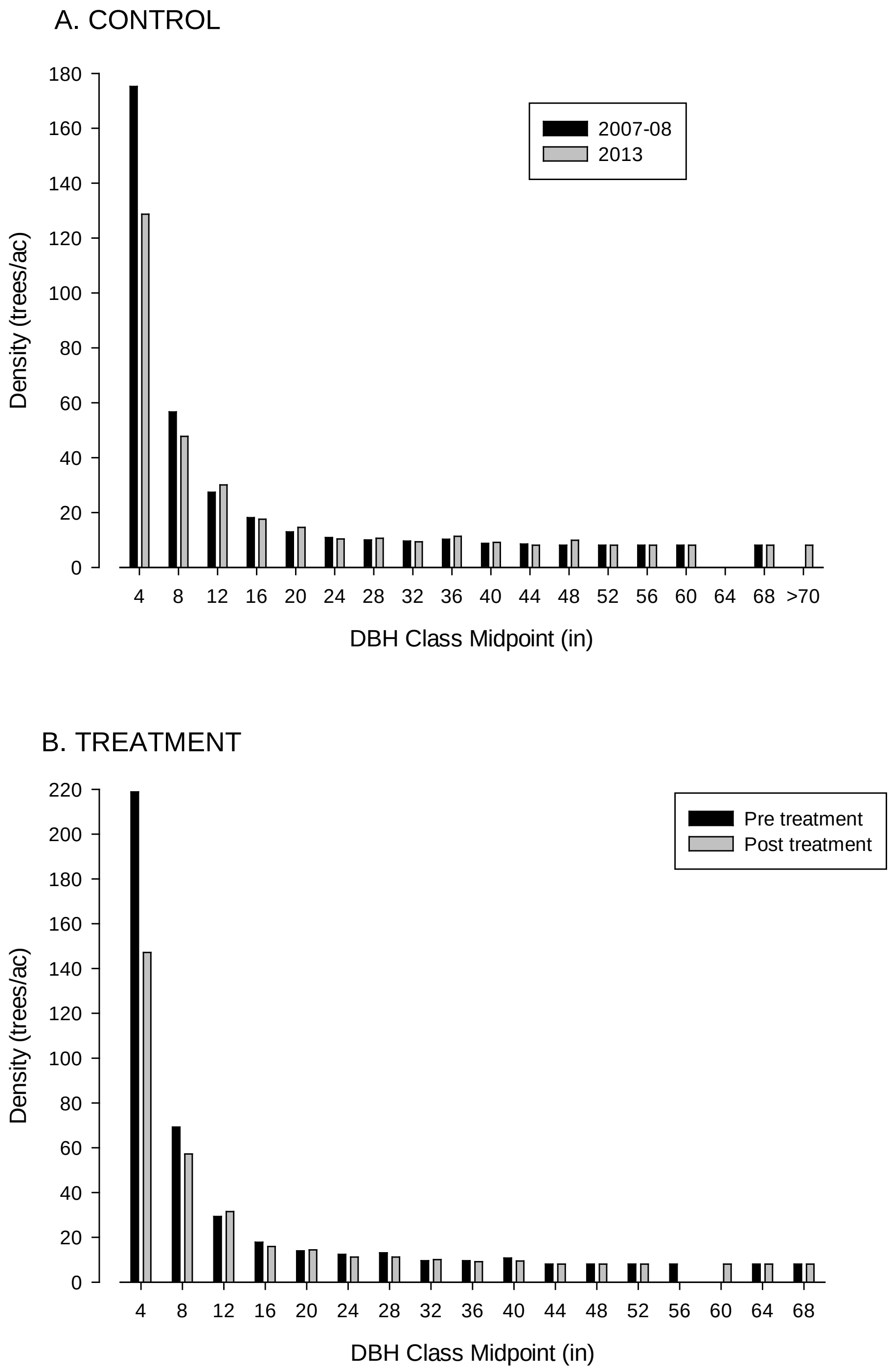


Figure A9: Changes in tree diameter distributions in the Last Chance site in the Sierra Nevada, CA. Pre-treatment results based on data from the 2007-08 inventory data collected from plots in the core grid. Post-treatment results based on data from 2013 inventory. DBH class represents 4-in dbh classes.

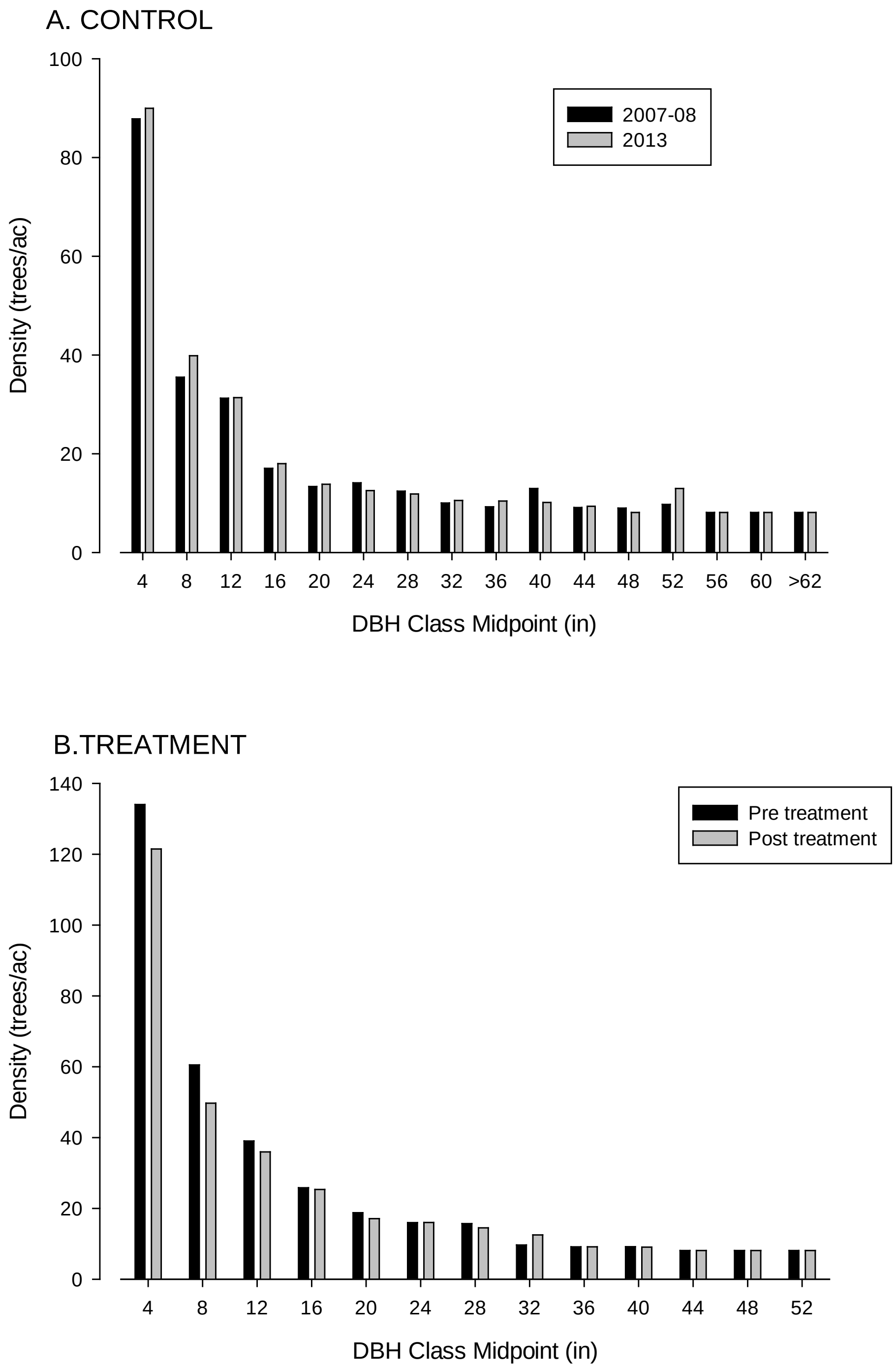
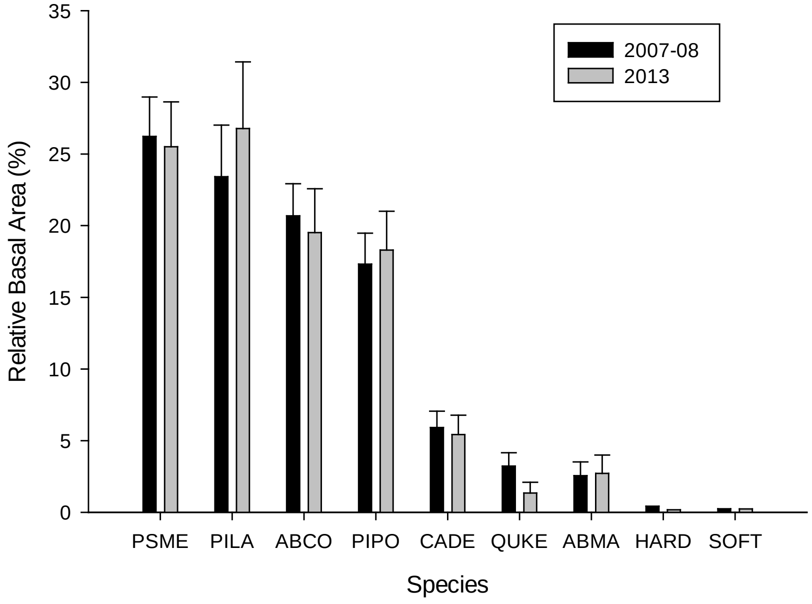


Figure A10: Changes in tree diameter distributions in the Sugar Pine site in the Sierra Nevada, CA. Pre-treatment results based on data from the 2007-08 inventory data collected from plots in the core grid. Post-treatment results based on data from 2013 inventory. DBH class represents 4-in dbh classes.

All the firesheds were dominated by tree species representative of the mixed conifer forest (Fites-Kaufman et al. 2007). While there was variation in species dominance between LC and SP and between control and treatment firesheds (Figure A11, Figure A12), implementation of SPLATs resulted in only modest changes in composition. At LC, the largest shift related to treatments was a 14% decrease in white fir (ABCO) with corresponding increases of 16% in ponderosa pine (PIPO) and 12% in sugar pine (PILA) (Figure A11). At SP, the fuel treatments reduced the relative basal area of the most dominant species in the fireshed -- incense-cedar (CADE) -- by 7% (Figure A12). White fir and black oak (QUKE) both increased by 9%.

A. Control



B. Treatment

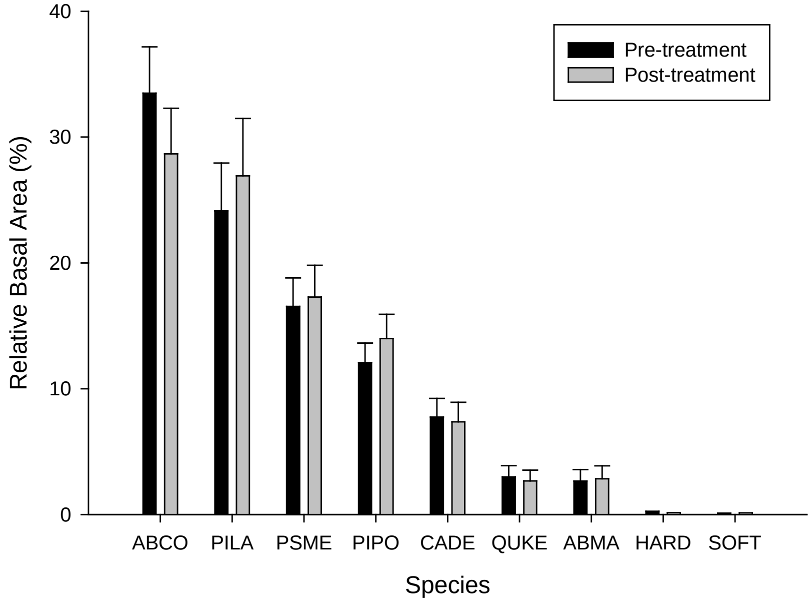
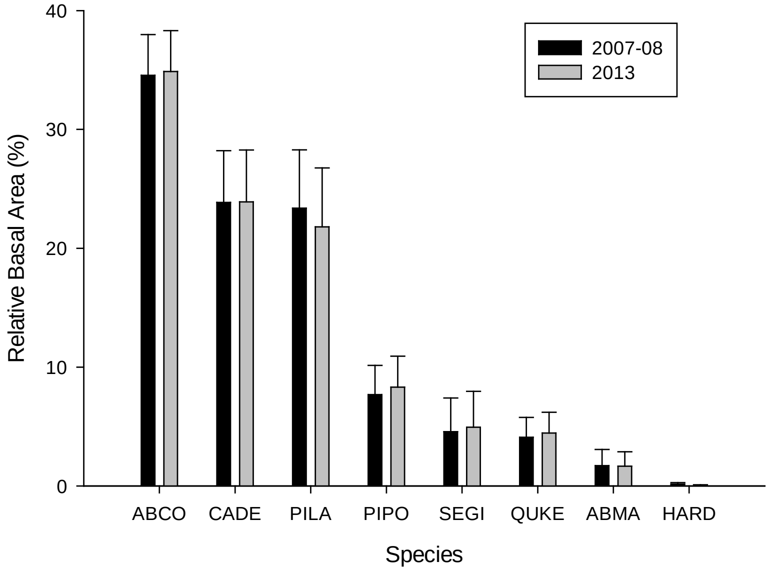


Figure A11: Changes in tree species composition in the Last Chance site in the Sierra Nevada, CA. Pre-treatment results based on data from the 2007-08 inventory data collected from plots in the core grid. Post-treatment results based on data from 2013 inventory. Means with standard errors reported. Species codes: ABCO, white fir (*Abies concolor*); ABMA, California red fir (*A. magnifica*); CADE, incense-cedar (*Calocedrus decurrens*); PILA, sugar pine (*Pinus lambertiana*); PIPO, ponderosa pine (*P. ponderosa*); PSME, Douglas-fir, (*Pseudotsuga menziesii*); QUKE, black oak (*Q. kelloggii*); HARD, other hardwood species; SOFT, other conifer species.

A. Control



B. Treatment

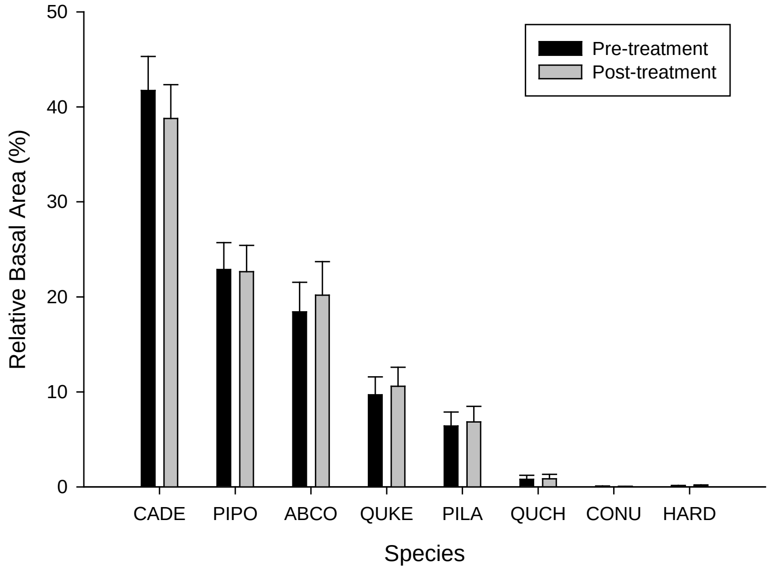


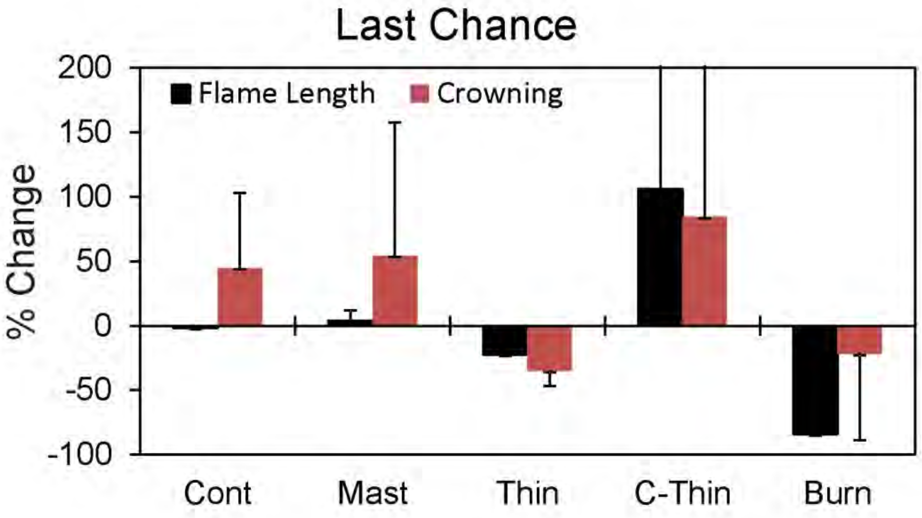
Figure A12: Changes in tree species composition in the Sugar Pine site in the Sierra Nevada, CA. Pre-treatment results based on data from the 2007-08 inventory data collected from plots in the core grid. Post-treatment results based on data from 2013 inventory. Means with standard errors reported. Species codes: ABCO, white fir (*Abies concolor*); ABMA, California red fir (*A. magnifica*); CADE, incense-cedar (*Calocedrus decurrens*); CONU, mountain dogwood, (*Cornus nuttallii*); PILA, sugar pine (*Pinus lambertiana*); PIPO, ponderosa pine (*P. ponderosa*); PSME, Douglas-fir, (*Pseudotsuga menziesii*); QUCH, canyon live oak (*Quercus chrysolepis*); QUKE, black oak (*Q. kelloggii*); SEGI, giant sequoia (*Sequoiadendron giganteum*); HARD, other hardwood species.

Fire Simulations

Despite similarities in weather and fuel moisture conditions (Table A2) and fuel model assignments (Table A3) used in the fire modeling, overall fire behavior tended to be higher at LC compared to SP. Differences are partly due to forest structure attributes; for example, average shrub cover and small tree density were higher at LC compared to SP (Table A4, Figure A7, Figure A9, Figure A10). FARSITE fire modeling showed that most treatments reduced flame length and fire type not only within the treated units (Figure A13), but also across the study areas (Figure A14). The largest decrease in average flame length was within prescribed fire (LC only) and thinning followed by mastication (SP only) treatment units. Cable logging at LC left activity fuels on site (Table A6), which resulted in a slash-blowdown fuel model being assigned, and consequently had higher post-treatment flame lengths and crowning. To estimate potential offsite effects from treatments we extracted FARSITE output pixel values within a 1,640 ft (500 m) buffer area outside treatment boundaries. There was a decrease of 23% and 44% in average flame length at LC and SP, respectively. Treatments were effective at decreasing the proportion of stand crowning in the buffer area by 51% at LC but not at SP (decrease of 1%).

Similarly, overall conditional burn probability (CBP; fire occurring with flame lengths > 6.6 ft) tended to be higher at LC (Figure A15) compared to SP (Figure A16). This was also reflected in the average fire size for either treatment scenario from the wildfire simulations (Year 0 in Figure A17). Topography and dominant wind direction influenced fire spread resulting in higher CBPs on the west side of the study area at LC and on the east side at SP.

There was a low to moderate decrease in hazardous fire potential (flame lengths > 6.6 ft) for the treatment fireshed relative to the control fireshed (Table A10). However, the effect of time (i.e., pre- to post-treatment changes in the control fireshed) was mixed; with decreases in both fire metrics at LC but only one at SP. Thus the treatment impact on hazardous fire potential varied with a greater reduction in the extent of the fireshed with flame lengths > 6.6 ft obtained for SP and a larger decrease in high conditional burn probabilities for LC (Table A10).



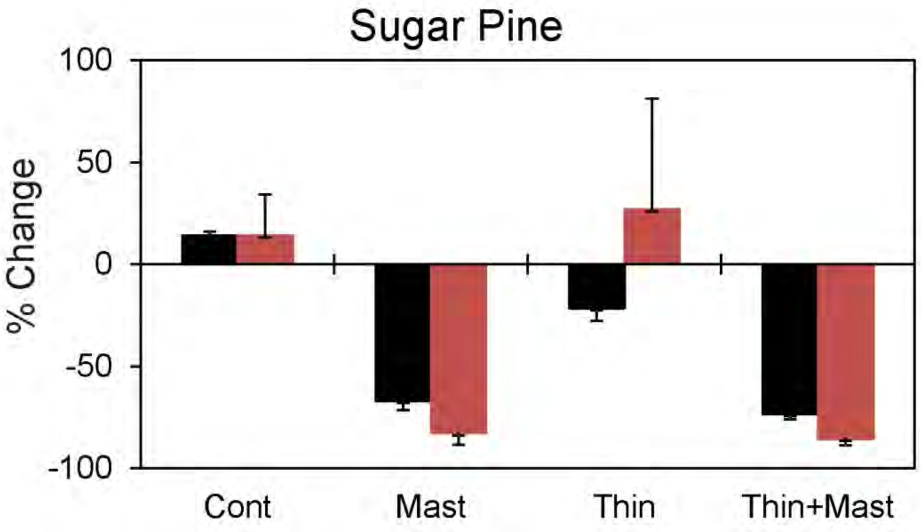


Figure A13: Changes in average flame length and proportion of the stand crowning by treatment type. Results based on comparisons of FARSITE pre- and post-treatment fire growth simulations. Cont, control; Mast, mastication; Thin, thinning; C-Thin, cable logging; Thin+Mast, thinning followed by mastication; Burn, prescribed fire.

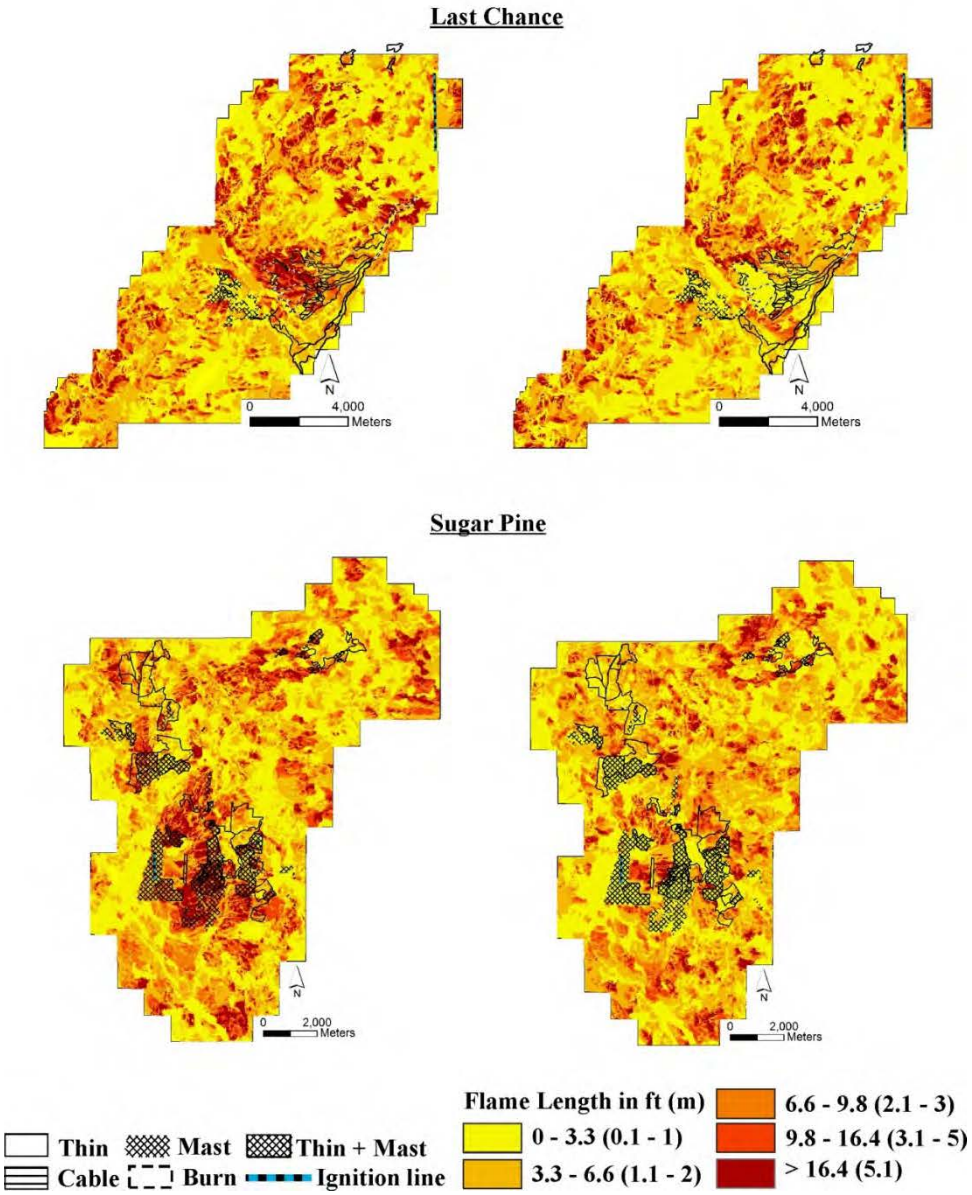
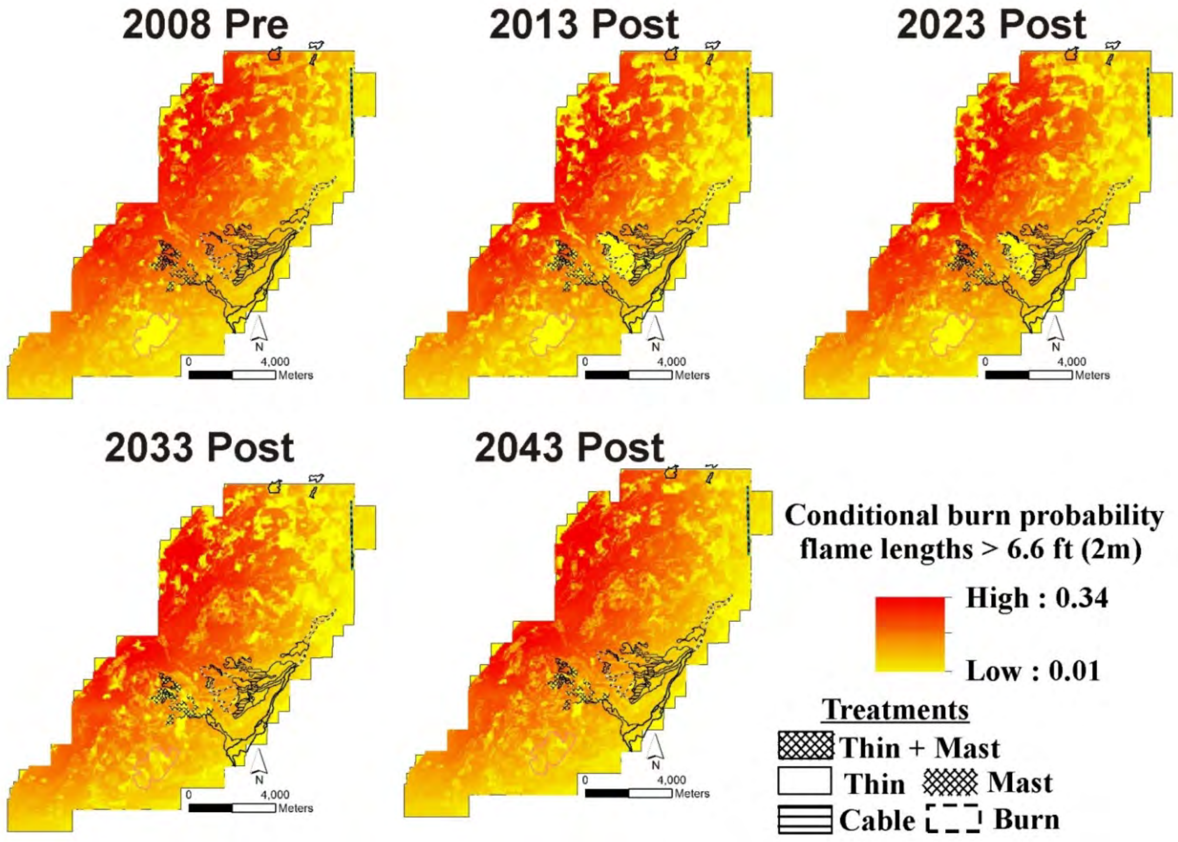


Figure A14: Simulated flame lengths for forest conditions pre- (left) and post-(right) implementation of SPLATs. Results based on FARSITE fire growth simulations. Models were parameterized with plot-level tree lists and scaled to stand polygons using vegetation map. The simulated wildfire occurs immediately after pre- and post-treatment plot measurements. Thin, thinning; Mast, mastication; Thin+Mast, thinning followed by mastication; Cable, cable logging; Burn, prescribed fire.

The lower post-treatment CBP relative to the pre-treatment scenario (2008) was evident across both study sites in 2023 and 2033, returning to pre-treatment levels by 2043 (Figure A15 and A16). Patterns of forest growth derived from the FVS showed either a leveling or continuous increase in most attributes, for both treatment scenarios, up to 30 years post-treatment (Figure A18, Figure A19). However, as indicated by the fire size comparisons (pre- and post-treatment without fire scenarios), the effects of SPLATs was negligible by 2033 at SP (Year 20 in Figure A17).



2008 Pre

2013 Post

2023 Post

2033 Post

2043 Post

Figure A15: Conditional burn probabilities for which flame lengths > 6.6 ft at Last Chance. Burn probabilities are reported for pre- and post-implementation of fuel reduction treatments as well as during 30 years of simulated forest growth. Estimates are based on 10,000 random ignitions under 90th percentile wind and fuel moisture conditions. Cable, cable logging; Thin, thinning; Mast, mastication; Burn, prescribed fire.

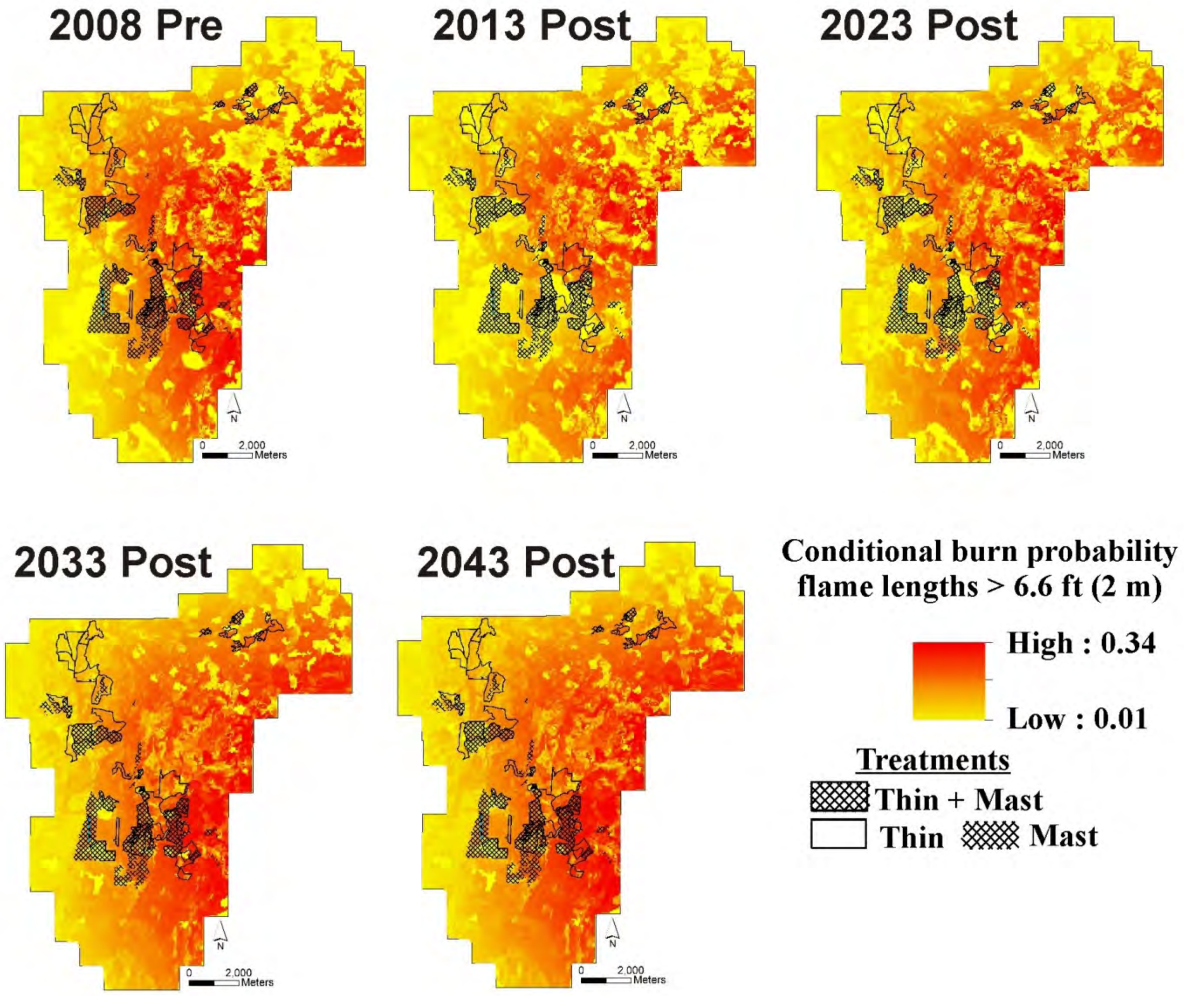


Figure A16: Conditional burn probabilities for which flame lengths > 6.6 ft at Sugar Pine. Burn probabilities are reported for pre- and post-implementation of fuel reduction treatments, as well as during 30 years of simulated forest growth. Estimates are based on 10,000 random ignitions under 90th percentile wind and fuel moisture conditions. Thin, thinning; Mast, mastication; Thin+Mast, thinning followed by mastication.

Incorporating effects of a wildfire and forest growth through FVS on both treatment scenarios show pronounced differences in recovery rates for most forest attributes (Figure A18, Figure A19), and therefore much different rates of change in CBP (CBP maps for fire scenarios not shown, see Figure A17). Following 30 years of forest growth in the fire scenario, the recovery towards pre-treatment averages was higher for the treatment scenario.

Table A10: Changes in fireshed-level fire behavior at both study sites. CBP, conditional burn probability for flame lengths > 6.6 ft (2 m).

Last Chance	**Control Fireshed**				**Treatment Fireshed**				**Treatment Impact**
	Pre	Post	**Δ**		Pre	Post	**Δ**		
Percentage of fireshed with flame lengths > 6.6 ft (2 m)	28.3	24.1	-4.2		32.9	22.5	-10.4		-6.2
Percentage of fireshed with CBP > 0.1	54.3	40.5	-13.8		59.3	40	-19.3		-5.5
Sugar Pine	**Control Fireshed**				**Treatment Fireshed**				**Treatment Impact**
	Pre	Post	**Δ**		Pre	Post	**Δ**		
Percentage of fireshed with flame lengths > 6.6 ft (2 m)	25	28.7	+3.7		29.3	25.3	-4		-7.7
Percentage of fireshed with CBP > 0.1	67.3	54.3	-13		29	12.3	-16.7		-3.7

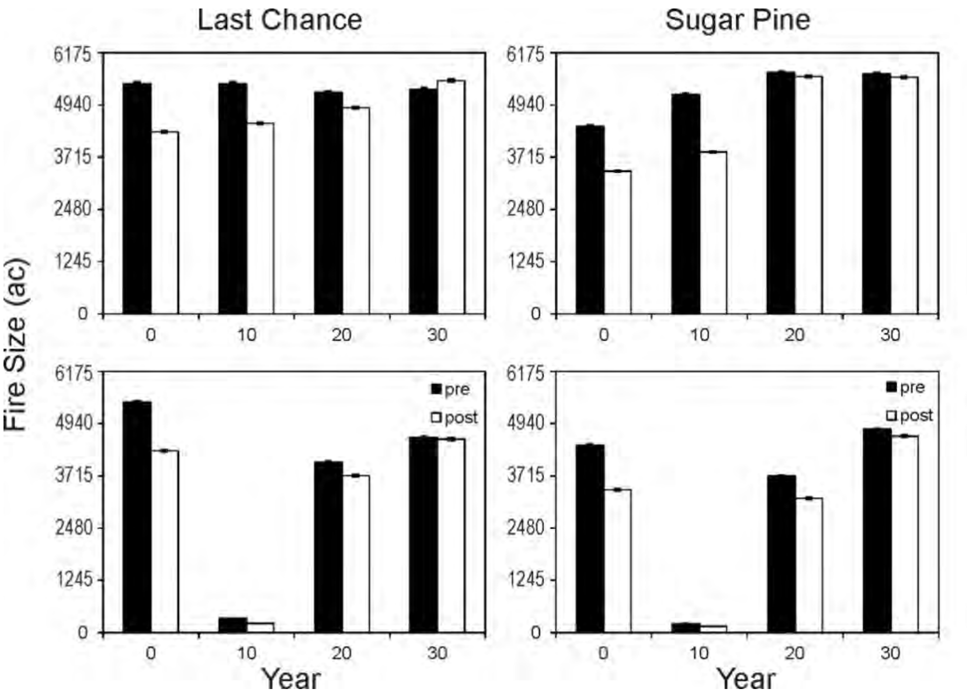


Figure A17: Average (1 standard error) fire sizes for wildfire simulations performed using RANDIG. Fire sizes are reported for all four treatment-fire scenarios (see Table A1), with pre- and post-implementation of fuel reduction treatments reflected at Year 0, and without (top) and with (bottom) incorporating the effects of a FARSITE wildfire simulation expressed at Year 10. The simulated fire occurs immediately after Year 0 is measured. For all four scenarios, RANDIG simulations were performed during 30 years of simulated forest growth. Estimates are based on 10,000 random ignitions under 90th percentile wind and fuel moisture conditions.

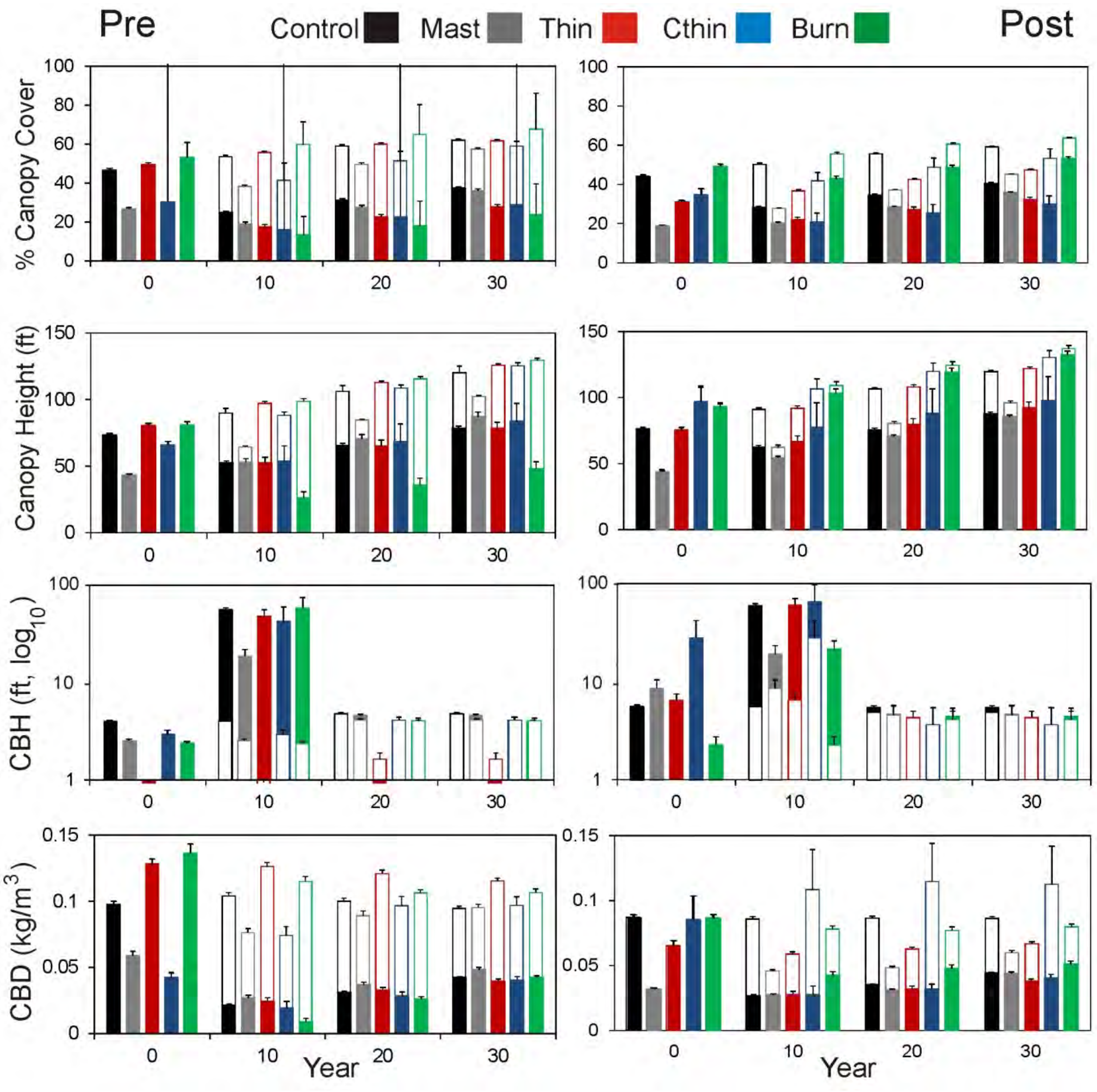


Figure A18: Average (one standard error) forest stand attributes, by treatment type, for all four fire-treatment scenarios at Last Chance. Treatment scenarios are pre- and post-implementation of fuel reduction treatments reflected at Year 0, combined with (filled bars) and without (open bars) incorporating the effects of a FARSITE wildfire simulation, with differences shown at Year 10. The simulated fire occurs immediately after Year 0 is measured. Attributes were calculated for each scenario during 30 years of simulated forest growth. Cable, cable logging; Thin, thinning; Mast, mastication; Burn, prescribed fire; CBH, canopy base height; CBD, canopy bulk density.

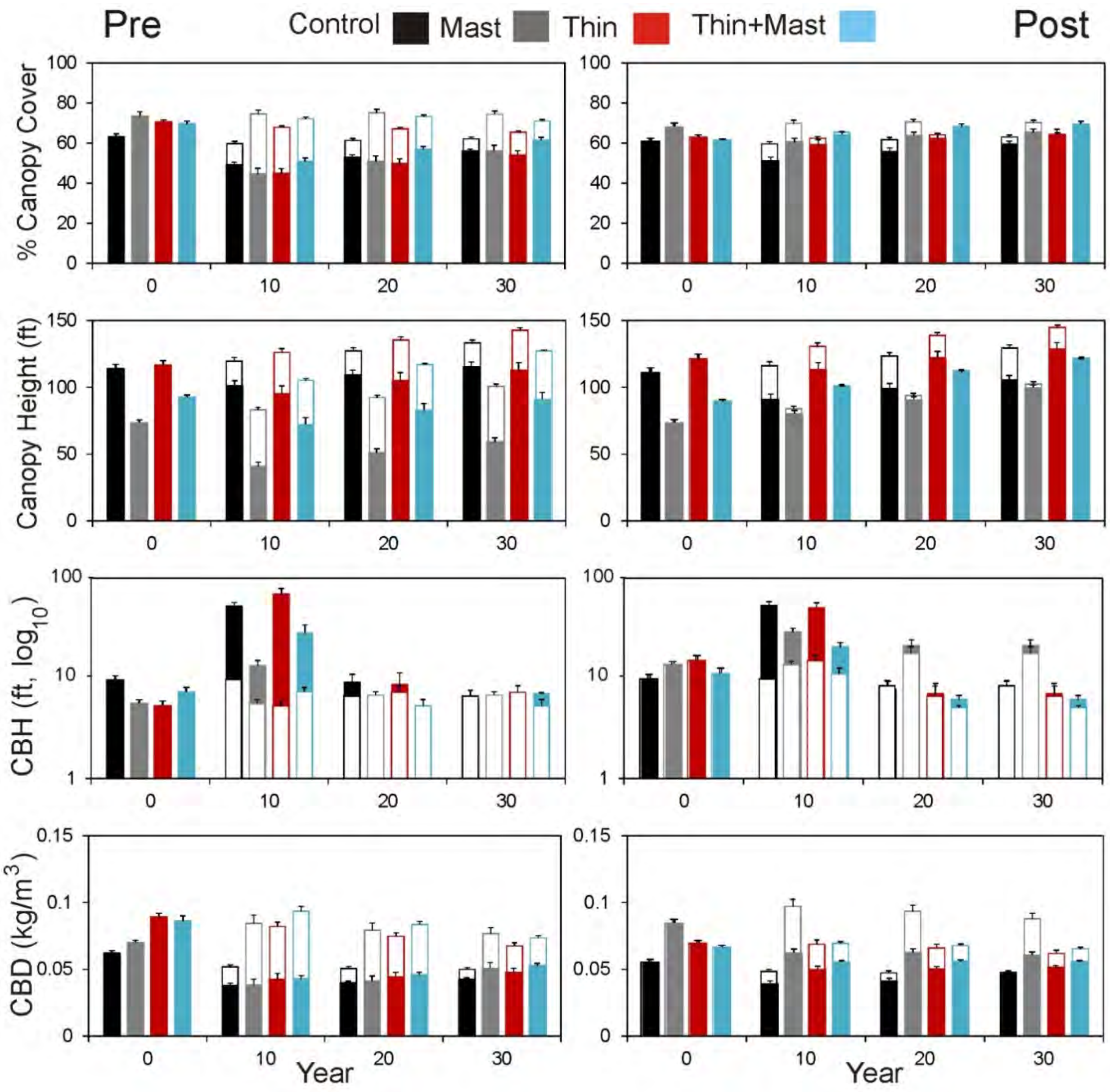


Figure A19: Average (one standard error) forest stand attributes, by treatment type, for all four fire-treatment scenarios at Sugar Pine. Treatment scenarios are pre- and post-implementation of fuel reduction treatments reflected at Year 0, combined with (filled bars) and without (open bars) incorporating the effects of a FARSITE wildfire simulation, with differences shown at Year 10. The simulated fire occurs immediately after Year 0 is measured. Attributes were calculated for each scenario during 30 years of simulated forest growth. Thin, thinning; Mast, mastication; Thin+Mast, thinning followed by mastication; CBH, canopy base height; CBD, canopy bulk density.

Integration

Pre-treatment crown fire potential was much higher at LC (Figure A20A) compared to SP (Figure A20B) in the treatment fireshed. The effect of SPLATs on CBP is evident at Year 0 (no fire scenario, blue bars in Figure A20), a 28% and 34% decrease at LC and SP, respectively. This difference wanes over time to only 2-4% by Year 30. Following essentially a zero CBP for either scenario immediately following simulated fire (red bars in Year 10), by Year 20 the recovery in CBP towards initial values (blue bars in Year 0) for the treatment scenario (light red bar) reached 67% at LC and 96% at SP. For the no treatment scenarios at Year 20 (stripe red bar) the recovery was slower, reaching 44% and 72% at LC and SP, respectively.

Overall the modeling results show consistent improvements in forest health with SPLATs. At both sites, a higher fraction of the pre-treatment basal area was retained (red bars) with SPLATs when there was a simulated fire (Figure A21). The treatment effect was greater at LC (Figure A21A). In Year 10 at LC, SPLATs reduced overall losses due to fire from 52% (no SPLATs, 0.48 fraction retained) to only 34% (with SPLATs, 0.66 fraction retained). As the forest grew, these differences were maintained through Year 30 (Figure A21A). In contrast, under the no-fire scenario, SPLATs improved growth efficiency more at SP. Between Year 0 and Year 10, growth efficiency was more than double with treatments (Figure A21B). At LC, small increases in growth efficiencies with SPLATs only emerged 20 years after the fire (Figure A21A). Despite the small relative improvement in growth efficiency at LC, in absolute terms trees at LC had a much higher growth efficiency. For example, at Year 10 in the untreated, no-fire scenario, growth efficiency at LC was 7.1 ft2/ac per unit leaf area. This efficiency was almost ten times greater than the rate at SP -- 0.8 ft2/ac per unit leaf area. Apparently, the relatively small changes in density and canopy cover associated with SPLATs lead to disproportionately large improvements in growth efficiency at the site that started with more basal area and higher canopy cover (Table A4).

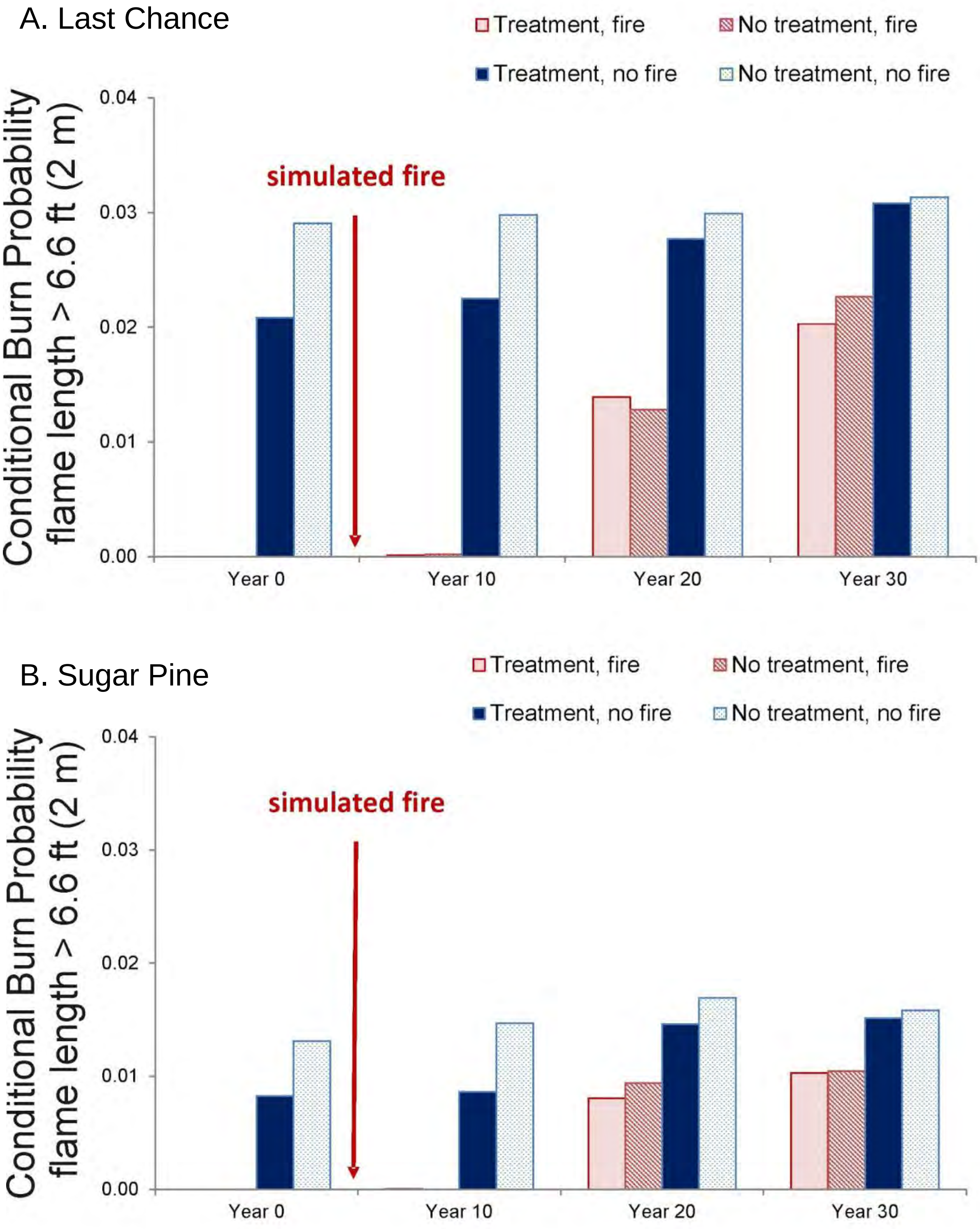
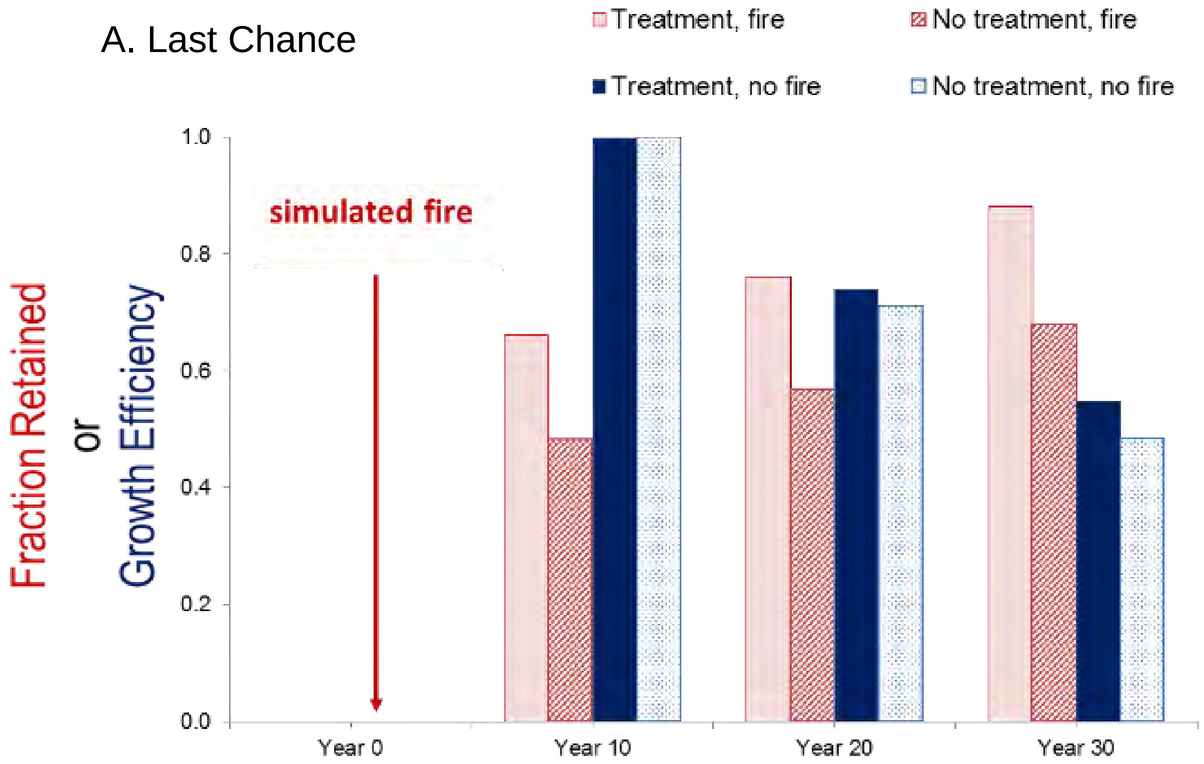


Figure A20: Changes in conditional burn probability by treatment and time. Results based on fire and forest growth simulations. Models were parameterized with plot-level tree lists and scaled to the fireshed using remote sensing. The simulated fire occurs immediately after Year 0 is measured. Results for the treated fireshed only.


A. Last Chance

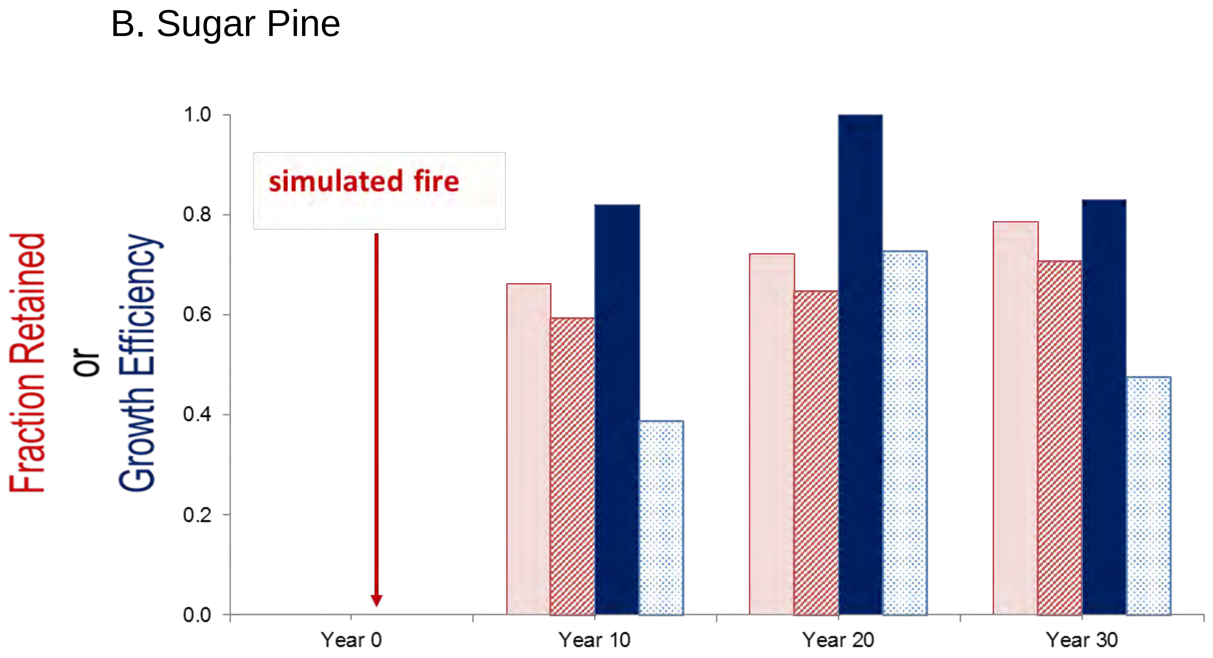

B. Sugar Pine

Figure A21: Trends in measures of forest health by treatment scenario. For the fire scenarios, forest health is expressed as the fraction of the Year 0 basal area that is retained (red bars). For the no fire scenarios, forest health is expressed as the relative growth efficiency (blue bars). The simulated fire burns immediately after Year 0 is measured. Results for the treated fireshed only.

DISCUSSION

Response to SPLATS

Our results demonstrate that SPLAT networks as implemented according to the Sierra Nevada Forest Plan Amendment (USFS 2004) do reduce the risk and effects of uncharacteristically severe fire. This conclusion is based on a fully implemented treatment project, with a detailed inventory plot network, incorporating simulated wildfire effects to model fire behavior and forest growth. Comparable studies of SPLATs on fire behavior in fire-frequent conifer forests support this conclusion (Ager et al. 2007, Moghaddas et al. 2010, Collins et al. 2011, 2013). Our results are also consistent with SPLAT theory (Finney 2001) in that fire behavior was reduced not only in treated areas but also across the landscape, particularly on the leeside of treatments (Weatherspoon and Skinner 1996, Collins et al. 2013). Fuel treatments that targeted both ladder and surface fuels (e.g., thinning and prescribed fire at LC, thinning followed by mastication at SP) were the most effective at reducing simulated fire behavior (Stephens et al. 2009, Moghaddas et al. 2010).

When we scaled our results via landscape imputation and simulation modeling, results suggest that SPLATs improved forest health as measured by the fraction of basal area retained (fire scenario) and growth efficiency (no-fire scenario). The increase in the fraction of basal area retained in the treated firesheds with a simulated problem fire (Figure A21) is the expected outcome given that SPLATs reduced the probability of trees being exposed to damaging flame lengths (Figure A20). In the no-fire scenario, ecological theory (e.g., Ford 1975) and forestry practice (e.g., Lemmon and Schumacher 1962) predict improved growth resulting from a reduction in tree density. Indeed we did detect absolute increases in growth. For example, at SP basal area increased in the treated fireshed at a rate of 0.89 ft^2/ac per year – a rate more than double that of the control fireshed (0.34 ft^2/ac per year). In contrast at LC, there was no treatment related increase in absolute basal area in the model results. Both LC firesheds grew fast at an average rate of 2.8 ft^2/ac per year. However, by focusing on growth efficiency as the measure of tree vigor, we did see improvements realized at both sites (Figure A21). As noted by Waring (1983) and supported by Zierel (2004), the ratio of foliage extent to tree growth is a sensitive indicator of tree vigor. Thus, the increase in growth efficiency at both sites implies that the trees in the treated firesheds are healthier and less susceptible to mortality agents (Waring 1985).

Fire

Based on our simulations, fuel treatment scale and intensity should have the capacity to modify landscape fire behavior at both sites for two to three decades. Last Chance has an overall higher fire risk compared to Sugar Pine as indicated by the higher fireshed-level CBP, which is attributed to differences in forest structure--Sugar Pine has lower tree density and higher basal area and canopy base height-- and management history. It appears that hazard in untreated areas continues to increase (Collins et al. 2013), which is also demonstrated empirically at the stand-level by Stephens et al. (2012). This increased hazard in untreated areas over time may reduce the overall effectiveness of the fuel treatment network. Although we do not model it, maintenance treatments that would reduce surface fuels, namely prescribed fire, would probably extend treatment longevity across both landscapes. This is especially true considering most of the treatments focused on reducing ladder fuels, resulting in augmented surface fuels or a negligible change compared to pre-treatment fuel conditions.

The overall 4% reduction in potential fire behavior after SPLATs were installed at the Sugar Pine site is small and does not reduce the potential for high severity fire as much as intended by the project. Since this southern Sierra Nevada site is within the Pacific Fisher's range the intensity of fuels treatments were limited. Almost no change in the forest canopy was detected and surface fuels were still moderate after treatment because of no use of prescribed fire mainly because of air quality constraints. Ladder fuels were the main component removed at this site which can lower the probability of passive crown fire (Agee and Skinner 2005, Stephens et al. 2009) but can still leave the overall landscape at relatively high risk to severe fire.

The overall goal of protecting the Pacific Fisher is logical but leaving large forested landscapes that are the core of its habitat with high fire hazards is likely to fail in the long-term, especially with warming climates. A recent paper that analyzed 1911 landscape-scale (> 25,000 acres) forest structure from mixed conifer and ponderosa pine forests in the southern Sierra Nevada found high heterogeneity in structure before the impacts of harvesting or fire suppression

(Stephens et al. 2015). In 1911, total tree basal area ranged from 4 – 261 ft^2 $acre^{-1}$ (1 to 60 m^2 ha^1) and tree density from 1 – 67 trees $acre^{-1}$ (2 - 170 ha^1)(based on trees > 12 inches dbh). Comparing forest inventory data from 1911 to the present indicates that current forests have changed drastically, particularly in tree density, canopy cover, the density of large trees, dominance of white fir in mixed conifer forests, and the similarity of tree basal area in contemporary ponderosa pine and mixed conifer forests. Average forest canopy cover increased from 25–49% in mixed conifer forests, and from 12–49% in ponderosa pine forests from 1911 to the present. Current forest restoration goals in the southern Sierra Nevada are often skewed toward the higher range of these historical values, which will limit the effectiveness of these treatments if the objective is to produce resilient forest ecosystems into the future, as was found in the Sugar Pine site. Allowing more of the mixed conifer forests in the Sugar Pine area to received treatments that produced forest structures similar to those found in 1911 would have reduced potential fire behavior more than the 4% observed in this study.

One of the main limitations in evaluating the effectiveness of landscape fuel treatments is the reliance on simulated fire behavior from a single fire. Recent studies have been critical of commonly used fire behavior modeling techniques (Alexander and Cruz, 2013). In particular, these and other studies (Hall and Burke, 2006) have noted a general under prediction of crown fire. Characterization of surface and ladder fuels, represented as surface fuel models and canopy base height in commonly used modeling software, are the most influential inputs determining predicted fire behavior (Hall and Burke, 2006). In addition to their importance in capturing static assessments of altered fuel conditions in treated areas (e.g., Moghaddas et al., 2010), surface fuel models and canopy base height are essential for dynamic characterizations of changing surface and ladder fuels over time as well (e.g., Seli et al., 2008; Collins et al., 2011, 2013). Despite the importance of these two input variables, little work has been done to analyze the sensitivity of landscape fire behavior predictions, thus assessments of landscape fuel treatment effectiveness, to changes in these two variables. Furthermore, the coupling of forest dynamics models with landscape-scale fire behavior models is being implemented operationally in forest planning (e.g., Collins et al., 2010). Our findings provide guidance in the use of these models, which potentially improve planning outcomes and management on-the-ground.

Our previous research showed that stand canopy base heights (CBH), when projected using the forest dynamics models in FVS, increased considerably over time in untreated stands (Collins et al. 2011). This occurs at a rate that is difficult to justify ecologically, especially given the large proportion of shade-tolerant species present in many stands. Since predictions of hazardous fire potential are sensitive to CBH, modifications have been made by manipulating regeneration ingrowth levels (Collins et al. 2011, 2013). For this study, in addition to ingrowth levels used in Collins et al. (2011), we modified the default CBH in FVS by using the FVS output from the previous cycles, thereby slowing the rate of change. For fire scenarios we only modified the last cycle (2043) by using CBH values from the previous cycle (2033). While CBH still increased over time, this resulted in a more stabilized, realistic change in CBP over time.

It is likely that the fuel model selection logic we developed had an impact on conditional burn probability and fire size outputs over the simulated duration. Our assumptions that thinned and burned stands progressed from moderate-load conifer litter to high-load conifer litter surface fuel models and, by the final cycle, entered into the untreated selection logic may or may not represent realistic fuel recovery (Collins et al. 2011). Our fuel model succession logic was aided by Davis et al. (2009), in which transitions from one fuel model to the next were based on both fire severity and time since fire. Very little research has been done in this area, and more empirical studies of fuel recovery after wildfires, prescribed fires, and mechanical fuel treatments are needed to form robust methodologies for dynamically assigning fuel models in long-term simulation studies.

Finally, a source of error in our study is the use of a stand-level model (FVS-FFE) to generate fire behavior modeling inputs across our study landscape. Our approach used a base vegetation map to delineate stands, with vegetation and fuel data from over 600 field plots in an attempt to capture the diverse vegetation conditions across our large study areas, allowing for a more detailed quantification of vegetation structure and fuels, which are then simulated independently for the study duration. The base map combined the lidar data with multispectral aerial imagery to predict composition and structure in a 20x20 m^2 grid (Su et al. 2015b). This “pixel-based” product was then aggregated to stands using an object-of-interest segmentation method (Appendix B-Spatial in this report). Aggregating pixels to stands in order to create the continuous vegetation structure and fuel inputs needed to execute the fire models introduces abrupt transitions at stand boundaries. These transitions could potentially lead to unrealistic fire behavior predictions across the landscape. Correlating surface fuel models and forest conditions is a major limiting factor in fire behavior modeling research (but see Lydersen et al. 2015). Lidar data has unlimited potential to provide quantitative information at finer spatial scales that will inevitably help improve fire behavior and fire effects modeling. Despite these potential sources of error, and the uncertainties associated with FVS-FFE projections, our analyses capture the effects of the fuel treatment network in both study sites reasonably well.

Forest health

The implementations of SPLATs at Last Chance and Sugar Pine led to only minor immediate effects on forest structure and species composition. While we did detect the post-treatment increase in overstory tree mortality due to thinning, fireshed-scale changes related to forest health were more subtle. Indeed based on the plot inventory data, none of the structural changes were statistically different from the baseline trends observed in the control firesheds (Table A8, Table A9). Several factors account for this lack of structural change. The management priorities at both sites focused on reducing surface and ladder fuels with explicit goals to retain large trees and maintain canopy cover (USFS 2009, 2010). Thus treatment impacts were greatest for understory tree density and shrub cover with minimal shifts in canopy cover and big tree density (Table A8, Table A9). Also only a fraction of the landscape was treated. Thus the majority of plots received no treatment (Table A5). Finally at LC, trends in the control fireshed also seemed to “track” management goals. For example, tree basal area and density declined between 2007/08 and 2013 in the control fireshed at LC (Table A8). In the case of understory trees, the decrease was substantial (24%) and statistically significant (t-test, $p < 0.05$). These structural changes were also reflected in the fire models. Both fire behavior metrics at LC declined in the control fireshed under post-treatment conditions (Table A10). There was no obvious explanation for the observed decrease in understory tree density aside from self-thinning dynamics in a maturing stand (Vospernik and Sterba 2015).

Changes in tree species composition were also modest (Figure A11, Figure A12). At LC, reducing white fir dominance while increasing the pine component was an explicit treatment goal (USFS 2009). To some extent this target was met. Treatments at LC accounted for a decline in the relative basal area of white fir (14%) with corresponding increases in both ponderosa and sugar pine (Figure A11B).

Both sites identified the need to reduce stand densities in order to improve the resiliency, growth, and vigor of the remaining trees (USFS 2009, USFS 2010). While results from the FVS growth models support the contention that SPLATs did improve tree vigor (Figure A11), forest growth and yield simulators like FVS struggle to predict tree mortality accurately (Hamilton 1990, Battles et al. 2008, Robards 2009). Thus ultimately the measure of success of treatments in terms of tree vigor is to improve tree survival. This criterion is explicitly stated in the LC environmental impact assessment (USFS 2009). Subsequent treatment impacts on tree mortality can be tracked directly by repeat measurements. In addition, Collins et al. (2014) demonstrated a promising method to measure changes in forest resilience caused by fuel treatments. In fact, Collins et al. (2014) applied growth-mortality models developed for LC as part of the SNAMP pre-treatment field campaign. The initial work plan for SNAMP envisioned a post-treatment follow-up to provide empirical support to the model results, but the abbreviated post-treatment period (1-2 years) was too short to measure the tree growth response. Thus future work should prioritize documenting the growth response in order to quantify treatment impacts on future forest vulnerability.

Summary

There were clear differences in the extent and intensity of the treatments between LC and SP (Table A5, Figure A7). SPLATs impact on fire behavior and forest health was further modified by the ecological and historical differences between the two sites. The treated fireshed at SP supported a mixed conifer forest that was more crowded with bigger trees (Table A4) but exposed to a lower initial fire hazard (Table A10). Thus there was a dichotomy in the response to SPLATS. In terms of modifying fire behavior, the impact of SPLATs was greater at LC; in terms of improving forest health, the impact was greater at SP. The longevity of the impacts differed as well. The gains in growth efficiency were maintained through time while the reductions in flame lengths dissipated with time (Figure A20, Figure A21).

Results from SNAMP support the promise of SPLATs. Coordinated treatments across part of the landscape can help minimize the hazards posed by severe fires and at the same time meet forest health objectives. However, as noted above, to fully realize the potential of SPLATs further refinements are needed. For example, prioritizing surface and ladders fuels may be an effective means to decrease the risk of crown fire (Safford et al. 2012) while preserving structural elements (e.g., large trees and high canopy cover) important to wildlife species dependent on old-forest characteristics (Zelinski et al. 2013); it may not create gaps of sufficient size to recruit disturbance-dependent trees like ponderosa pine and sugar pine (York et al. 2011). Devising solutions that support the integrity and function of Sierra Nevada forest ecosystem will require more strategic thinking (e.g., North et al. 2009, North 2012, Stephens et al. 2014). Given the extent of the changes wrought by past management and the challenges posed by global change, the successful strategy will also need to plan for a great deal more management activity in the forest (North et al. 2015).

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The California Spotted Owl: Current State of Knowledge

Forest Service

Pacific Southwest Research Station

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The California Spotted Owl: Current State of Knowledge

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Technical Editors

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Pacific Southwest Research Station
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Abstract

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This conservation assessment represents a comprehensive review by scientists of the current scientific knowledge about the ecology, habitat use, population dynamics, and current threats to the viability of the California spotted owl (*Strix occidentalis occidentalis*). It is based primarily on peer-reviewed published information with an emphasis on new scientific information that has emerged since the first technical assessment for the California spotted owl (CASPO) was conducted in 1992. Substantial new information and insights exist for owls inhabiting the Sierra Nevada, but much less exists for populations inhabiting the central and southern California parts of its range. Spotted owls are habitat specialists that are strongly associated with mature forests that are multistoried or complex in structure, and have high canopy cover, and an abundance of large trees and large coarse woody debris. Most California spotted owl habitat is concentrated in mid-elevation forests of the Sierra Nevada, which consist primarily of ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson), mixed-conifer, white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and mixed-evergreen forest types. Currently, there are about ~2 million ha (~5 million ac) of suitable habitat in the Sierra Nevada, with 75 percent occurring on national forests. These habitat conditions have been demonstrated to have a strong positive association with key vital rates (e.g., occupancy, adult survival, reproductive success), which drive population persistence.

All studies published since CASPO have demonstrated that owl populations on national forests in the Sierra Nevada have declined over the past 20 years. A preponderance of evidence suggests that the past century's combination of timber harvest and fire suppression has resulted in forests that have a considerably higher density of trees but a reduced density of large-diameter trees and logs, a greater density of shade-tolerant fire-sensitive tree species, and an increase in forest fuels. These conditions have resulted in reduced habitat quality, increased habitat fragmentation, and increased risk of high-severity fire in the Sierra Nevada. Climate change is projected to have significant effects on Sierra Nevada forests, including exacerbating the risk and impacts from high-severity fires, which in turn is likely to affect spotted owl habitat and populations. The specter of additional threats in the form of competition from the newly invading barred owl (*Strix varia*) and environmental contaminants, as well as the continuing dearth of information on central and southern California populations, further raises concerns about the fate of California spotted owl populations. Maintenance of a viable population of spotted owls in the Sierra Nevada and throughout its range will depend on effective, long-term owl conservation practices embedded in an overall management strategy aimed at restoring resilient forest structure, composition, and function, including reducing the risk of large-scale high-severity fires while reducing the risk of habitat loss to the owls.

Keywords: California spotted owl, *Strix occidentalis occidentalis,* conservation assessment, national forest, Sierra Nevada, forest resilience, USDA Forest Service, viability, wildfire.

Contents

Preface

The chapters that comprise this compendium provide an assessment of recent scientific knowledge of the California spotted owl—the information that has been published since “The California Spotted Owl: A Technical Assessment of Its Current Status” in 1992. In addition, we included two chapters that are relevant to spotted owl conservation (fire, forests, and climate change in chapter 5; and threats to the owl in chapter 7). As noted in chapter 1, the assessment team limited the scope of the summary of recent California spotted owl research, conducted no original analysis (other than to attempt a synthesis, chapter 9), and limited the number of topics.

The process followed by the assessment team (consisting of the authors of the chapters) began with a meeting in April 2014 in Davis, California, to outline the scope and goals of the assessment, assign individual chapters, and discuss issues related to the owl and its conservation. Individual authors then worked alone or in collaboration with coauthors to complete the chapters which they were assigned. I reviewed and edited draft chapters, which were then sent to all remaining team members for internal team review. Second revisions were returned to me, and, if necessary, I provided additional editing to prepare the papers for peer reviews. Chapter 9 was a synthesis and context of chapter information, written by Dr. Zachariah Peery. A first draft was reviewed and discussed by coauthors and team members over several months. To facilitate completion of chapter 9 and the final details of other chapters, the team convened for a second time in December 2014 in Davis, California. Following this meeting, team members revised their chapters again, and I reviewed and compiled them into a single file. This file was then sent by Dr. Peter Stine, team leader, to the California Regional Office of the U.S. Forest Service in June 2015.

Prior to completion of the chapters, the Pacific Southwest Region (Region 5) selected anonymous reviewers and handled the review process. The team received the anonymous peer review comments in early August 2015 and the Region 5 staff review comments in mid-August. Team members then created individual response documents to these reviews. I edited and compiled the individual responses into a composite response document using a consistent style, but did not alter the content of responses. This response document was then returned to Region 5 peer-review coordinator.

The team did not create a detailed response document to specific comments made by the regional staff because many of the comments overlapped those of the peer reviewers, and others were not relevant given the goals and constraints of the assessment. Regardless, the chapter authors made a good-faith effort to incorporate the suggestions made by regional staff so that they could be accommodated without compromising the scientific and professional integrity of the document.

The team then revised their chapters based on the anonymous peer reviews and the Region 5 staff reviews and in accordance with their commitments made in their responses to reviewers. I read these revised chapters as they were completed, and they were then sent individually to PSW for a policy review between mid-October and early November 2015. Chapter 9 was completed last owing to multiple discussions among the coauthors to settle on language that was acceptable to all coauthors. The authors of chapter 9 acted in good faith to achieve language that they felt was scientifically defensible yet reflected the existence of differences of interpretation of information or the implications of the published information. After several policy reviews were conducted by PSW from October 15, 2015, to April 2016, I made specific recommendations on the policy comments to each chapter author. The authors edited their chapters once again and returned them to PSW in January 2016. A final courtesy review of the final draft chapter was sent to the Region, which resulted in additional requests for revision.

The team held a final conference call in late February to discuss the issues related to the demarcation between what might be considered implied direction to managers by scientists and what constituted a direct, logical interpretation of scientific information. Authors agreed to continue with the review process, but with heightened attention to the issues of scientific independence and integrity of the document. The team received a final station's policy review of the January version of chapter 9 on March 10. The authors addressed the review comments to the extent they felt was appropriate but resisted any changes that would have altered the context of the original text. At the beginning of May, after 11 months of reviews, the full manuscript was accepted by PSW.

In summary, the roles of the technical editors were to ensure consistency of writing style among chapters, to facilitate responses by authors to reviewer comments at several stages of review, and to recommend changes or additions to authors about content and prose of chapters. However, the editors had no ultimate authority or discretion to reject specific chapters or to force authors to comply with editorial and content recommendations of any type. Moreover, the review process was completely outside the jurisdiction of the editors (as it should have been, given that editors were also authors of chapters).

Although the release of the GTR was delayed because of disagreements between the authors and managers about what constituted management recommendations vs. implications of research, we feel the chapters provided an accurate summary and synthesis of recent California spotted owl research. The knowledge gained about California spotted owls since the publication of the 1992 technical assessment led by Dr. Jared Verner will provide a substantial basis for constructing a scientifically defensible conservation strategy for the California spotted owl.

R.J. Gutiérrez

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Executive Summary

Introduction

The California spotted owl (*Strix occidentalis occidentalis*) occurs in the Sierra Nevada, the mountains of central coastal California, and the peninsula and Transverse Ranges of southern California. It is a species of conservation concern because of the potential impacts of forest management and high-severity fire on its habitat—primarily closed-canopy forest. The first California spotted owl technical assessment "The California Spotted Owl: A technical Assessment of it's current status" (CASPO) was published in 1992. It was developed to help guide forest management in the Sierra Nevada and southern California mountains. Since CASPO, much has been learned about the ecology of California spotted owls, but the complexity of managing owl habitat, forests, and wildlife also has increased because of declining forest health, climate change, diseases, and invasive species. Moreover, the population status of owls in the Sierra Nevada is no longer uncertain—populations are declining on national forests.

This document represents a comprehensive overview of the current knowledge about the ecology, habitat use, and population dynamics of the California spotted owl as well as existing and potential threats to its viability. For this assessment (as in CASPO), we divided the range of the California spotted owl into two major physiographic provinces: the Sierra Nevada and the mountains of southern California (including the Transverse Ranges of southern California and portions of the Coast Range of central California). Tehachapi Pass was used as the demarcation between the regions. The majority of new information pertains to the Sierra Nevada population, so all but chapter 8 primarily address the Sierra Nevada population. The science team that produced the assessment was assembled to provide expertise in owl biology and other relevant disciplines (experts in climate change, fire and fuels management, forest ecology, remote sensing, and vegetation ecology). Ideally, this assessment will help inform future options for management and activities ranging in scales from site-specific projects to large landscapes to the entire range of the owl.

Biology and Ecology

The three subspecies of the spotted owl are recognized by the American Ornithologists' Union: northern (*S. o. caurina),* California (*S. o. occidentalis*), and Mexican *(S. o. lucida*). The ranges of the northern and California spotted owls are parapatric (ranges immediately adjacent). For purposes of owl management and conservation, Pit River has been recommended as the management dividing line between these two subspecies although there is evidence that both subspecies occur on either side of the river.

Spotted owls have a monogamous mating system, with territorial pairs forming relatively long-term pair bonds and occupying large home range areas. Spotted owls sometimes break pair bonds (i.e., "divorce"); birds that break pair bonds or whose mate has died form new pair bonds with other birds, often in different territories. Spotted owls are territorial (i.e., exclude other pairs or individuals from the core of their home range) and exhibit strong fidelity to their territory. The territory is typically smaller than a home range. Although the sizes of territories have not been estimated, home ranges are relatively large (about 400 to 1200 ha [1,000 to 3,000 ac]), and home ranges of adjacent owls often overlap.

Spotted owls are primarily active at night when they hunt, defend, socialize, and conduct exploratory movements. They sleep, conduct self-maintenance, and guard young during the day while roosting in complex-structured forests. These forests provide thermal and protective cover, and the same roost sites are often used consistently over many years. The areas around nest and roost sites serve as the center of activity for spotted owls. An owl can forage anywhere within its home range.

Owls have evolved long lifespans and low reproductive rates as mechanisms to mitigate the negative effects of short-term, unpredictable environmental conditions (such as weather variability and disturbance frequency). Annual reproduction by California spotted owls is extremely variable, ranging from no young produced within an area to nearly all birds producing young. These biological features have led some scientists to suggest that the owl exhibits a "bet hedging" life history strategy, meaning that the lack of reproduction at a site for one or more years does not necessarily reflect low site quality, but rather it could reflect temporarily poor environmental conditions that cause owls to postpone reproduction until conditions improve.

Spotted owls prey primarily on medium-sized small mammals, particularly dusky-footed and big-eared woodrats (*Neotoma* spp.) at lower elevations and flying squirrels (*Glaucomys sabrinus)* at higher elevations. However, they prey on many other species, such as mice, pocket gophers, voles, birds, lizards, and insects.

Predators of spotted owls include the great horned owl (*Bubo virginianus*), northern goshawk (*Accipiter gentilis*), and red-tailed hawk (*Buteo jamaicensis*). The invasion of the barred owl (*Strix varia*) in western North America has been of substantial concern for spotted owl conservation because it is a dominant competitor.

Habitat Characteristics and Use

Spotted owls are habitat specialists that are strongly associated with mature forests that are multistoried or complex in structure and have larger trees, higher canopy cover, and more coarse woody debris than does the general landscape. Several hypotheses have been generated to explain why owls select old/mature forests (such as nest site requirements, ambient temperature moderation, or prey availability). They use large, old trees and snags as structures for nests. Here they nest in cavities, broken tree tops, and occasionally on debris platforms such as nests of other species or mistletoe brooms. In mixed-conifer forests, the average nest tree is 124 cm (49 in) in diameter at breast height (d.b.h.) and 31 m (103 ft) tall with an average nest height of 23 m (74 ft). Nests trees in hardwood forests have an average diameter of 76 cm (30 in) and an average nest height of 12 m (38 ft). Owl site occupancy and adult survivorship increase when there is a greater proportion of area of the nest stand containing high canopy cover and high basal area in an owl territory.

Spotted owls are central-place foragers so they concentrate their activities in a "core area" around nests and roosts, with foraging activity decreasing as distance increases from nests or roosts. The "core area" refers to the area that contains the nesting, roosting, and foraging habitat that is essential to each pair's survival and reproductive success. It is commonly considered to be consistent with the territory and is often portrayed in analyses as a circle with a radius that is half the average distance between adjacent nests (i.e., nearest neighbor distance). Occupancy, site colonization, adult survival, and reproductive success are positively associated with the proportion of the core area containing structurally complex conifer forest with large trees and high canopy cover. Concomitantly, reproductive success is negatively correlated with the proportion of nonforested areas and forest types that are not used by owls for nesting or foraging.

Current management on the National Forest System (NFS) centers on protection of 121 ha (300 ac) of high-quality habitat (protected activity center [PAC]) around the nest site as a means of maintaining average habitat conditions within the core use area. One study showed that the current size specified for spotted owl PACs may be adequate to maintain occupancy of territories. Another study showed that mechanical tree removal on ≥20 ha (49 ac) of a PAC was negatively correlated with site colonization and occupancy. Because of the limited number of studies, the contribution of PACs to owl conservation still needs study.

Spotted owl foraging habitat is characterized by a mosaic of vegetation types and seral stages including but not limited to mature forest. Spotted owls often forage in areas having high-contrast edges as well as in interior forest patches (i.e., with few edges). The juxtaposition of mature closed-canopy forest with other cover types is correlated with higher reproductive output and intermediate survival rates in northern spotted owls, which in turn may reflect higher prey diversity and abundance where there is a mosaic of cover types available to owls.

Habitat characteristics of most spotted owl prey have remained largely unstudied in the Sierra Nevada. In general, the dominance of flying squirrels in the diet increases as elevation increases—the reverse is true for woodrats. In the Sierra Nevada, northern flying squirrels are associated with mature forest stands with patches of moderate-to-high canopy closure (>70 percent), large live or dead trees (>75 cm d.b.h. [>30 in]), thick litter layers (≥2.5 cm [≥0.1 in]), and sparsely distributed coarse woody debris or understory cover. In lower elevation forests, woodlands, and shrublands of the west-side Sierra Nevada, woodrats are positively associated with oak cover or large oak density (>32 cm [>13 in] d.b.h.).

A home range is the area used by an individual to meet its requirements for survival and reproduction—consistently, owl home ranges contain a greater abundance of large trees and greater proportion of mature forest than is available on the landscape. Generally, California spotted owl home ranges are larger in the northern Sierra Nevada ([>1000 ha [>2,500 ac]) and smaller in the southern Sierra Nevada (<1000 ha). Owl home ranges contain a mosaic of cover types; however, home range size increases as heterogeneity increases, suggesting that high cover type heterogeneity can negatively affect habitat quality. Data sources to describe habitat characteristics across large geographic areas such as home ranges have proven to be inaccurate and inconsistent among studies, making it difficult to derive specific and reliable home range characteristics to inform management.

Population Distribution and Trends

As reported in CASPO, there appear to be no significant gaps in distribution of owls in the Sierra Nevada. The majority of owls occur within the mid-elevation, mixed-conifer forests on the west slope of the Sierra Nevada. We could not determine the relative population density or size between public and private land in the Sierra Nevada because there has been no published estimate of the number of owls occupying private land in the Sierra Nevada.

Since CASPO, data collected on five long-term California spotted owl study areas have provided substantial empirical data on demographic rates and population trends. Of these five study areas, four were in the Sierra Nevada—three on national forests (Lassen, Eldorado, and Sierra) and one within Sequoia and Kings Canyon National Parks. Meta-analyses of these data have shown substantial variation in reproductive rates (number of young fledged per territorial female for which reproduction was assessed) among the four areas. Reproduction has declined over time on the Eldorado but has been relatively constant on the other study areas.

Reproductive rates have been correlated with both climatic conditions and habitat characteristics. Reproductive rates were negatively correlated with higher precipitation and colder temperatures during the previous winter or early nesting season and positively correlated with the presence of closed-canopied forest, respectively. Key vital rates—reproductive rates at both the nest and territory scales, as well as the survival of adults—appear to be closely tied to habitat characteristics, namely a positive association with the amount of forest with dense canopy and larger trees.

All studies published since CASPO have demonstrated that owl populations on national forests in the Sierra Nevada have declined over the past 20 years. Both the finite rate of a population increase (λ) and the realized rate of change (Δ_t) have shown negative trends over the past 20 years. The greatest population declines have occurred on the Lassen and Eldorado National Study Areas. However, one study in two national parks, Sequoia and Kings Canyon, showed a stable population. These findings removed the uncertainty expressed in CASPO about the status of population trends in the California spotted owl.

Sierra Nevada Forest Conditions

Most of the California spotted owl's habitat is concentrated in mid-elevation forests of the Sierra Nevada, which are made up primarily of ponderosa pine, mixed-conifer, white fir, and mixed-evergreen forest types. The majority of the range of California spotted owl is occupied by NFS lands, with private lands and national parks making up almost all the rest. These forests have changed substantially since the arrival of Europeans. Management practices (fire suppression, logging, and grazing) on national forests and private lands have largely shaped current forest conditions in the Sierra Nevada. There are five national parks in the Sierra Nevada and southern Cascades covering 1.74 million ac that contain substantial suitable spotted owl habitat. Management of these parks is directed toward building ecosystem resilience to cope with changing climates, primarily using prescribed fire and managed wildfire to accomplish conservation objectives.

Until 1990, similar management objectives and silvicultural prescriptions were used on both NFS and private lands. Prior to 1900, logging occurred mainly near mining operations and communities, with most logging occurring on private lands. Timber harvest in the Sierra Nevada peaked in the post-World War II years and then stabilized starting in the 1960s. The CASPO report noted four key changes in forest conditions that occurred from 1850 to 1992: (1) the loss of old, large-diameter trees and associated large downed logs; (2) a shift in species composition toward shade-tolerant, fire-sensitive tree species (i.e., from pines to fir and cedar); (3) increases in fuel loads associated with the mortality of small-diameter trees; and (4) the presence of fuel ladders (ground to canopy) that facilitate crown fire. We found no new information that was contrary to this historical view (but see climate change effects below).

With the adoption of the California spotted owl guidelines following CASPO, management of national forest and private forests diverged significantly in the mid-1990s. Timber harvest dramatically decreased on NFS lands such that private lands produced more than 80 percent of the timber volume from 1990 to 2013. Nearly 400 000 ha [1 million ac] were logged on private land between 1990 and 2013 in the Sierra Nevada, with most logging occurring in the southern Cascades and northern Sierra Nevada. In contrast, about (265 000 ha [665,000 ac]) were logged during about the same time on national forests, with most logging occurring in the northern Sierra Nevada.

Current estimates are (about 4.9 million ac [2 million ha]) of suitable habitat, with about 75 percent, 7 percent, and 18 percent occurring on NFS, national parks, and either private or other government lands, respectively. About half of all suitable habitat is classified as the Sierra Nevada mixed-conifer vegetation type, and this type is mostly (about 75 to 80 percent) on NFS lands, which demonstrates the critical role of NFS lands for owl conservation in the Sierra Nevada.

The preponderance of evidence suggests forests have a considerably higher density of trees than forests of presettlement times because of fire exclusion and logging that allowed the regrowth of dense tree stands. Moreover average canopy cover of presettlement forests has been estimated to be as low as 22 percent but ranging from 8 to 37 percent. However, a less accepted estimate of presettlement forests based on Forest Inventory and Analysis data and on historical tree data suggests that presettlement forests had greater density than suggested by others. Despite these differences, most studies suggest presettlement forests were spatially complex across landscapes, including the presence of early seral vegetation (e.g., dense conifer regeneration, and shrubs) and denser mature forest stands within a matrix of generally low-density stands. Numerous studies have demonstrated that high frequency (5- to 15-year return intervals) of low-severity fire maintained low-density stands across much of the landscape, resulting in the dominance of large, fire-resistant trees. This is particularly the case for yellow pine (*Pinus ponderosa* and *P. jeffreyi*) and mixed-conifer forest types within the Sierra Nevada.

Fire is a critical ecosystem process throughout the Sierra Nevada, but that process is changing because of fire exclusion and climate change. Current trajectories of fire size and impact, along with a predicted doubling of the likelihood of future fires, suggest a future in which the frequency and proportion of stand-replacing fires in the Sierra Nevada will exceed both current and past levels. Such changes have the potential to reduce forest regeneration.

Estimates of the effects of climate change predict an upward elevation shift of plant species and communities, an expansion of grassland, savannah and shrub-dominated ecosystems, and a general reorganization of forested ecosystems. Increases in tree stress and large-tree mortality are expected among these vegetation changes. Climate projections also suggest the potential for conversions of all vegetation type with increasing warmer and drier future climate scenarios, including the forests upon which California spotted owls currently depend.

Forest heterogeneity in the Sierra Nevada is strongly influenced by water availability and fire. Mesic and riparian sites are dominated by the greatest densities of large overstory trees, have high basal area and canopy cover, and have an abundance of large snags and logs. Slope steepness and slope position (e.g., ridgetop, midslope, valley bottom) influence forest heterogeneity because they affect the reception and retention of water. While overstory forest patterns are closely associated with climatic water deficit, understory conditions are strongly shaped by fire.

Heterogeneity within forest types that are fire adapted (historically affected by frequent fires) can be characterized by the interspersion of individual trees, clumps of trees, and openings or gaps (i.e., ICO structure). The small-scale heterogeneity characteristic of historical forest conditions are hypothesized to confer multiple desirable functions: openings may inhibit crown fire spread under most weather conditions and may be as effective as fuel breaks with regularly spaced trees with wide crown separations; and the variable microclimate and vegetation conditions between the three conditions may enhance forest drought resilience and provide greater habitat diversity for both plants and animals. Intentionally creating these conditions by either mechanical treatments or prescribed fire is likely to be challenging.

Mapping Forest Conditions Past, Present, and Future

Mapped data are essential to public land managers and researchers to identify and characterize wildlife habitat across scales, to monitor species and habitat change, and to predict and plan for future scenarios. National forest managers in the Sierra Nevada use maps to aid conservation planning for sensitive species. They require the ability to estimate important habitat metrics accurately across spatial scales to account for variation in a species' needs. However, creating accurate maps can be challenging because landscapes exhibit great variability in composition, cover, and topography, and reflect a complex legacy of fire and logging effects.

Aerial photographs provide spatially detailed records and remain a valuable data source for habitat despite the increase in the number and types of digital sensors available to managers and scientists. Aerial photographs predate satellite imagery; in California, imagery archives include images from the 1930s onward. Further, the spatial detail provided by aerial photography is high, even when analog photographs are digitized. Finally, when digitized, aerial photographs (e.g., digital orthophoto quadrangles) can be analyzed with powerful image analysis techniques.

Approaches to mapping wildlife habitat have been varied. Data used to create maps describing owl habitat have been gathered from field surveys; black and white or color air photos; or digital aerial imagery, and other maps such as timber survey; Landsat-derived vegetation; and fire-severity maps. Remotely sensed imagery at both fine spatial resolution (e.g., 1 m [3 ft]) and moderate resolution (e.g., 30 m [98 ft]) has also been used to create maps.

Vegetation maps derived from Landsat data have been used widely to study California spotted owl habitat. The broad spatial coverage of Landsat and the spectral detail of its sensors have been found useful to map species groups and canopy cover but cannot detect the residual tree component of forests in forests dominated by the medium-sized trees necessary for owls to use these forests. Additional sources of vegetation data useful to create maps of owl habitat are color infrared aerial photographs, National Agricultural Imagery Program (NAIP) imagery, and Google Earth, but have yielded varying levels of success. Some studies have shown that some Landsat maps have error rates that can lead to erroneous conclusions about changes in habitat conditions. The NAIP imagery has shown greater promise for accurately mapping tree size, canopy cover, and vegetation type.

LiDAR (Light Detection and Ranging) is a laser-based technology that provides detailed, extensive, and accurate vegetation structure data, which are key elements of species' habitats. LiDAR provides data suitable to estimate many vegetation characteristics typically associated with California spotted owl habitat.

In particular, the ability to map individual trees, tree sizes, and canopy cover are enhanced by analysis of LiDAR data.

An essential step in map development is assessing the map's accuracy. The best method for doing this is to compare classified map values against field-verified values (creating an error matrix). Using field validation methods, spotted owl researchers generally have created maps with greater than 80 percent accuracy using aerial photography and 76 percent accuracy using Landsat. But all such large-scale maps of owl habitat thus far created have not contained the "residual tree" component that appears critical for owls. Mapping technology has been and will continue to be critical to understanding owl habitat relationships and inform their conservation.

Population and Habitat Threats

The CASPO provided four factors as either threats or potential threats to the viability of California spotted owl populations: (1) timber harvest and forest management, (2) wildfire, (3) development of gaps in owl distribution across the Sierra Nevada, and (4) human population growth and development. Since then, most of these conditions persist or have worsened, while additional factors have emerged as threats to California spotted owl population viability: invasion of the barred owl (*Strix varia*) into the Sierra Nevada; climate change that could affect owls and their habitat; and disease, parasites, and contaminants (namely rodenticides) that could lead to owl mortality.

Three studies have explicitly addressed the threat of timber harvest and wildfire at territory and landscape spatial scales with mixed results. Whereas multiple studies have shown the importance of critical amounts of mature conifer forest for owls, they have been mixed in their ability to elucidate their cause-and-effect relationships. For example, one study showed that loss of ≥20 ha (50 ac) of mature forest within a territory resulted in a decline in the probability of territory occupancy. Further, territories with greater amounts of mature conifer forest had higher probabilities of being colonized and lower probability of being unoccupied relative to territories with lower amounts of mature conifer forest. Another study was unable to relate habitat change due to fire or logging directly to owl vital rates, but the amount of mature, high canopy cover forest was positively related to owl survival, reproduction, population growth rate, and occupancy. There is only a single published study on the effects of logging on the owl, which showed a 43 percent reduction in occupied owl sites. Although causative linkages have not been established, these high rates of decline are coincident with the greater amount and extent of logging on public and private lands.

Studies relating owl demographic parameters to habitat patterns indicate the importance of territory-scale habitat conditions such as the amount of complex-structured mature forest present and an intermediate amount of habitat edge between forest and other vegetation types. This pattern has also been reported for owls whose territories have been affected by mixed-severity fires, including low amounts of stand-replacing fires. However, there is significant uncertainty about the amounts of edge and fine-scale heterogeneity that might be beneficial to owls or how best to achieve this heterogeneity.

Recent research indicates that California spotted owls can persist on territories burned by low-moderate severity and mixed-severity (i.e., low-moderate fires with inclusions of high severity) wildfire. The amount of high-severity fire that owls can tolerate within their territory is unknown. Occupancy of sites by owls after fire appears to be a function of the amount of suitable habitat remaining after fire, the amount of suitable habitat burned at high severity, and whether postfire salvage logging was conducted. Postfire salvage logging may negatively affect postfire habitat suitability and confounds our understanding of owl response to fire.

Development of gaps in owl distribution in the Sierra Nevada could have negative demographic effects because dispersal among geographic areas likely would be reduced. Spotted owls in the Sierra Nevada have low genetic diversity so fragmentation and isolation of owl populations in the future could lead to increased risk to long-term viability. The CASPO had a list of eight land areas of concern (AOCs) within the Sierra Nevada where potential gaps in the distribution could develop because (1) naturally fragmented distribution of habitat and owls occurs, (2) populations become isolated, (3) habitat becomes highly fragmented, and (4) areas occur where crude density of owls becomes low. Evidence indicates that the threat of gaps in distribution has likely increased since CASPO as a function of habitat loss and fragmentation. Documented owl population declines in Lassen and Eldorado National Forests (AOCs 2 and 4, respectively), along with uncertainty about the status of owls in the northern Lassen, Tahoe, Stanislaus, and Sequoia National Forests (AOCs 1, 3, 5, and 8, respectively) where extensive forest management treatments have occurred contribute to the increased threat of gaps developing in the distribution of owls.

Human population continues to grow in the main area of owl distribution on the west slope of the Sierra Nevada, which has raised the risk to owl habitat. Wildland-urban interface (WUI) zones are typically heavily managed to reduce fuels and the risk of fire to protect communities. About 50 percent of known owl sites occur within areas designated as WUIs. Disturbance resulting from human recreation and management activities also can potential affect California spotted owls. Impacts from recreation can range from the presence of hikers near owl nests and roosts to loud noises made by motorized vehicles. Research studies have varied in their findings about the effects of disturbances on owls.

Barred owls have invaded the range of both northern and California spotted owls. Because barred owls are having a major negative impact on northern spotted owls, it is predicted they will have a similar impact on spotted owls in California. Competition between barred and spotted owls occurs because of broad overlap in habitat use, similar diets, and choice of nests. Barred owls are behaviorally dominant. Through 2013, 51 barred and 27 "sparred" (hybrids between the two species) owls, and 1 unknown have been detected in the Sierra Nevada. No barred owls have been reliably documented in either southern or central coastal California. Experiments are occurring to test the effects of barred owl removal on northern spotted owls and to assess whether removal is a feasible management strategy to reduce competition with spotted owls. If left unchecked, barred owls have the potential to extirpate spotted owls from the Sierra Nevada.

Climate change is projected to have significant effects on Sierra Nevada forests, which in turn would affect spotted owls. Increases in temperature and changes in precipitation patterns may have direct effects on spotted owl physiology, survival, reproduction, recruitment, and population growth. Climate change may also precipitate indirect effects through mechanisms such as (1) changes in habitat distribution, abundance, and quality; (2) increasing high-severity wildfire; (3) increasing mature/large-tree mortality caused by drought, insects, and disease; (4) changes in prey distribution, abundance, and population dynamics; (5) changes in interspecific interactions with competitors and predators; and (6) changes in disease dynamics associated with changing temperature and precipitation patterns.

Although little information exists on the threat of disease, parasites, and contaminants on spotted owl populations, the potential for impacts from these elements is concerning. The primary threats are West Nile Virus, ectoparasites, and endoparasites. West Nile virus is primarily a mosquito-borne flavivirus that has recently invaded North America and is highly lethal to owls. Several species of ectoparasites and endoparasites have been identified in spotted owls. Diseases and parasites can interact with other stressors to affect either the condition or survival of individuals. Environmental contaminants have not been identified as current ecological stressors on California spotted owls; however, recent reports of high exposure rates of fisher (*Pekania pennanti*) to rodenticides across the southern Sierra Nevada are likely to have implications for spotted owls because they feed on rodents. For example, 62 percent (44 of 71 owls) of barred owls tested positive for rodenticides on the Hoopa Reservation in northern California.

The Spotted Owl in Southern and Central Coastal California

Spotted owls in southern and central coastal California have received much less attention than those inhabiting the Sierra Nevada because of economic (effect of habitat conservation measures on timber harvest) and social issues (community desire for naturally functioning ecosystems). Yet there has been continued concern over the status of owl populations in this region since CASPO. The owl in this region is distributed from Monterey County and Tehachapi Pass south through the coastal, Peninsular, and Transverse Ranges to Mount Palomar near the Mexican border. The presumption is that owls in the Sierra San Pedro Martir in Baja California Norte are California spotted owls as well.

There are four major cover types used by spotted owls in southern California: riparian/hardwood forests and woodlands, live oak (*Quercus chrysolepis* Liebm.)/big cone-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) forests, mixed-conifer forests, and redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.)/ California laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.) forests. Unlike in the Sierra Nevada, most owls occur in cover types other than mixed-conifer forest because mixed-conifer forest is only found at the highest elevations in most of these isolated mountain ranges. Thus, they are found over gradients of habitat within these mountain ranges. Yet, site-specific characteristics of territories and nest sites follow patterns seen in the Sierra Nevada owl habitat selection.

The spotted owl in southern California is unique among west coast spotted owl populations because it occurs as a presumed metapopulation—distinct populations that function independently, yet their dynamics are interrelated because of dispersal among populations. Metapopulation structure is presumed, but there is a lack of documented movement among populations to confirm this presumption. One analysis in CASPO revealed key properties of this theoretical metapopulation. One property was that the San Bernardino population was critical to the persistence of the entire metapopulation because the many small populations in the region would benefit from having this large population be a source of immigrants. A later simulation study suggested that the metapopulation would likely either go extinct within the next 30 to 40 years or would undergo a substantial decline but not go extinct. If there is little or no dispersal among populations, as current studies indicate, the risk of local population extinctions increases.

Crude densities (density across the landscape) of owls in southern California are lower than densities in other areas of California, which suggests that there is higher spatial fragmentation of suitable habitat within populations in southern California; however, ecological density (density within suitable

cover types across the landscape) is comparable to at least one population of northern spotted owls prior to its recent decline. This suggests that the habitat in southern California has a similar capacity for supporting spotted owls as the more mesic forests in northwestern California. Like populations in the Sierra Nevada, fecundity of owls is variable among years and influenced by the age of owls (subadults have lower fecundity than adults) and weather. In southern California, survival was related to age (survival higher in older age classes) and precipitation in the preceding winter.

The most complete data on territory occupancy and population trend in southern California exists for the San Bernardino Mountains within the San Bernardino National Forest, and suggests that this key population has declined. This study occurred from 1987 through 1998, with additional monitoring of known owl territories from 2003 through 2011. The San Jacinto population was studied less intensively and sporadically from 1988 through 2011. Both populations have shown significant declines (about 50 percent) in territory occupancy and for the San Bernardino a significant decline based on estimates of vital rates.

Connectivity among populations is critical to the persistence of the spotted owl in this region, and it is a function of barriers and dispersal habitat. In CASPO, urban and suburban development and the loss of riparian areas were reported to be threats to the metapopulation because they were barriers to dispersal among populations. The current situation is worse than at the time of CASPO because development continues unabated within both the Los Angeles Basin and the surrounding deserts. Further, two new types of barriers pose potential threats to dispersal: wind farms and large reservoirs. Many wind turbines have been erected in several areas that could serve as potential dispersal corridors between mountain ranges and between the southern California region and the Sierra Nevada. At the time of CASPO, reservoirs were not specifically considered a barrier to dispersal, but at least one owl drowned in its apparent attempt to cross one in the area between the San Bernardino and San Gabriel Mountains.

Habitat loss could result from fires and salvage logging, as well as habitat loss and disturbance from urban development and recreation. There are as yet no restrictions on logging of trees on private land within the range of the owl other than those imposed by the California Forest Practices Act. Habitat is also being lost or fragmented as a result of primary and secondary (i.e., vacation) home building. However, there is no longer any commercial timber harvest on national forests within the owl’s range in southern California. Post-CASPO assessments of riparian habitat found no evidence for loss of riparian habitat owing to the water diversion threat that was listed as a potential threat in CASPO. Yet such loss remains a potential threat as does the threat of channelization to control waterflow (i.e., flood protection). Wildfire has long been a concern because of its potential impact on owls and their habitat, but its overall effect on owl populations is not clear. Given the loss of habitat owing to other factors (e.g., urbanization and drought), fires are likely a contributing factor to owl declines. A myriad of additional threats to habitat and owls exist in the southern California and coastal populations, including disturbance from human recreation, drought, air pollution, mining, marijuana cultivation, invasive species, disease, cumulative effects of small-scale management actions, and climate change.

Synthesis and Interpretation Within the Context of Public Forest Management

In this final chapter, we identify and discuss key scientific findings that have emerged since the CASPO report in 1992. We also discuss priorities for future research that could enhance the successful conservation of California spotted owls and their habitat, and we acknowledge when uncertainty limits well-founded conclusions and articulate potential differences in interpretation of the scientific literature where such differences exist.

Conservation of California spotted owls in the Sierra Nevada will require maintaining a well-distributed population of owls of sufficient abundance that the population will be resilient to the effects of climate change and other environmental stressors. Establishing a set of biologically based conservation benchmarks would be valuable to indicate the status of spotted owl populations and to prompt additional or alternate conservation measures.

Maintaining a viable population of spotted owls on public lands in the Sierra Nevada will be an outcome of effective, long-term owl conservation practices embedded in an overall management strategy aimed at restoring resilient forest structure, composition, and function. Conserving spotted owl populations and restoring ecosystem resilience are complementary objectives when management activities reduce the loss of old forest and owl habitat to drought and large high-severity fires. A reasonable guiding philosophy is to manage Sierra Nevada forests in ways that combine the objectives of spotted owl conservation, fuels management, and drought resilience, while also recognizing that forests are dynamic ecosystems that will support a range of vegetation types and structures that vary over space and time. In practice, however, implementing effective fire-management and ecosystem restoration programs that do not also pose risks to spotted owls will be challenging.

Two paradigms emerged as part of this assessment regarding tradeoffs between the potential short-term negative impacts and possible long-term benefits of fuel and restoration treatments on spotted owls.

- One paradigm holds that forest management treatments within spotted owl habitat pose risks to spotted owls because their populations have declined and restoration treatments commonly entail the reduction of canopy cover and canopy complexity, and even the removal of some large trees. Thus, a strategy focused on conserving and enhancing existing owl habitat would be the most effective approach to conservation.
- The alternative paradigm holds that increases in the spatial extent of high-severity fire and other disturbances to forests (e.g., prolonged drought, insects, and disease) pose the primary proximate threat to spotted owl population persistence, owl habitat, and forest ecosystems in the Sierra Nevada. Thus, a strategy that reduces the risk of large, high-severity fires would be the most effective approach to conservation.

The following key findings and points of consensus regarding new scientific information are relevant to both owl conservation and forest restoration in the Sierra Nevada:

- Spotted owls have declined in abundance on some national forest lands in the Sierra Nevada over the past two decades.
- The density of large and defect trees has declined in Sierra Nevada forest as a result of historical (pre-CASPO) timber harvesting; these habitat elements may well be contributing to recent spotted owl population declines, and restoring large trees is expected to benefit both spotted owls and forest resilience.
- A century of fire exclusion has led to an increase in the size of high-severity fires owing to the accumulation of surface and ladder fuels, and a concomitant high risk of habitat loss resulting from large high-severity fires.
- Restoring low- to moderate-severity fire regimes to the mixed-conifer zone could help achieve both spotted owl conservation and forest restoration goals.
- Habitat conditions in owl territories that are located in areas with high burn probabilities or low drought tolerance may not be viable in the long term—conservation and restoration focused in areas that can sustain suitable habitat conditions may align the distribution of owl habitat with forest restoration goals.

Different habitat features are important to spotted owls at each of several spatial scales, and considering these scale-specific requirements will facilitate the development of forest conditions that minimize risk to owls and promote resilient forest ecosystems. The scales of greatest importance are the owl's activity center, territory, and home range, embedded within the broader forested landscape. Desired conditions for each scale of ecological importance, as well as the implications of recent research for achieving these conditions via forest management are as follows:

- **Activity center scale**: Maintaining high-quality nesting and roosting habitat at known spotted owl activity centers will likely enhance occupancy and demographic performance. Forest structural characteristics known to be important at this scale are likely to be maintained or even enhanced through low-intensity vegetation treatments intended to reduce the risk of high-severity fire and drought-induced large-tree mortality.
- **Territory scale (outside of activity centers)**: Spotted owl occupancy and fitness within territories appear to be positively related to the acreage of high-quality habitat. Given climate change predictions and the likely implications for fire and tree mortality, reducing these risks to forests within territories is likely to benefit spotted owl populations.
- **Home range scale (outside of territories)**: Spotted owl home ranges are characterized by heterogeneous forests containing a mosaic of vegetation conditions. At this scale, greater emphasis can be placed on fuels management and forest restoration, particularly approaches that enhance forest resilience, landscape heterogeneity, and spotted owl foraging habitat.
- **Landscape scale (matrix between home ranges)**: A landscape of heterogeneous forests containing a mosaic of vegetation conditions including patches of old forest is likely to promote the recruitment of new spotted owl territories. Fuels and restoration treatments (including prescribed and managed fire) that promote landscape heterogeneity in forest conditions and reduce risks for high-severity fire are likely to be beneficial to spotted owl conservation in the longer term.

Recent research indicates that California spotted owls persist in territories that experience low-moderate severity and mixed-severity wildfire and that small patches of high-severity fire may enhance foraging conditions for spotted owls. However, high-severity fire can also have a negative effects on spotted owls. Salvage harvesting within such landscapes, particularly high-intensity salvage (removal of most snags), could invoke or exacerbate negative impacts on spotted owl habitat via the removal of snags and ultimately the reduction of coarse woody debris on the forest floor.

Barred owl range expansion into the northern Sierra Nevada, particularly given the profound impacts they have had on northern spotted owls, could warrant control measures. Control measures would be most effective while barred owls still occur at low densities in the Sierra Nevada. The momentum of range expansion and abundance is expected to increase exponentially once barred owls have reached a critical, as yet unknown, density.

A set of "conservation benchmarks" would be valuable to indicate the status of California spotted owl populations. Such benchmarks could be used to evaluate monitoring results and gauge whether management activities are effectively accomplishing their intended objective of conserving spotted owls, or whether additional conservation measures need to be implemented, within an adaptive management framework. For example, potential demographic metrics of spotted owl population status upon which conservation benchmarks could be based include abundance, population trends, and geographic distribution.

Despite considerable resources devoted to improving our understanding of the ecology and status of the California spotted owl, important uncertainties and knowledge gaps remain that could be addressed through future monitoring or research investments.

- It remains unclear what environmental or anthropogenic factors are responsible for observed population declines of the California spotted owl.
- A greater understanding about the effects of fuel and restoration treatments and wildfire on California spotted owls is needed to inform forest management that is intended to recover owl populations and restore ecosystem resilience in Sierra Nevada forests.
- Considerable uncertainty remains about the owl's distribution and winter ranges in the mountain ranges of southern California, the foothills of the western Sierra Nevada, and the Coast Ranges, and the significance of these local and regional owl populations to the species' rangewide persistence.
- To achieve a regional-scale inference based on sampling of owls, a regional-scale, occupancy-based monitoring program would be highly complementary to the information provided by the demographic monitoring and would facilitate the assessment of barred owl impacts.
- Nonforested vegetation (e.g., montane chaparral) distributed within a mosaic of forest types may constitute important foraging habitat, particularly when juxtaposed with closed-canopy forests and may confer fitness (survival and reproduction); however, such linkages have not yet been demonstrated conclusively for California spotted owls.

- A greater understanding of the vegetation conditions that shape the abundance and distribution of important prey species in the Sierra Nevada would inform the development of effective stand- and landscape-scale forest management strategies to enhance spotted owl foraging habitat.
- Future studies could further our understanding of potential climate change effects by linking expected changes in owl distribution to shifts in vegetation communities and change in fire dynamics—an effort that would benefit from integrative efforts involving wildlife, forest, and fire ecologists.
- There are many outstanding needs for mapping of wildlife habitat, including the mapping of snags, large trees, and large broken-top trees; the development of improved metrics to quantify vertical canopy structure; and the development of tree species distributions in mixed-conifer forests.

Chapter 1: Introduction

Peter A. Stine and Patricia N. Manley[1]

The California spotted owl (*Strix occidentalis occidentalis*) occurs across a large portion of California, including the portion of the southern Cascade Range south of the Pit River that abuts the Sierra Nevada and throughout the Sierra Nevada, the mountains of central coastal California, and the Peninsular and Transverse Ranges of southern California. The future of the California spotted owl is of concern because of population trends over the past few decades, the potential impacts of forest management, and the threat of high-severity fire on its primary habitat of closed-canopy forest. Data from demographic studies conducted in three locations in the Sierra Nevada show that populations have been declining over the past 20-plus years (e.g., Conner et al. 2013, Tempel et al. 2014). The majority of the current range of the owl occurs on public lands, primarily national forests.

Regulatory Context

The U.S. Forest Service (USFS) is required, under the new 2012 National Forest Management Act (NFMA 2012) Planning Rule (36 CFR 219; Federal Register 2012), to identify potential species of conservation concern and provide an assessment of existing information for those species. A species of conservation concern is defined as:

> …a species, other than federally recognized threatened, endangered, proposed, or candidate species, that is known to occur in the plan area and for which the regional forester has determined that the best available scientific information indicates substantial concern about the species' capability to persist over the long-term in the plan area.

The California spotted owl is considered a species of conservation concern (FS Handbook 1909.12 § 12.52c-d), thus the USFS is directed to identify and assess information relevant to this species. A technical assessment of its status and threats is a valuable, if not essential, step in informing effective conservation measures and strategies. Among other applications, the information presented in this assessment will inform revisions of the USFS Land and Resource Management Plans for the 15 national forests within its range.

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The first technical assessment for the California spotted owl “The California Spotted Owl: a Technical Assessment of Its Current Status” or (CASPO) was initiated in 1991 (Verner et al. 1992). It was developed to help guide management direction for national forest project planning in the Sierra Nevada and southern California mountains (Verner et al. 1992; see below for more details). The interim management guidelines recommended in CASPO were followed by the national forests in the Sierra Nevada until the Sierra Nevada Forest Plan Amendment record of decision (ROD) was released in 2001 and then amended in 2004. The ROD (USDA FS 2004) provided some specific standards and guidelines for California spotted owl habitat based on a science synthesis created for the forest plan amendment process. Additionally, the 2004 ROD focused on fuels treatments because loss of owls and their habitat as a result of catastrophic wildfires was considered a significant threat to the species. Much has been learned about the ecology of California spotted owls since CASPO, but there has been no comprehensive assessment of this new information. New information in the published literature needs to be assessed to improve our understanding of its significance and relevance to management and future research. Periodic syntheses and assessments also help bring cohesion to the interpretation of new information, thereby guiding its application to management. Over the 25-year period since CASPO, many site-specific research projects, long-term demographic monitoring, basic ecological research, and specific project monitoring activities have occurred throughout the range of the California spotted owl. Dozens of peer reviewed publications have resulted from these activities (e.g., see chapters 2, 3, 4, 7, and 8), and given forest plan revision activities and growing concerns for the status of the spotted owl, it was timely to generate an updated assessment to support and inform conservation and management efforts.

1992 California Spotted Owl Technical Assessment

The information benchmark for our assessment was CASPO (Verner et al. 1992). The CASPO represents the last effort to comprehensively summarize what is known about this subspecies throughout its range. It was developed over a 1-year period by a technical team dedicated solely to this task. The CASPO was conducted in response to the designation of the northern spotted owl (*S. o. caurina*) in 1990 as a federally listed threatened species, the recognition that forest managers in California would benefit from an assessment of the current status of the California subspecies, and the need to develop a scientifically defensible plan for the conservation of the California spotted owl. The CASPO received direction from the California Spotted Owl Assessment Team Steering Committee, whose members represented several state of California (Resources Agency, Board of Forestry, Department of Fish and Game, and Department of Forestry and Fire Protection) and federal entities (U.S. Department of Agriculture Forest Service; and U.S. Department of the Interior Bureau of Land Management, Fish and Wildlife Service, and National Park Service).

The charter for CASPO specified submission of a report to the steering committee on the current status of the California spotted owl following "accepted scientific standards and practices." The 285-page CASPO report was intended to provide guidance for managing owl habitat as forest plans were revised and more information about the owl was learned to justify either deviation from the strategy or to support a long-term conservation strategy based on fulfilling critical information needs of the owl. The technical assessment had the following objectives:

1. Present, analyze, and interpret relevant information currently available on the biology of the owl—its distribution, abundance, density, movements, breeding biology, diet, demography, habitat associations, etc.
2. To the extent possible, characterize the attributes of various habitats used for foraging, roosting, and nesting by the owl throughout its range in California.
3. Evaluate current land management practices throughout the range of the owl, recognizing that more detailed information may be available for some land ownerships than for others.
4. Evaluate a range of options to achieve an amount and configuration of suitable habitat to provide for the long-term maintenance of the owl throughout its range.
5. Identify research, monitoring, and inventory programs needed to answer existing critical questions and to provide for adaptive management of the owl in the future.

Lessons Learned From the Northern Spotted Owl

Although the northern spotted owl (*Strix occidentalis caurina*) is a different subspecies within a different ecoregion, many of the challenges and successes in conservation efforts associated with this federally threatened species over the past 24 years are applicable to the California spotted owl (USFWS 2011). Our assessment makes no attempt to incorporate the large body of work published on the northern spotted owl, but the five primary topic areas of the 2011 Recovery Plan clearly reflect the critical information needed to address the conservation and management of spotted owl populations and habitat:

1. Conservation of existing spotted owl sites and high-value spotted owl habitat.
2. Ecological forestry and active forest restoration approaches to meet the challenges of climate change and altered ecological processes.
3. The threat posed by barred owls (*Strix varia*) and management options to address those threats.
4. The potential need for state and private lands to contribute to spotted owl recovery in areas with substantial mixed ownership.
5. Development of a population and habitat modeling framework as a decision-support tool to better inform future land management decisions.

Expanding Challenges in Spotted Owl Conservation

The complexities of managing habitat that supports viable populations of species associated with mature forests have continued to grow in recent decades. At the time of CASPO, concern about fire centered on sufficient fire suppression measures, climate change was not a primary focus for Forest Service scientists and managers, and as the barred owl had just recently invaded the range of the northern spotted owl, there was uncertainty about its impact on the spotted owl (Verner et al. 1992). Since CASPO, we have observed significant declines in spotted owl populations across its range (Conner et al. 2013, LaHaye and Gutiérrez 2005, Tempel et al. 2014; chapters 4 and 8); an increase in the size and severity of wildfires (chapter 5); a growing recognition of the essential role of active fire in forest restoration, and the dual role that fire can play as a destructive and constructive process (chapters 5 and 9); the challenge of balancing forest restoration using fire and increasingly strict air quality objectives and constraints (Quinn-Davidson and Varner 2012); a clearer understanding of the impact of high-severity burned forests in sustaining owls in a dynamic landscape where fire is likely to become more prevalent (Bond et al. 2009; chapter 7); the emergence of diseases, such as West Nile virus (Ishak et al. 2008; chapter 7); and the significant threat that the invasion of the barred owl has on spotted owl population persistence (Gutiérrez et al. 2007; chapter 7). Against this background, uncertainty posed by climate change in California, most notably in the form of extended droughts, is predicted to exacerbate many of these observed challenges in addition to unforeseen effects on owl populations and their prey (Millar and Stephenson 2015). These emerging issues have joined, not replaced, those recognized at the time of CASPO, namely the impact of habitat loss and fragmentation through logging and urbanization, the uncertain impact of water diversions to serve increasing demands with (now) decreasing supplies, and the uncertainty of imperfect information about the ecology, vulnerabilities, and primary drivers of population trends. Perhaps the most troubling of all is the overwhelming evidence that uncertainties about how to conserve the California spotted owl are now confounded by the uncertainty about how to conserve forest ecosystems in light of the increasing threat of high-severity fires and climate change. This excerpt from the northern spotted owl recovery plan pertaining to habitat conservation and management in dry forest ecosystems illustrates the conservation conundrum we face (USFWS 2011: III-20):

> Changing climate conditions, dynamic ecological processes, and a variety of past and current management practices render broad management generalizations impractical. Recommendations for spotted owl recovery in this area also need to be considered alongside other land management goals—sometimes competing, sometimes complimentary—such as fuels management and invasive species control. In some cases, failure to intervene or restore forest conditions may lead to dense stands heavy with fuels and in danger of stand-replacing fires and insect and disease outbreaks. In general, we recommend that dynamic, disturbance-prone forests …should be actively managed in a way that reconciles the overlapping goals of spotted owl conservation, responding to climate change and restoring dry forest ecological structure, composition and processes, including wildfire and other disturbances.

The management of forested landscapes entails many considerations. In addition to the concerns raised above, there are other species of conservation concern (including candidate species for listing under the Endangered Species Act of 1973 [ESA 1973]) that also occupy the mid-elevation multilayered, mature forests that California spotted owls use. In particular, the pacific fisher (*Pekania pennanti*), another old-forest-associated species of concern, is found in the southern Sierra Nevada where its range almost entirely overlaps that of the California spotted owl. Therefore, management of California spotted owl habitat may have complementary or competing objectives with other old-forest-associated species. This could be especially important when considering the cumulative effects of multiple conservation strategies on meeting ecosystem management and ecological restoration objectives.

This Conservation Assessment

This conservation assessment for the California spotted owl was initiated in response to a request by the Pacific Southwest Region of the USFS to provide a scientific foundation for a comprehensive conservation strategy for National Forest System lands within the owl's range. The intention of this assessment was to provide a comprehensive overview of the best available scientific information about the ecology, habitat use, population dynamics, and existing and potential threats throughout the geographic range of the California spotted owl, as well as its implications for land management within the context of the broader landscape. It was also intended to specify and clarify to the degree possible the complex interactions of owl populations, forests, and landscape dynamics, and address these topics from the perspective of different areas of scientific expertise in order to provide a more comprehensive perspective on management challenges and opportunities. In a few cases, different authors reached different conclusions about particular topics; when this occurred, authors worked together to provide additional clarification on the range of perspectives and their respective foundations. Ideally, this assessment will help inform future options for management ranging in scale from site-specific projects to large landscapes to the entire range of the owl. Land managers must reconcile many objectives and demands, including conserving the full suite of native species associated with forest ecosystems within their jurisdiction. We intended this assessment to inform that reconciliation.

The geographic coverage of this assessment includes the entire range of the subspecies—the Sierra Nevada, the Transverse Ranges of southern California, and portions of central coastal California (Gutiérrez et al. 1995). However, the majority of the owl population occurs in the Sierra Nevada, and this is also where most of the new information has been generated over the past 20 years. Thus, this assessment is focused primarily on the Sierra Nevada, with a largely independent update of the southern and coastal California populations addressed only in chapter 8.

The Owl Assessment Team members, the authors of this assessment, were assembled to represent expertise relevant to the conservation and management of the California spotted owl and its habitat (see appendix). This team provided expertise not only in owl biology but also in several related disciplines, including climate change, fire and fuels management, forest ecology, remote sensing, and vegetation ecology.

The forests in which the owl lives have changed significantly in composition and structure over at least the past 100 years as a result of human activities and will be subject to additional human influences and other stressors in the coming decades. This assessment provides a comprehensive summary of the state of knowledge in relevant topic areas, many of which were also addressed in CASPO. The latest understanding of the biology of the spotted owl is provided in chapter 2. Chapter 3 provides a thorough reporting of the current knowledge of habitat associations and use. Population distribution and trends based on demographic monitoring and other research results are summarized in chapter 4. The assessment then transitions to the environmental context for owl populations and habitat, starting with an overview of current and projected future forest conditions in mid-elevation conifer forests of California in chapter 5, followed by habitat mapping and analysis technology in chapter 6. Chapter 7 summarizes the primary threats that owl populations and habitat face currently and into the foreseeable future. Given the relative paucity of information on spotted owl population status and trends in southern California, an overview of what we do know is presented entirely in chapter 8. The assessment concludes with a synthesis and interpretation of California spotted owl research within the context of broader land management challenges presented in chapter 9.

This assessment does not evaluate explicit habitat management options for the long-term maintenance of the owl throughout its range, but rather it attempts to identify key elements that appear to be critical to the success of any conservation effort, and it explores implications for future research and management. This assessment does not provide an evaluation of monitoring and inventory program needs necessary to provide for adaptive management of the owl, but it does identify future research investments that could reduce key uncertainties as management proceeds.

Although this assessment addresses only one species, it reflects the situation facing old-forest ecosystems and associated species in dry forest ecosystems of the Sierra Nevada and southern California. The essential role of fire in restoring the resilience of forests in the range of the California spotted owl, juxtaposed with the threat that high-intensity wildlife poses to suitable spotted owl habitat given current forest conditions, and the uncertainty of impacts to owls of forest treatments to reduce the risk of high-intensity fire creates challenges for both scientists and managers. The role of forest management and the use of managed wildfire and prescribed fire emerge as dominant themes across the chapters of this assessment, and the final chapter provides an evaluation of common ground between owl conservation approaches and management to restore forest resilience.

Information Sources Consulted

Substantial monitoring of owl populations, field research, and analysis of data have been completed since CASPO. Five geographically distinct demographic study areas were established either before or approximately coincident with CASPO to examine apparent survival probability, reproductive output, and population trends. The five areas were on the Lassen National Forest, Eldorado National Forest, Sierra National Forest, the adjoining Sequoia and Kings Canyon National Parks, and the San Bernardino Mountains. These study areas represented a broad spectrum of habitat and management conditions in the Sierra Nevada and the largest population in southern California (Franklin et al. 2004). Although the San Bernardino Mountains demography study ended in 1998, it has been the source of the majority of information from southern California. A summary of the latest scientific information on the southern California owl populations was developed in 2011 by the San Bernardino National Forest[2] but not published. Many other research projects were conducted throughout the range of this subspecies within this time period, contributing significantly to the current body of knowledge about the owl.

The information used in this assessment is based almost exclusively on peer-reviewed, published literature. The team was not solely dedicated to this task but, as it was a minor allocation of their professional responsibilities, we limited the review to (1) published information), (2) only a limited scope of northern spotted owl work, and (3) no data compilation or analysis of raw data. As such, it was a much more limited and constrained (by time and money) effort relative to CASPO. It was not possible within the constraints of this assessment to access unpublished reports and archived data that may exist and that could be relevant to this assessment. Resources used to inform this assessment are individually referenced and cited in each chapter.

The Process and Product

This assessment is published as a Pacific Southwest Research Station (PSW) general technical report, as was the previous CASPO report. General technical reports provide the opportunity for a detailed reporting of information, a rigorous peer review process, and an easily accessible outlet. The technical peer review was conducted by an anonymous, independent group of four scientists who represented the same scientific disciplines covered by the content of the report. The comments of the reviewers were individually addressed through a scrupulous revision process. The document also was subject to management review by Region 5 staff, and to a policy review by PSW.

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Chapter 2: The Biology of the California Spotted Owl

R.J. Gutiérrez, Douglas J. Tempel, and M. Zachariah Peery[1]

Introduction

The spotted owl (*Strix occidentalis*) is one of the most studied raptors in the world (Lõmus 2004) because forest management throughout its range has the potential to negatively affect owl populations. Information on the California spotted owl (*S. o. occidentalis*) has been summarized in several literature reviews (e.g., Gutiérrez 1996; Gutiérrez and Carey 1985; Gutiérrez et al. 1995; Keane 2014; Roberts and North 2012; USFWS 1990, 1993, 2003, 2006; Verner et al. 1992a). However, the first comprehensive review of the biology of the California spotted owl was conducted by Verner et al. (1992a). Verner et al. (1992a) also served as a foundational chapter for the California spotted owl technical assessment "The California Spotted Owl: A technical Assessment of it's current status" (CASPO) and its recommended owl management strategy (Verner et al. 1992b). Much has been learned about the biology of the California spotted owl since CASPO including new methods of data analysis to provide scientifically defensible results (Gutiérrez 2004, 2008). In this chapter, we summarize new information on the natural and life history of the California spotted owl that has been gathered primarily since CASPO (Verner et al. 1992b), but we also include new research about other owl subspecies (northern and Mexican spotted owls, *S. o. caurina* and *S. o. lucida*, respectively) when it is applicable to the California spotted owl. We cite the *Birds of North America* spotted owl account (Gutiérrez et al. 1995) for most information about northern and Mexican spotted owls published before 1995 rather than citing the original sources. Relatively more ecological knowledge is available for the northern spotted owl owing to its longer history of conservation concern and its commingling with old-growth forest protection issues (Gutiérrez et al. 1995, 2015; Redpath et al. 2013). Although this chapter is about the general biology of California spotted owls, most of the salient ecological information on habitat use and population dynamics is treated separately in chapters 3 and 4, respectively, of this assessment because those topics are particularly critical for understanding current population trends and developing

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future forest management plans. Indeed, we know more about spotted owl habitat and population dynamics than of most other species of conservation concern (Gutiérrez 2008, Lõhmus 2004). Finally, we occasionally include the theoretical underpinnings to support inferences we make about some new research findings.

Taxonomy

The three owl subspecies named above (northern, California, and Mexican) are the only subspecies recognized by the American Ornithologists' Union (AOU 1957). Whether the subspecies is a useful or valid taxonomic delineation is a much debated topic among ornithologists (e.g., Barrowclough 1982, Mayr 1982). This seemingly esoteric subject has been elevated as a topic of significance for the conservation of spotted owls because "subspecies" is a category recognized under the Endangered Species Act as a biological unit that can be considered for listing. This general subspecies controversy has led some to question the validity of some listing decisions using subspecies as a conservation unit because it has not always been clear that designated subspecies were phylogenetically distinct from other populations of a species (e.g., Zink 2004). In the case of the spotted owl, the subspecies boundaries are well defined so the subspecies as currently recognized are valid taxa (Zink 2004).

Typically, subspecies in birds have been recognized on the basis of plumage variation. For the spotted owl, the northern subspecies has the darkest brown plumage with the smallest white spots, and the Mexican subspecies has the lightest plumage with the largest white spots. California spotted owls are thought to be intermediate between them. However, these plumage characteristics exhibit clinal variation so they have not been useful for identification of subspecies in the field (Barrowclough 1990). Recent research using DNA analysis now shows a clear genetic differentiation among the subspecies (Barrowclough et al. 1999, 2005: chapter 4; Haig et al. 2004). Interestingly, California spotted owls are more closely related to Mexican than to northern spotted owls (Barrowclough et al. 1999, Haig et al. 2004). VanGelder (2003) also showed that vocal structures of the three subspecies supported the subspecies relationships that were defined by the mtDNA analysis of Barrowclough et al. (1999).

While the distributions of the two west coast subspecies and the Mexican subspecies are allopatric (separated in space), the distributions of northern and California spotted owl subspecies are parapatric (i.e., adjacent to each other in space; see fig. 2-1). This latter distribution pattern would enhance the likelihood of genetic introgression (exchange of genes between the subspecies). Indeed, introgression between northern and California spotted owls occurs and there is a cline of overlap

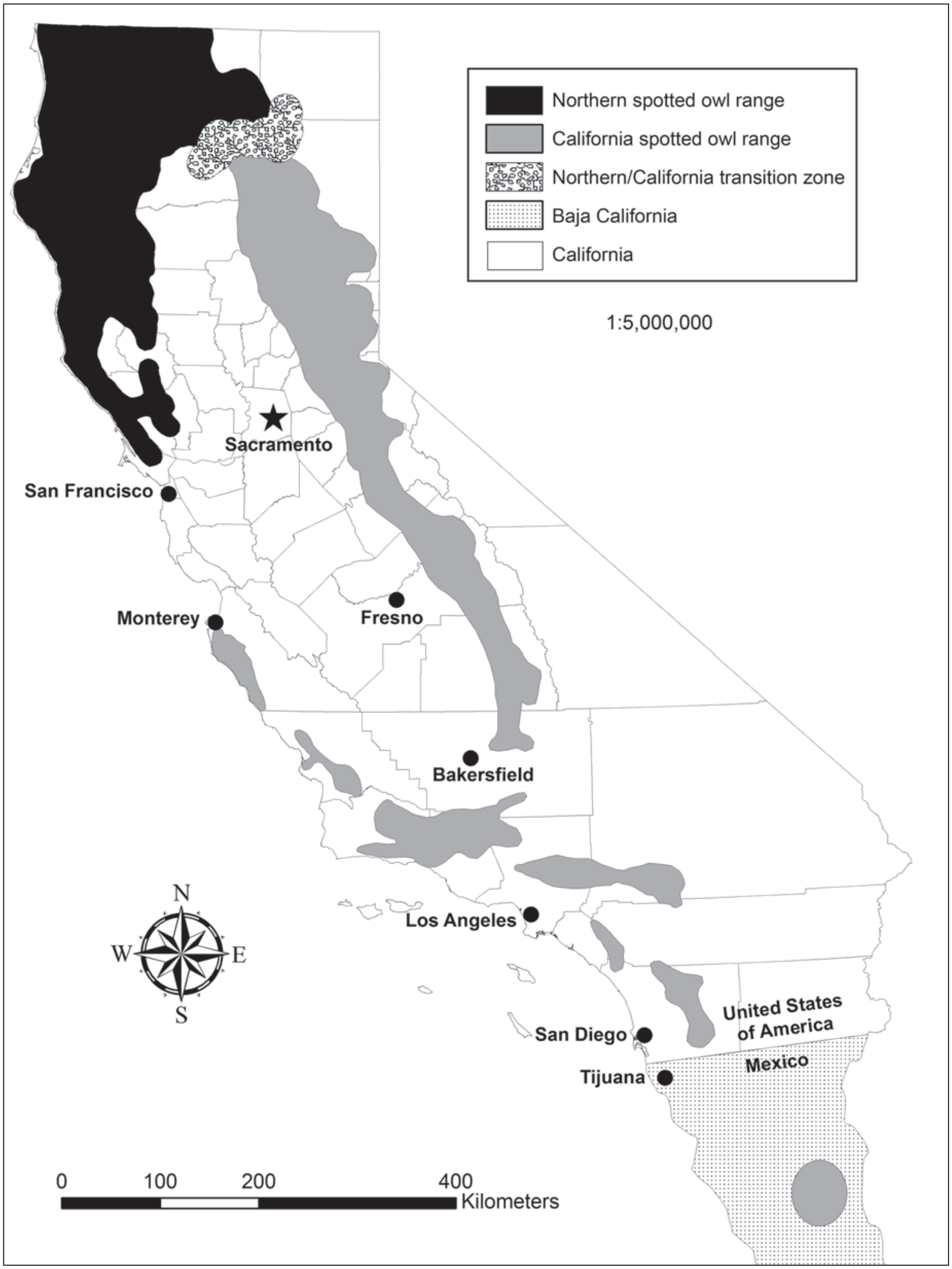

Figure 2-1—Range of the northern and California spotted owls (*Strix occidentalis caurina* and *S. o. occidentalis*, respectively) in the Sierra Nevada and their zone of overlap in northeastern California.

in northeastern California near the Pit River (Barrowclough et al. 2011; fig. 2-1). For purposes of owl management and conservation, the Pit River is recommended as the management dividing line between the northern and the California subspecies (Gutiérrez and Barrowclough 2005). Thus, the Hat Creek Ranger District of the Lassen National Forest is that unit of U.S. Forest Service managed land where the transition of the northern and California subspecies occurs (fig. 2-1).

Of relevance to this assessment is the systematic relationship of California spotted owls occupying various mountain ranges in southern and central coastal California. This relationship was unknown at the time of CASPO (Verner et al. 1992a). Although the "island" populations in southern California were traditionally classified as California spotted owls, those in central coastal California were thought to be either California or northern spotted owls owing to potential connectivity with populations in the south or proximity to birds in the north (i.e., northern spotted owls). Recent mtDNA analyses demonstrates that owls found in the Santa Lucia Mountains (i.e., the most northerly population of spotted owls on the central California coast) and birds from several southern California populations belong to the California spotted owl taxon (Barrowclough et al. 2005).

Genetic studies reveal that California spotted owls have low genetic variation. Barrowclough et al. (1999) proposed three hypotheses for this low genetic variation. The first was that there was a demographic population bottleneck (the population declined for unknown reasons, which led to loss of genetic variability). The second was that there was a selective sweep of a superior genotype. The third was that there was a founder event; a few founder owls immigrated to the Sierra and established a population, which provided a limited genepool for the population. At this time, these hypotheses have not been tested explicitly, but some could be tested using other genetic markers and tools (see chapter 9).

Ecology

The extensive research on spotted owls has allowed scientists to develop substantial insight about the life history strategy of the spotted owl. It is clear from this research that the spotted owl is a K-selected species, meaning that natural selection has favored the evolution of long lifespans and low reproductive rates as mechanisms to mediate the negative effects of unpredictable environmental conditions (in terms of weather variability, disturbance frequency, and other random events in nature). This life history strategy has led some scientists to suggest that they likely exhibit a "bet-hedging" life history strategy (Franklin et al. 2000, 2004). Understanding the spotted owl's basic ecology is essential for developing predictions about the effects of disturbance. The effect of fire, logging, fuels treatments, and drought stress on habitat (and perhaps individuals) related to climate change on different life history parameters (survival, reproduction, dispersal) and social structure and processes needs to be evaluated within the context of the owl's evolutionary history. For example, disturbance at the nest may cause nest desertion, and disturbance that lowers habitat quality may precipitate either territory abandonment or divorce (e.g., breaking of pair bonds) (Gutiérrez et al. 2011). The bet-hedging strategy predicts a species can overcome short-term negative factors but will have more difficulty overcoming the relatively longer term impact of reduction in habitat quality. Underpinning its evolutionary strategy is the nature of the animal itself—how it behaves, its social system, and how those relate to its reproductive ecology, survival, and dispersal.

Behavior

Vocalizations—

Spotted owls communicate using a variety of hoot, whistle, chitter, and "bark" vocalizations (Gutiérrez et al. 1995). They use a four-note hoot and a series (a long series of hoots based on a foundational four-note hoot) call when defending their territories. These two vocalizations are likely also used for pair bond maintenance and expressing excitement, respectively (Gutiérrez et al. 1995). VanGelder (2003) reported that the vocalizations of California spotted owls from the Sierra Nevada appeared to be adapted to forests having higher vegetation complexity than is found in forests occupied by Mexican spotted owls because vocalizations attenuated less when experimentally broadcast into foliage. Moreover, the structure of vegetation where spotted owls were found was a good predictor of song structure. These results indicated that vegetation structure exerted selection pressure on the structure of owl vocalizations.

Social system and territoriality—

Spotted owls have a monogamous mating system, with pairs forming relatively long-term pair bonds (Gutiérrez et al. 1995). However, spotted owls sometimes break pair bonds (i.e., "divorce") after failing to produce young; birds that break pair bonds or whose mate has died will form new pair bonds with other birds (Blakesley et al. 2006; Gutiérrez et al. 1995, 2011). Coincident with their mating system and territoriality, California spotted owls show strong site fidelity (Berigan et al. 2012). Thus, frequent breeding dispersal (indicating lower site or mate fidelity) could be indicative of disruption of their social system.

Spotted owls are territorial, which means they defend an area by excluding other pairs or individuals from the core of their home range (Gutiérrez et al. 1995). For this reason, owls are dispersed rather than clumped within landscapes.

Moreover, core areas of California spotted owls tend to be spatially static over time (Berigan et al. 2012). For example, in the Sierra Nevada, spotted owl territories are more dispersed than expected by chance, and sites having similar occupancy rates are dispersed rather than being clumped (Seamans and Gutiérrez 2006). Unbiased estimates of adult survival derived from even very small sampling areas indicate that territorial owls generally do not shift territories or undergo breeding dispersal from an established territory (Blakesley et al. 2010, Gutiérrez et al. 2011, Zimmerman et al. 2007).

The risk of divorce or leaving a territory when a mate dies is significant. First, if a bird leaves its territory as a result of divorce or mate death, it will be unfamiliar with the landscape in a new territory, which places it at a disadvantage (e.g., no knowledge of locations of good foraging patches) (Hirons 1985). Second, divorce incurs other risks such as failing to find a new mate or finding a new mate that is not as high a quality as the one divorced. For example, Gutiérrez et al. (2011) reported that birds that lost mates because of a mate's presumed death (mate never detected again on the study area) tended to improve their reproductive success, whereas it was not clear that birds who divorced also improved their reproductive success. Thus, understanding the reasons why birds divorce may have important management implications if forest management activities that lead to disruption of pair bonds negatively affect demographic processes.

Not all spotted owls are territorial, and these nonterritorial individuals are called "floaters" (Franklin 1992). Some floaters are younger birds in search of their first territory, but others seem to be birds that have left a territory and become nonterritorial for unknown reasons. These floaters can occur within or outside the home ranges of territorial birds, but it is unknown whether they are tolerated by resident birds or simply not detected by resident pairs because they do not attempt to defend an area using vocalizations. Although floaters do not contribute to the reproductive output of a population, they can influence population dynamics because they provide a pool of birds that could colonize vacant territories or pair with single birds (Franklin 1992).

The territory (the area that is actively defended by birds) of a pair is likely smaller than their home range although no one has precisely estimated the size of the areas they will actively defend (i.e., their true territories). Rather, from a management perspective, the concept of territory has been "approximated" by various derivations of a "core area" such as a protected activity center or PAC (an area of about 121 ha [300 ac]) that was created to anticipate the likely essential areas used for nesting and roosting, but not for foraging or even territorial defense (Verner et al. 1992b). Other researchers have attempted to estimate the core area (the area of concentrated use) of both northern and California spotted owls (Bingham and Noon 1997) and to examine how well PACs accommodate long-term use by spotted owls for nesting and roosting (Berigan et al. 2012). Based on their assessment of the Lassen demographic study population, Bingham and Noon (1997) suggested that the core area for California spotted owls was about 813 ha (2,009 ac), which was substantially larger than the designated size of a PAC (about 121 ha [300 ac]). One reason for this disparity was that Bingham and Noon (1997) estimated the core area based on analysis of radiotelemetry data, whereas PACs were designated by contiguous association of preferred habitats at and around nests and primary roosts (Verner et al. 1992b).

Intraspecific interactions—

Members of a pair of spotted owls divide roles when nesting. Females incubate eggs and brood young, while males provision females with food so they can maintain incubation with little interruption (Gutiérrez et al. 1995). Males defend the territory at this time more predictably than females. Thus, males are often detected first in occupancy surveys, while females that are actually present at the same sites may go undetected until later surveys. When eggs hatch, the owlets are guarded and fed by both parents, but the female tends to continue brooding (Gutiérrez et al. 1995).

Because spotted owl home ranges are relatively large, it is likely impossible for territorial pairs to defend their entire home range from other spotted owls, so home ranges of adjacent owls often overlap (Gutiérrez et al. 1995). Because spotted owls are central-place foragers, they expand their activities outward from their nests or roosts to forage on prey that is patchily distributed and that can be depleted through predation within those foraging patches (Carey et al. 1992, Carey and Peeler 1995, Ward et al. 1998). Thus, their activity declines within far patches relative to close patches as distance from the territory center increases owing to travel time. They engage in conspecific interactions with “neighbors” (i.e., adjacent territorial owls) and “strangers” (non-neighbors and dispersing owls) through hooting vocalizations, and these hooting bouts intensify as foreign owls encroach on areas near the territory center. Spotted owls apparently recognize their neighbors because Waldo (2002) experimentally demonstrated the “dear enemy hypothesis” for spotted owls, where territorial spotted owls responded more strongly to broadcasts of the vocalizations of a stranger than a known neighbor. The adaptive advantage of such a conspecific response is that territorial owls do not have to expend energy defending a territory from an individual with whom they have already established a territory boundary.

Inbreeding is a conspecific interaction that is generally considered maladaptive because of the potential for the expression of deleterious alleles. Inbreeding can occur between distant and close relatives (siblings, half-siblings, and parents with offspring). A comprehensive analysis of inbreeding has not been done for spotted owls, but “incest” (inbreeding of close relatives) has been reported for both northern and California spotted owls (Carlson et al. 1998).

Interspecific interactions—

Spotted owls in California are not apex predators in their food chain. Great horned owls (*Bubo virginianus*) are sympatric, larger, and can prey on spotted owls (Gutiérrez et al. 1995). However, spotted and great horned owls do not usually use the same habitats; great horned owls typically occupy more open habitats than spotted owls (Johnson 1992). Moreover, the simulated presence of great horned owls in the territories of spotted owls does not suppress calling behavior in spotted owls (Crozier et al. 2005), which suggests that great horned owls either are not generally a threat to spotted owls or they are not likely to be in the same habitats. Finally, spotted owls will sometimes nest in the same stand as great horned owls even though great horned owls are known to prey on spotted owls (Gutiérrez et al. 1995).

The invasion of the barred owl (*Strix varia*) in western North America has raised concern over the potential for this species to negatively affect spotted owls (Gutiérrez et al. 2007, USFWS 1990). Barred owls were first documented in California in 1981, and by 2004, one barred owl has been detected as far south as Kings Canyon National Park in the southern Sierra Nevada (Dark et al. 1998, Steger et al. 2006). The barred owl invasion has been of substantial concern for spotted owl conservation and will be covered in detail in chapters 7 and 9. Spotted owls also interact with other species on a daily basis. For example, they are routinely mobbed by other bird species (Gutiérrez et al. 1995), and they are victims of kleptoparasitism, when other species steal prey the owls have cached (Hunter et al. 1993).

Activity patterns—

Spotted owls are primarily active at night. They hunt, defend, socialize, and conduct exploratory movements at night (Gutiérrez et al. 1995). However, they also can be active at dusk when they often socialize and begin to hunt, but they will opportunistically prey on species that are active during the day (Gutiérrez et al. 1995, Laymon 1991). During the day, however, they primarily sleep, conduct self-maintenance, and guard young while roosting in complex-structured forests (Gutiérrez et al. 1995). Roost stands are often areas used consistently by owls over many years (Berigan et al. 2012). The areas around nest sites, together with roost sites, serve as the center of activity for spotted owls (i.e., a prediction of central-place foraging theory) (Carey and Peeler 1995). Their night time foraging locations can be anywhere within the home range, both within the core area and well beyond it (Williams et al. 2011).

Although spotted owls are most active at night, there are periods during the night when they are more active than others. For example, activity is highest during the periods 1 to 3 hours after sunset to 1 to 3 hours before sunrise (Gutiérrez et al. 1995). These general activity periods have been quantified by Delaney et al. (1999), where the highest prey delivery rates occurred at these times. Owls progressively increase prey delivery rates to the nest as young mature, while females spend less time in attendance of young as the brood-rearing period progresses (Delaney et al. 1999).

Response to human activities—
The spotted owl has long been recognized for its tame behavior because it often tolerates close approach by humans (Gutiérrez et al. 1995). Tameness has often been mistaken for adaptability or lack of disturbance effects in animals. However, many studies have shown that animals may exhibit no outward signs of stress when they are actually having a physiological stress response (Beale 2007). Indeed, a study of northern spotted owls suggested that birds had elevated levels of corticosterone, a stress hormone whose metabolites can be detected in feces, when living near roads or areas that had been logged (Wasser et al. 1997). In contrast, Tempel and Gutiérrez (2004) analyzed corticosterone metabolites in feces of spotted owls from the central Sierra Nevada and found that corticosterone levels were best explained by the breeding state of individuals and how samples were stored in the field, rather than by the presence of roads or habitat type.

In another assessment of spotted owl response to humans, Swarthout and Steidl (2003) conducted an experimental study of the behavioral response of Mexican spotted owls to recreational hikers and showed that Mexican spotted owls changed certain activity patterns in response to both high levels of recreation use and to the presence of observers. They suggested that spotted owls were tolerant to moderate levels of disturbance (i.e., noise not within 100 m [328 ft] of roosting birds, <50 hikers per day), but high levels of recreational activity could cause disturbance (Swarthout and Steidl 2003). Swarthout and Steidl (2003) results also suggested that researchers should minimize their time and activities when working near spotted owls.

Reproductive Ecology

Reproduction is a vital rate that contributes to population growth and will be covered in chapter 4. However, it is important to set the context of the spotted owl's reproductive ecology in both relative and evolutionary contexts. Spotted owls exhibit the lowest reproductive rate among North American owls (Johnsgard 1988).

Mean reproductive output (number of young produced per female) across years has varied among the five long-term demography monitoring areas in the Sierra Nevada and southern California (0.555 to 0.988 young/female) (Blakesley et al. 2010, Franklin et al. 2004; see also chapter 4 for details). Moreover, the range in annual reproduction by California spotted owls is extremely variable, ranging from no young produced within a demographic study area in a given year to nearly all birds nesting (Blakesley et al. 2010, Franklin et al. 2004, Seamans and Gutiérrez 2007b, Tempel et al. 2014). As previously noted, this highly variable rate of reproduction coupled with a high survival rate has given rise to the hypothesis that California spotted owls, like northern spotted owls, exhibit a bet-hedging life history strategy (Franklin et al. 2000, Stearns 1976). In the case of the California spotted owl, natural selection has favored the evolution of high survival rates that allow the owls to forgo breeding in "bad" years so they can breed in "good" years. Bad and good are relative terms here and can mean the difference between years of high and low prey or years of inclement or mild weather during the critical nesting period. The significance of this bet-hedging strategy is that lack of reproduction at a site for a few years does not necessarily mean the site is of low quality, but rather it could be related to overall poor environmental conditions leading to absence of reproduction (Stoelting et al. 2014).

There are several environmental or ecological factors that have been examined to explain patterns of reproduction in California spotted owls. Reproductive success is often correlated with annual variation in weather (LaHaye et al. 1997, MacKenzie et al. 2012, North 2002, North et al. 2000, Seamans and Gutiérrez 2007b, Stoelting et al. 2014). The focus on the relationship with weather and vital rates is common because weather is easily measured and can be used to infer both indirect and direct potential effects on owls (e.g., it influences plant growth and thus prey populations, which affects energy budgets of owls). The influence of weather on reproduction is, however, confounded by the substantial variation in the distribution and abundance of the owl's prey (Ward et al. 1998). Weather can potentially affect spotted owls directly either by increasing energy demands of owls, increasing the risk of exposure of eggs when females have to leave the nest, and interfering with hunting and indirectly by influencing plant growth, which affects population dynamics of owl prey (Franklin et al. 2000, Rockweit et al. 2012, Seamans and Gutiérrez 2007b, Weathers et al. 2001).

A peculiar element of reproductive variability in spotted owls, including California spotted owls, is an alternating pattern of high and low years of reproductive output (Blakesley et al. 2010, Franklin et al. 2004). This pattern has been labeled the even-odd effect of reproductive output in owl population studies (Franklin et al. 1999, 2004). North (2002: 118) also reports "distinct annual fluctuations" of good and bad years of reproduction. Why this pattern occurs is unknown, but a logical hypothesis is that there is a "cost of reproduction" borne by owl pairs successfully raising young (Forsman et al. 2011, MacKenzie et al. 2009). That is, birds that reproduce successfully in one year are less likely to breed in the subsequent year because there is an energetic cost to reproduction that presumably reduces the condition of females (MacKenzie et al. 2009, Stoelting et al. 2014). However, Stoeling et al. (2014) simulated the even-odd cycle in California spotted owls and found that the observed cost of reproduction was insufficient either to generate or to maintain this even-odd pattern. Stoelting et al. (2014) hypothesized that some external, widespread environmental factor was likely responsible for generating and maintaining this cycle (see also North 2002). Interestingly, the even-odd effect in northern spotted owls appears to be waning with time (Dugger et al. 2016).

Other observations about individual costs of reproduction have been linked to California spotted owls. California spotted owls typically fledge one to three young (Gutiérrez et al. 1995), with three young in a brood being uncommon (Tempel et al. 2014). There are records of four-egg clutches or broods, but these are extremely rare, having been recorded only twice in southern California (Dunn 1901, LaHaye 1997). Thus, a question arises about the optimal clutch (brood) size for owls. Peery and Gutiérrez (2013) showed that when juveniles fledge from broods of two they have a greater survival probability than if they fledge either from a single or triplet brood. More importantly, this effect carried over to subadult and adult age classes. This occurs even though it should be more difficult for parents to provision two chicks than one chick. Finally, Peery and Gutiérrez (2013) reported that indices of territory quality, based on chick survival, were positively correlated with indices of territory quality based on parental reproductive output.

Whether owls successfully breed at sites also seemed to influence whether they will remain on those sites. For example, Gutiérrez et al. (2011) showed that owls having higher reproductive output compared to the entire population were less likely to disperse. While their result was confounded by mate quality (i.e., a bird might be more likely to stay at a site if they have a "high-quality" mate), they also found that owls were less likely to leave sites where owl reproduction was higher than the population average, which partially controlled for the effect of mate quality because these long-term effects accounted for multiple owls occupying the same sites.

The distribution and abundance of owl prey is another key factor that influences spotted owl reproductive success. Yet, studies of owl prey have lagged behind the study of other aspects of owl ecology even though prey are central to understanding the ecology of a predator (Newton 1979). The reason for this lack of study is simply that prey studies are costly, rather than failure by scientists to recognize this obvious connection (Gutiérrez 1985b). Much of our knowledge about spotted owl prey comes either from studies of northern spotted owls or the small mammal literature, although there are exceptions (Waters and Zabel 1995, Waters et al. 2000, Zabel and Waters 1997). However, there have been several studies relating spotted owl habitat to owl reproduction and others enumerating prey in the diet (see below).

Barrows (1985, 1987) first showed that California spotted owls took relatively larger prey when they were nesting, and they shifted their diet from larger to smaller prey when they failed in their breeding attempt. Thrailkill and Bias (1989) also found that diets of breeding owls contained more large prey by both frequency and biomass than nonbreeding owls. These early diet studies were both relatively limited either in terms of sample size (number of territories sampled in breeding and nonbreeding categories) or pellets collected per territory. These sample size limitations were overcome by Smith et al. (1999) who collected over 8,000 pellets from 109 territories in the San Bernardino Mountains over several years. They found that successful nesting owls had a greater percentage of biomass of large prey than small prey in diets relative to nonnesting owls. However, there was no difference in size of prey eaten between successful nesters and those pairs that attempted to nest but failed, suggesting that nests failed for reasons other than prey dynamics. However, the relationship between large prey in the diet and propensity for breeding was not clearly established for owls inhabiting the Sierra National Forest (Munton et al. 2002). Although it seems logical that spotted owl prey may be affected by abundance of pine seed production and thus affect owls, North (2002) found no such relationship in the southern Sierra Nevada.

Evaluating habitat quality is challenging because owls and sites are confounded (see “Management Implications” below). That is, it is difficult to partition the effect of “high-quality” individuals from the quality of the habitat (when there are two or more potentially explanatory factors whose effects are difficult to distinguish, they are said to be confounding). Recognizing these confounding effects, LaHaye et al. (1997) found in the San Bernardino Mountains that owls nesting in lower elevation oak (*Quercus chrysolepis* Liebm.)/big cone fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) cover types had higher reproductive output than those nesting in other higher elevation cover types (LaHaye et al. 1997). Hunsaker et al. (2002) showed that owls occupying sites having canopy cover greater than 50 percent had greater productivity, and these sites also had higher occupancy rates than sites with lower canopy cover. North (2002) reported that owls in certain territories almost always produced young, even in bad years. North's finding could be related either to variation in territory quality, variation in owl quality, or an interaction between the two, but North did not have sufficient data to examine these possibilities. However, he reported that owls which occupied higher quality territories (weighted by reproduction output) used the same nests repeatedly, whereas owls occupying lower quality territories used a nest only once, which suggested local site factors were important in addition to broad regional influences.

Habitat Associations

California spotted owl habitat associations are provided in detail in chapter 3. However, we here provide some generalities and hypotheses about habitat use and their relevant ecological context. Spotted owls are primarily forest inhabitants. Their habitat selection and habitat requirements are among the most controversial issues related to spotted owl conservation because of the economic implications of habitat conservation and the design of forest management plans. However, we present some general concepts related to owl habitat and the evolution of habitat selection in California spotted owls.

Theoretically, habitat quality of a species should be reflected in individual home range size and, therefore, the spacing and density of individual territories in a population. For spotted owls, a specific hypothesis about this theory could be that home range sizes should be smaller in areas of higher habitat quality. Yet, because of territorial interactions (see next paragraph), there will be a threshold of population density, regardless of relative habitat quality. However, the relationship between density thresholds relative to habitat quality in different landscapes is unknown.

One avenue to assess habitat quality is to observe patterns of animal space use as a function of the predictions derived from ecological theory because predictions of theory can be tested with empirical data. This has been done as two general theories of habitat selection have been investigated in spotted owls—the ideal free and ideal despotic theories (Fretwell 1972, Fretwell and Lucas 1969). The ideal free theory predicts that if animals have perfect knowledge of their environment (i.e., are "ideal"), they will select the best habitat first and sequentially select lower quality habitats when higher quality ones are occupied. The ideal despotic theory predicts that territorial animals will exclude (i.e., are "despots") other individuals of the same species from occupying the same habitats (i.e., territorial behavior prevents simultaneous space use regardless of habitat quality because of intraspecific competitive exclusion). Recent evidence suggests California spotted owls follow an ideal despotic distribution of habitat selection because occupancy is correlated with “territory fitness” (“territory fitness” is a measure of territory quality based on the survival and reproduction of all owls that occupy that territory over time) (Zimmerman et al. 2003). In a seemingly counterintuitive observation, territorial behavior also seems to influence habitat selection by owls native to an area because owls immigrating into a population settle closer to territorial pairs than do owls from that population who are switching territories within the population (i.e., immigrant owls may be using presence of conspecifics as cues to settle in suitable habitat) (Seamans and Gutiérrez 2006). This suggests that both behavioral factors and intrinsic habitat quality influence habitat selection by spotted owls. Territorial behavior can constrain the allocation of space (habitat) among individuals of a population (there is an upper limit for density) and serve as a cue to naïve owls about territorial quality.

Much has been discussed about the use of private lands by California spotted owls in the Sierra Nevada because in some places, public and private lands occur in near-alternating parcels and commercial timberland is abundant (Bias and Gutiérrez 1992, Gutiérrez 1994, Moen and Gutiérrez 1997). Private and public lands often have been managed differently, which may result in different dominant forest types and forest structure. Irwin et al. (2007) studied foraging owls on primarily private land in the northern Sierra Nevada and found that owls tended to forage near nests, small streams, and areas with a diversity of conifer species and hardwoods versus areas dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). In an area of alternating public-private ownership parcels (i.e., “checkerboard” ownership pattern) in the central Sierra Nevada, spotted owls rarely used private land for nesting and roosting (Bias and Gutiérrez 1992, Gutiérrez 1994, Moen and Gutiérrez 1997). This result has been enigmatic because spotted owls occur elsewhere on private land in the Sierra Nevada (Irwin et al. 2007, Roberts 2015[2]). The findings from the central Sierra Nevada have also prompted work to determine if this pattern is related to placement of nest sites relative to hard edges (spotted owls placed their nests farther from edges than predicted by chance [Phillips et al. 2010]) and their use of private land for foraging (Williams et al. 2014). In the latter study, the researchers found that owls used private land proportionately less than its availability when foraging, even when controlling for central-place foraging tendencies.

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Habitat structure—
The structure of spotted owl habitat has long been of interest because original research suggested that spotted owls were old-growth dependent (e.g., Carey 1985, Forsman et al. 1983). Subsequently, the nature of owl-habitat relationships has been expanded to include the concept of forest structure (Solis and Gutiérrez 1990). This concept suggests that California spotted owls are habitat specialists because they select an array of forests and forest structures that are different than what is generally available on the landscape (Gutiérrez et al. 1992, Verner et al. 1992a). For example, they select sites that have larger trees, higher canopy cover, and more coarse woody debris than occurs on sites available to them (chapter 3). Research on the structure of spotted owl vocalizations also supports this forest-structure relationship because it appears California spotted owl vocal structure evolved in response to "complex" forest structure (VanGelder 2003). Song is the fundamental way by which most birds communicate (defend territories, attract mates, maintain pair bonds), and thus there is a large body of research on the adaptive nature of vocalizations relative to habitat that a species occupies.

Several hypotheses have been generated to explain why owls select old/mature forests (e.g., nest site selection, ambient temperature moderation, availability of prey), and these hypotheses are relevant under the habitat structure selection hypothesis (Carey 1985, Forsman et al. 1983, Gutiérrez 1985a). To these, we add an additional hypothesis that the owls themselves have evolved in fire-adapted forest ecosystems because all landscapes spotted owls now inhabit experience some type of historical fire regime. In addition, their resilience to fire of low and moderate severity is consistent with this fire-adapted hypothesis. Under either a predominantly accepted hypothesis that a frequent, low- to moderate-severity fire regime was the historical norm in the Sierra Nevada (chapter 5) and an alternative that posits a mixed-severity fire regime prevailed in the West historically (e.g., DellaSala and Hanson 2015 and references therein; SNEP 1996), there is uncertainty about the precise distribution and abundance of various forest types and structures under historical fire regimes. This uncertainty is underscored by the fact that the current sites spotted owls use for nesting and roosting in the Sierra Nevada indicate that there was a relatively high density of large trees on the landscape in many places. That is, the large, old trees at current owl sites were present in presettlement times (Gutiérrez et al. 1992). The importance of this uncertainty is that it can lead to different predictions for desired future conditions of forests. To this end, we propose that neither of these hypotheses about historical fire regimes is inconsistent with creating and maintaining suitable spotted owl habitat (e.g., under the predominant fire paradigm, the structure of old-growth forests that were under a suppression regime returned to a condition likely to be suitable for owls, at least in terms of diameter distribution of trees and size of trees, after two cycles of return fire) (Lydersen and North 2012). Hence, the forest structure hypothesis is important to consider when thinking about appropriate management actions. In addition, because fire suppression has led to unnaturally high densities of trees in most places and owls often inhabit these areas, we think that describing suitable owl sites as "dense" may obfuscate the discussion about spotted owls. For one, the word "dense" is a normative term and, therefore, conjures different visualizations among people about both tree density and vegetation structure, which then leads to concerns about such things as spotted owl habitat being a fire hazard, susceptibility of trees to insects and diseases, and effects of climate change on forests. For another, there are many forests that do not have spotted owls because either they have such a high density of trees or high foliage volume that it may impede hunting by owls, or they have low prey densities (these were among the original hypotheses linking owls to old-growth forests). Consequently, as qualitative expressions to aid discussion, the terms "multistoried structure" or "complex-structured forest" seem more appropriate terms to describe owl habitat than does the term "dense" because most dense forest stands without tree age or size structure do not harbor owls. In this context, complex-structured forests do not necessarily have to have the density of trees that often occurs in stands following long periods of fire suppression. Moreover, achieving this type of forest structure does not seem incompatible with reintroduction of fire as a natural process (Lyderson and North 2012).

Disturbance—

The effect of disturbance on owls and their habitat has been a concern, particularly the effect of large, high-severity fires and associated salvage of fire-killed trees. These can potentially affect owls negatively (Clark et al. 2011, 2013; Lee et al. 2013, 2015b; see also chapters 3 and 4). Moreover, climate change will likely increase the frequency of these types of fires. Research has shown that low- and moderate-severity fires have little or no effect (acute or chronic) on spotted owls (Bond et al. 2002, Roberts 2008, Roberts et al. 2011). This result has not been surprising given that spotted owls evolved in forests that experienced fire frequently. One study of radio-marked owls showed that owls will forage in areas that have been burned (Bond et al. 2009) while another study showed that owls foraged at the edge of burns (Eyes 2014). Studies of territory occupancy showed that mixed-severity fires had no effect on owls (Lee et al. 2012, Roberts 2011) while high-severity fires had negative effects (Clark et al. 2013, Lee et al. 2013). However, the owl territories in studies by Clark et al. (2013) and Lee et al. (2013, 2015b) were also affected by salvage logging. Lee and Bond (2015a) reported a high occupancy rate of owl territories in the first year following the very large Rim Fire in the southern Sierra Nevada. Recently, however, Jones et al. (2016) demonstrated a strong first-year impact of the King Fire in the central Sierra Nevada on California spotted owls. Almost all territories that were occupied prior to the fire, but experienced >50 percent high-severity fire, became unoccupied following the fire—with several owls moving to the less severely burned territories. Moreover, GPS-tagged owls exhibited strong avoidance of high-severity fire burned patches, particularly those in the main, high-severity patch. Currently, additional research has been undertaken to examine the longer term impacts of the Rim Fire on the owl population studied by Lee and Bond (2015a; Keane 2015[3]). Differences in the inferred effects of the Rim and King Fire studies could be the result of more patchily distributed high-severity-fire burned patches in the Rim Fire, or differences in methodology between the two studies (e.g., the King Fire study used marked birds, whereas the Rim Fire study did not). Ongoing work at both sites will provide more perspective on the relative and longer term impacts of these fires and whether there are different outcomes to fire effects, as these early studies indicate.

Similarly, logging, especially when used as a treatment to reduce fire hazard, is of particular concern (Verner et al. 1992b) because logging treatments will be a mechanism to reduce fuel loading in forests. Logging has long been presumed to negatively affect spotted owls through loss of habitat (Gutiérrez et al. 1995). Effects of logging have been demonstrated recently both indirectly and directly. Seamans and Gutiérrez (2007a) showed that occupancy declined when at least 20 ha of high-canopy, mature forest was lost from a territory, but they did not partition losses attributable either to logging or fire. Tempel et al. (2014) showed that the proportion of high-canopy, mature forest was the best predictor of occupancy by owls. In their study, the owl population had declined by 50 percent over the sampling period, so the assumption was that disturbance by various kinds of logging was partially responsible for the decline. Finally, Stephens et al. (2014) demonstrated experimentally that logging treatments designed to reduce fire risk resulted in a loss of owls. As noted above, there appears to be a compounding effect on occupancy of salvage logging following fire in owl territories (Clark et al. 2013; Lee et al. 2013, 2015b).

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Diet

The general diet of spotted owls has been well described in the literature (Gutiérrez et al. 1995). Spotted owls prey primarily, by biomass, on medium-sized small mammals, particularly dusky-footed woodrats (*Neotoma* spp.) and flying squirrels (*Glaucomys sabrinus*) (Gutiérrez et al. 1995). However, they eat a wide array of other small mammals, such as mice and voles, as well as birds, lizards, and insects. Flying squirrels are found in closed-canopy forests, usually at higher elevations than woodrats. Woodrats also use closed-canopy forests and oak woodlands, early-seral-stage forests (e.g., clearcuts and fire-disturbed landscapes), and shrub cover types. Recent studies have generally confirmed past observations of owl diet, but there have been some notable differences recorded (see below).

Diet analysis has been a mainstay of owl studies because owls regurgitate indigestible parts of their prey as consolidated "pellets," which can be found at roost and nest sites (Marti 1987). These pellets contain bones, hair, nails, beaks, feathers, scales, and exoskeletons. So it is somewhat surprising that only three reports on diet composition based on pellet analyses have been published since CASPO (Munton et al. 1997, Munton 2002, Smith et al. 1999). Owls generally swallow small prey whole and dismember larger animals to swallow smaller chunks. However, they often decapitate prey and when they do this, they swallow the head first and then the body, or cache the body to eat later (Gutiérrez et al. 1995). They will also swallow the head of a prey item and give the rest of the prey to young. For these reasons, strict protocols have been observed when enumerating prey items to avoid double counting individuals in a sample (Marti 1987).

Munton et al. (1997) identified 664 prey remains from 520 pellets found at 11 territories in low-elevation (300 to 586 m [984 to 1,923 ft]) oak and riparian deciduous cover types in the Sierra and Sequoia National Forests of the southern Sierra Nevada. They identified 20 species of prey of which mammals comprised 96 percent, by biomass, of the diet. Woodrats and pocket gophers (*Thomomys* spp.) comprised 80 and 11 percent of the biomass, respectively. Interestingly, the contribution of woodrats, mice, and birds to the diet was lower during the breeding season than nonbreeding season, and the contribution of voles and pocket gophers to the diet showed the opposite pattern. This could mean either that the diversity of prey in the diet increased during the breeding season, the results were a function of sampling limitations, or the results were a function of annual variation in diet among pairs (Munton et al. 1997).

Munton et al. (2002) expanded their earlier study of lower elevation cover types by examining 1,140 pellets collected at territories between 305 and 2316 m (1,000 and 7,600 ft) on the Sierra National Forest. In addition, they added 1 year of data (1998) to their original 6-year study. Their sampled sites in this 2002 study included all those sites from the 1997 study except for the low-elevation sites on the Sequoia National Forest. They identified 2,038 individual prey items from 1,140 pellets. As before, woodrats dominated (74 and 82 percent biomass in diet in nonbreeding and breeding seasons, respectively) the diet in oak woodlands and riparian-deciduous forests (i.e., low elevation), whereas in conifer forests at higher elevations, northern flying squirrels comprised 77 percent of the prey biomass in the diet. Pocket gophers comprised the second most important food by biomass at both low and higher elevations. These results were different from earlier studies reported for the mid- to high-elevation owl habitats in the central Sierra Nevada (Laymon 1988, Thrailkill and Bias 1989) where woodrats tended to dominate in the mid-elevation forest types, suggesting that there were differences in the prey community between the central and southern Sierra Nevada.

Smith et al. (1999) reported on a large study of owl diet in the San Bernardino Mountains of southern California. They sampled the entire population of territorial owls, 109 territories, between 1987 and 1991, and identified 8,441 individual prey in pellets. Dusky-footed woodrats (*N. fuscipes*) were the most important prey by both percentage frequency (42) and biomass (74). They also found that the proportion of biomass attributed to woodrats increased as elevation increased, which was opposite to other owl diet studies where the proportion of the diet attributable to woodrats decreased with increasing elevation (e.g., Verner et al. 1992a). They found that their large sample size resulted in reasonably precise estimates of woodrats on a territory-by-territory basis but not pocket gophers, which might explain why Munton et al. (2002) found a preponderance of pocket gophers in the diet (i.e., a few sites with large samples of pocket gophers might have skewed the results). In the San Bernardino study, flying squirrels were uncommon in the mountain range and constituted only 3 percent of the biomass of the diet. This latter result was likely related to flying squirrels being at the southern edge of their range, and their low abundance did not provide owls an alternative prey source at high elevations as they did in the Sierra Nevada. Diet studies of Mexican spotted owls have revealed that both medium-sized small mammals like woodrats and smaller mammals like mice and voles (e.g., *Peromyscus* spp. and *Microtus* spp.) can be important for reproduction in owls (Ward 2001). Thus, reproduction can occur when there are high populations of various prey species, and these prey populations can differ among years, habitats, and regions.

Cause-Specific Mortality

Predation—

Spotted owls are subject to predation by great horned owls, northern goshawks (*Accipiter gentilis*), and red-tailed hawks (*Buteo jamaicensis*) (Gutiérrez et al. 1995). Great horned owls can potentially prey on adults or young, and goshawks will take juvenile owls (Gutiérrez et al. 1995). In addition, one likely case of predation of an adult spotted owl by a barred owl has been reported (Leskiw and Gutiérrez 1998).

Accidents—

Accidents are an additional source of mortality in spotted owls. There are records of spotted owls dying from collisions with automobiles and tree branches (Gutiérrez et al. 1985, Williams et al. 2011). In addition, there is one record of an owl being electrocuted when perching on a power line or transformer (Gutiérrez et al. 1996).

Disease and infection—

The appearance and rapid spread of West Nile virus has been a concern because spotted owls, like other owls, are quite susceptible to the disease (Gancz et al. 2004). Louse flies (family *Hippoboscidae*), which are common external parasites of spotted owls (Hunter et al. 1994), were implicated in a West Nile outbreak among North American owls, including a spotted owl, in a captive holding facility in Ontario, Canada, so an existing vector for the virus is present in most spotted owl populations (Gancz et al. 2004). Hull et al. (2010) conducted a survey of antibody titers of California spotted owls and found no evidence of West Nile infection. However, because of the virus' apparent virulence to owls, it is doubtful that one could detect it through surveillance monitoring. Bacteria can also cause disease in spotted owls. Thomas et al. (2002) reported a fatal spirochetosis (an acute, septicemic disease) in a northern spotted owl, which was caused by a bacterium, *Borrellia* sp. It was unknown whether this disease regularly occurs in spotted owl populations.

Parasites—

Several survey screenings for hematozoa (blood parasites) have revealed that spotted owls harbor a variety of hematozoa such as *Plasmodium* sp., *Leucocytozoon* sp., *Haemoproteus* sp., *Trypanosoma*, *Atoxoplasma* sp., and microfilariae (Gutiérrez 1989, Ishak et al. 2008, Lewicki et al. 2015, Wood and Herman 1943). California spotted owl populations were found to have the highest rates of infection when compared to northern spotted owls, barred owls, and 387 other species of owls (Gutiérrez 1989, Ishak et al. 2008). Therefore, if the hematozoa that infect spotted owls has deleterious health consequences (e.g., compromising its immune system), then it could be an advantage to invading barred owls because barred owls have lower rates of hematozoa infection and hematozoa diversity (Ishak et al. 2008, Lewicki et al. 2015). Further, given the high rates of infection of California spotted owls, such an effect might be more pronounced in competitive interactions between this subspecies and the invading barred owl. Lewicki et al. (2015) tested several hypotheses relative to the consequences of the invasion of barred owls into the spotted owl's range and found support for two hypotheses about the relationship between invasive species and their parasites—the Enemy Release Hypothesis (ERH) and the Parasite Spillback Hypothesis (PSH). The ERH postulates that host populations of invasive species will harbor lower parasite species richness in their invaded ranges relative to their original ranges, while PSH postulates that invasive species will serve as reservoirs for native parasites, which will increase exposure of native species to native parasites, resulting in higher proportions of infective native species within populations (Lewicki et al. 2015: 1714). The ERH was supported by the finding that barred owls from the east coast had higher infection rates than barred owls from the west coast, but the PSH was supported by the finding that spotted owls had higher probabilities of infection than west coast barred owls (Lewicki et al. 2015).

Hunter et al. (1994) found seven species of ectoparasites belonging to five arthropod families either on live spotted owls or museum skins. The authors considered three species (a mite, a tick, and a flea) to be accidental on spotted owls because they typically are found on rodents, the normal prey of spotted owls. The remaining parasites were chewing lice (*Strigiphilus syrnii* and *Kurodaia magna*) and louse flies (*Icosta americana* and *Ornithoica vicina*). Of these parasites infecting owls as true hosts, *I. americana* was found on live California spotted owls, and an unidentified *Strigiphilus* sp. was found on a museum skin of an owl from Mariposa County in the Sierra Nevada. However, Bequaert (1952) found *O. vicina* on a California spotted owl. No helminth or other endoparasites have been reported from the California spotted owl but likely exist because they are found in northern spotted owl populations (Gutiérrez et al. 1995).

Chapter Summary

While most of the information gathered on spotted owls subsequent to CASPO has been devoted to monitoring population trends and spatial distributions (see chapter 4), much new biological information about California spotted owls has also been collected (see also chapters 3, 4, and 7). This new knowledge about spotted owl natural and life history has application to the management of the owl because it illuminates spotted owl requirements and responses of owls to disturbance (particularly logging and fire).

Studies of physiological stress in spotted owls suggest that many routine forest operations (e.g., trail maintenance, brush removal, timber cruising and marking) are not likely to affect owls if they occur beyond 100 m from the nest or primary roost site (Tempel and Gutiérrez. 2003). However, more intrusive activities like road building and timber harvest have greater potential to disturb owls and their seasonal restriction near owl nests should be maintained.

Because spotted owls defend their territory using vocalizations described above, they can be detected with high probability during surveys, given sufficient survey effort. Moreover, the site fidelity exhibited by a territorial pair and the consistency of their spatial location among years (Berigan et al. 2012) suggest that monitoring of spotted owls over large areas can be accomplished using call-based surveys (Tempel and Gutiérrez 2013). Indeed such call-based surveys have been the foundation of long-term demographic monitoring in the Sierra Nevada and southern California (Blakesley et al. 2010, Connor et al. 2013, Franklin et al. 2004, LaHaye et al. 2004, Tempel et al. 2014). However, the keys to unbiased call-based surveys are adequate survey effort (Tempel and Gutiérrez 2013), recognition of owl vocalizations by observers, year-to-year consistency within survey areas, and meeting the closure assumption of occupancy estimation (i.e., birds do not move in and out of surveyed areas; this is difficult to discern with unmarked birds). These studies have shown that spotted owls exhibit strong site fidelity, which has management implications. For example, Berigan et al. (2012) showed that owls used the same core areas, which contained a large proportion of the PACs established for their conservation for nesting and roosting over long time periods (>20 years). A PAC is designated whenever an owl is located on public land. However, the majority of PACs were delineated shortly after CASPO designed this concept in 1992. They now constitute essentially the only places where owls are currently found, suggesting that PACs are an essential management application. They could also represent the only remaining relatively large patches of nearly contiguous nesting/roosting habitat in the Sierra Nevada on public land. The PACs are also consistent management constructs relative to the hypothesis that spotted owls are central-place foragers. Thus, modifying PACs runs the risk of losing the owls within those PACs (see also chapter 8). The strong site fidelity of owls has several implications for management because birds may persist at sites even when site quality has been lowered because of disturbance(s), which makes it difficult to assess the effect of disturbance on spotted owls. Moreover, Seamans and Gutiérrez (2007a) showed a correlation with habitat change and territory occupancy, which suggests that maintaining key habitat areas is important to these birds.

Research on reproductive ecology provides numerous potential management implications, but there remains uncertainty about these implications. The relationship between brood size and territory quality suggests that territories can be ranked in terms of their contribution to the population, but presumed low-quality territories might actually be indicative of "low-quality" individuals inhabiting those sites. Moreover, territories with high turnover or low occupancy rates (which are currently presumed to be low quality) might actually improve as a result of forest succession and tree growth. The relationship between habitat and owl nesting success and reproductive output is important to managers because knowing which habitats might contribute to greater reproduction can inform management actions. Nevertheless, like other relationships involving reproductive output, habitat and individual quality are confounded. That is, are owls at a given site consistently successful because of the habitat conditions, the owls themselves (quality or experience), or both? This suggests, in addition to predictions from population viability theory, that "decommissioning" unoccupied PACs limits future options because PACs might be recolonized if they improve in quality with time (see Seamans and Gutiérrez 2007a). As another example, if owls exhibit low reproduction and PACs are removed for such reason, it will likely negatively affect the population because the bet-hedging life history strategy predicts that these owls will breed sometime and therefore may actually be important contributors to population demographic processes over the long term.

Franklin et al. (2000) suggested that good habitat may buffer owls against the effects of bad weather. That is, while managers cannot control weather, they can manage habitat and conserve existing high-quality habitat because such habitat confers survival or reproductive advantages to owls when bad weather occurs relative to lower quality habitat (Franklin et al. 2000). These research findings suggest that it is prudent, if not necessary, to maintain sufficient amounts of high-quality habitat (high canopy, large trees, complex-structured habitat) rather than low-quality habitat (i.e., habitats with forest condition metrics on the low end of the observed distribution used by owls).

Studies of diet analysis suggest that different management techniques could enhance prey habitat in low- and higher elevation habitats and among habitats within similar elevation zones. For example, at higher elevations in the Sierra Nevada, closed-canopy forests should be promoted to benefit the primary prey species (flying squirrel), but some amount of chaparral and early-seral stage forest can be maintained to benefit the primary prey species at lower elevations (woodrats).

In summary, substantial new information on California spotted owls has emerged since CASPO. This new information has the potential to inform management. Yet, there continues to be uncertainty about important aspects of the owl's biology, specifically how the owl is affected by disturbance (see also chapter 8).

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Chapter 3: California Spotted Owl Habitat Characteristics and Use

Susan L. Roberts[1]

Introduction

California spotted owls (*Strix occidentalis occidentalis*) establish large home ranges averaging about 1279 ha (3,160 ac) (table 3-1), and within these home ranges individual owls select habitat at different scales, depending on their activity. At the smallest spatial scale, the nest tree, it appears there is very limited flexibility in the requirements. However, as owls select habitat at larger scales and for different activities, from nest stand to core area to foraging habitat, there is greater variability in the habitat characteristics, which suggests greater flexibility in selection. Currently, researchers have not established definitions of the size of a nest stand or core area, nor have they reached consensus on how to calculate these aspects of owl habitat. This is at least partially because each researcher uses a certain method to estimate the nest stand or core area that is relevant only to the particular question they are investigating, and as those questions differ between research projects, the methods and definitions for those terms also differ. This chapter presents the current research describing spotted owl habitat characteristics and is organized by spatial scale, starting with the nest tree, followed by the nest stand, core area, foraging habitat, prey habitat, and finally the home range. Next is a brief assessment of the current research on the effects of fire on spotted owl habitat, and followed by relevant management implications.

Habitat Characteristics

Nest and Nest Tree Characteristics

California spotted owls are habitat specialists that are strongly associated with older, closed-canopy forests with multiple layers in the mid and upper canopies. All research shows they use large, old trees and snags as structures for nest and roost sites, embedded in a forest stand that has complex structure (Blakesley et al. 2005, Gutiérrez et al. 1992, Verner et al. 1992a). Owls nest in cavities, broken tree tops, and occasionally on platforms such as old nests or mistletoe brooms located in large conifers, oaks, and snags (Verner et al. 1992a). Often, these are the largest and oldest trees in the stand and many have structural defects, such as a broken or split tops that have multiple terminal leaders (North et al. 2000). In mixed-conifer forests

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Table 3-1—Estimates of individual California spotted owl home ranges in mixed-conifer forests for the breeding season from various telemetry studies using the 100 percent minimum convex polygon estimation method[a]

Study authors	Mean home range size	Home range standard error	Study area[a]	Sample size
	- - - - - -Hectares (acres) - - - - - -			
Zabel et al. 1992	2195 (5,423)	701 (1,731)	Lassen NF	9
Gallagher 2010	1653 (4,085)	336 (830)	Plumas NF	9
Call et al. 1992	1520 (3,756)	Not reported	Tahoe NF	5
Williams et al. 2011	946 (2,338)	Not reported	El Dorado NF, Tahoe NF	14
Eyes 2014	634 (1,567)	200 (494)	Yosemite NP	14
Zabel et al. 1992	728 (1,799)	65 (160)	Sierra NF	24

NF = national forest, NP = national park.

[a] Study results are organized by latitude of the study area from north to south.

of the Sierra Nevada, across 141 spotted owl nests, the owls show no preference for any particular tree species, and the average nest tree is 124 cm (49 in) in diameter at breast height (d.b.h.) and 31 m (103 ft) tall with an average nest height of 23 m (74 ft) (Gutiérrez et al. 1992, Roberts et al. 2011). Owls using nests with an overhead canopy of "high foliage volume" have higher reproductive success than owls using sites with low foliage volume (North et al. 2000). In hardwood forests, of the 13 nests observed, nests were typically in live hardwood tree species with an average nest height of 12 m (38 ft), and an average nest tree d.b.h. and total height of 76 cm (30 in) and 17 m (55 ft), respectively (Gutiérrez et al. 1992). Occasionally, owls nest in giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) or Coulter pine (*Pinus coulteri* D. Don).

Nest Stand Characteristics

Nest stands of California spotted owls typically have high canopy closure and cover (≥75 percent for both) [Note: when citing studies, we use terminology consistent with Jennings et al. (1999); however, many studies fail to accurately distinguish between canopy closure and cover (see chapter 5 for clarification)], an abundance of large (>61 cm [24 in] d.b.h.) trees, and multiple canopy layers comprising trees of different sizes, but numerically dominated by medium-sized trees (30 to 61 cm [12 to 24 in]) (Bias and Gutiérrez 1992, Blakesley et al. 2005, Chatfield 2005, Moen and Gutiérrez 1997, North et al. 2000, Roberts et al. 2011, Seamans 2005) (fig. 3-1).

There is no definitive estimate of the size of nest stands as each researcher used a stand size that was relevant to the question(s) they were investigating and

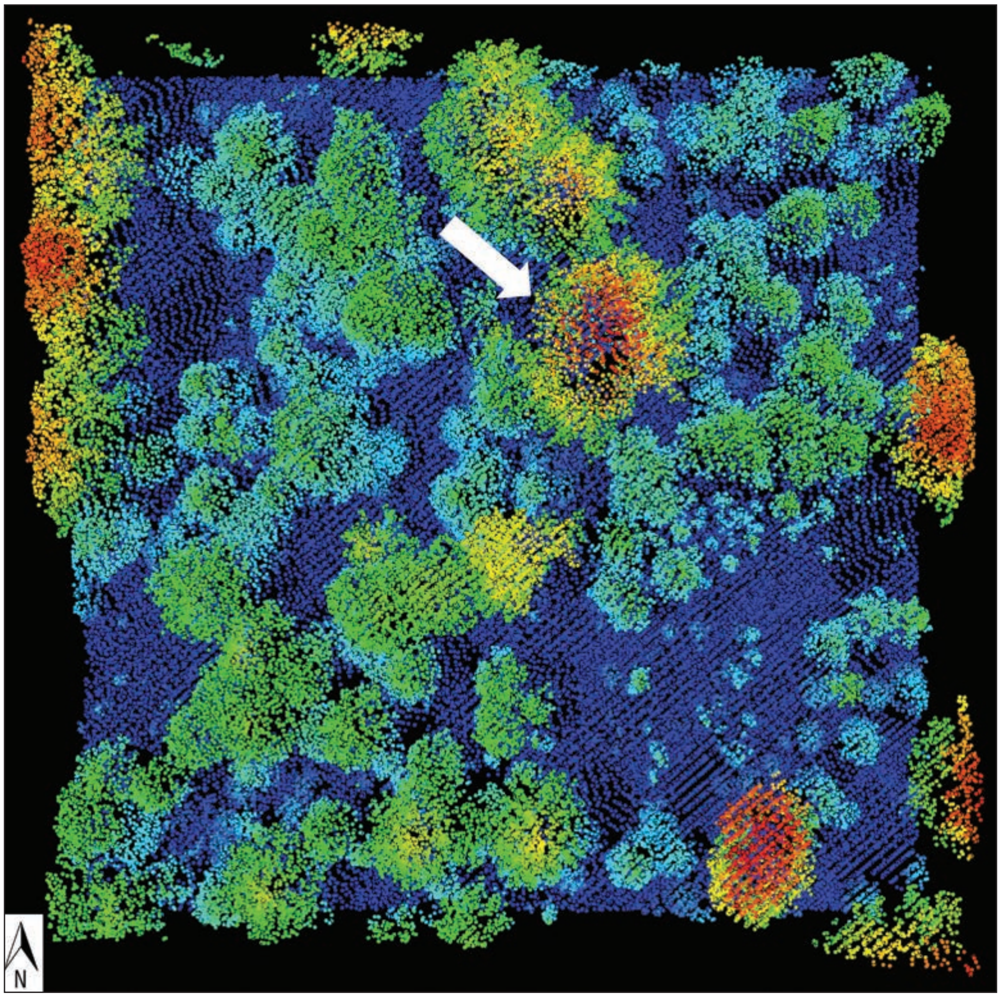

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Figure 3-1—Light detection and ranging (LiDAR) point cloud data of 1 ha (2.47 ac) illustrating multidimensional forest structure at a California spotted owl nest in a forest that burned at low to moderate severity 6 years prior to this LiDAR collection in Yosemite National Park, California. Tree heights are represented along a continuous color gradient with warmer colors (yellow to red) showing increasing crown height and bright blue showing ground level. The nest tree (50 m [167 ft] tall and 172 cm [68 in] diameter at breast height), is the tallest tree in the stand and located just northwest of center (see white arrow).

the methods they applied. Gutiérrez et al. (1992) reported that compared to random stands, nest stands had greater basal area of live trees and snags (42 to 80 m^2/ha [185 to 350 ft^2/ac] and 4 to 7 m^2/ha [19 to 31 ft^2/ac], respectively) and often had an abundance of large coarse woody debris (i.e., logs and large limbs on the ground). The association of large trees and snags and high canopy cover and closure were consistent regardless of the amount of area measured at the nest stand, which varied among studies (e.g., 0.04 ha [0.1 ac] in Moen and Gutiérrez 1997; 0.2 ha [0.5 ac] in North et al. 2000, Blakesley et al. 2005, and Roberts et al. 2011; or 40 ha [99 ac] in Chatfield 2005). Importantly, numerous studies showed that owl site occupancy and adult survivorship increased with a greater proportion of area of the nest stand containing these critical nest stand characteristics (e.g., high canopy cover or closure and basal area) (Blakesley et al. 2005, Chatfield 2005, Franklin et al. 2000, Roberts et al. 2011, Seamans and Gutiérrez 2007, Tempel et al. 2014).

Specific nest stand characteristics are highly correlated with juvenile spotted owl habitat selection. During the postfledging rearing period (after fledging and before dispersal), juveniles roosted within 800 m (875 yd) of the nest and in areas with high canopy closure (≥70 percent) and snag density (Whitmore 2009). Whitmore (2009) also estimated the mean area encompassing juvenile roosts was 125 ha (308 ac) suggesting this area around the nest provides critical habitat during a sensitive time (i.e., juvenile rearing). The complex vertical structure in late-successional forests (e.g., multiple layers in the mid- and upper canopy) provides deeper shading and protects juvenile and adult owls from overheating in areas that frequently reach 38 °C (100 °F) in summer (Barrows 1981, Weathers et al. 2001). This complex vertical canopy structure may also protect owls from predation. Phillips et al. 2010 showed owls select nest sites that are farther from high-contrast edges (i.e., mature forest patches that abruptly change to shrub-dominated or early-seral patches) than expected by chance despite other researchers observing owls foraging in those edge habitats.

Core Area Habitat Characteristics

As central-place foragers, spotted owls concentrate their activities around nests and roosts, with foraging activity reduced the farther they get from their nest or roost (Carey et al. 1992, Ward et al. 1998). This concentrated use area is commonly referred to as the “core area,” which is the amount of habitat a territorial owl or pair and young use consistently, including the nesting, roosting, and foraging habitat that contains vital habitat characteristics essential to each pair’s survival and reproductive success (Bingham and Noon 1997, Blakesley et al. 2005, Rosenberg and McKelvey 1999, Swindle et al. 1999, Williams et al. 2011). The core area is smaller than a home range, which is all of the area used by an individual owl.

Researchers have applied various criteria to identify and represent owl core use areas for the purpose of habitat analysis. Commonly, to delineate an area for habitat analysis that would be used by a territorial pair (by reducing spatial overlap between neighboring pairs), researchers apply either half of the minimum (0.8 km [0.5 mi]; Blakesley et al. 2005), or the average (1.1 km [0.7 mi]; Seamans and Gutiérrez 2007, Tempel et al. 2014) distance between adjacent nests (i.e., nearest-neighbor distance) as the radius to define their core area. These two examples define core areas of 203 ha (500 ac) and 400 ha (988 ac), respectively.

If radiotelemetry data is available, researchers can refine their core area sizes by using actual owl location data rather than estimating core use areas via distances between nests (e.g., Bingham and Noon 1997). Alternatively, Berigan et al. (2012) used 95 percent of each owl's locations to delineate a core area and averaged across all 38 of their radiotagged owls to define an average core area of 140 ha (347 ac) for their study.

Regardless of the amount of area different researchers use to define owl core area, the results of habitat analyses based on these defined areas demonstrate consistency in habitat characteristics of owl core areas. Occupancy, site colonization, adult survival, and reproductive success are positively associated with the proportion of the core area containing structurally complex conifer forest with large trees and high canopy cover (Blakesley et al. 2005, Seamans and Gutiérrez 2007, Tempel et al. 2014). Further, as the proportion of forest types that are not used for nesting (e.g., homogeneous forests consisting of only smaller, similar-aged young trees) increases in the core area, owl occupancy and reproductive success decline (Blakesley et al. 2005). However, the variation in the habitat classes available was relatively low (i.e., homogeneous habitat) where the non-nesting habitat mostly consisted of pole-sized stands, and there were not many other habitat types represented in their study area. This lack of variation in non-nesting habitat types could have potentially masked the influence of structural heterogeneity in core areas on owl occupancy and reproduction. Several other studies suggest that core areas of spotted owls have greater structural heterogeneity (e.g., increased edge between forest structure classes) than the nest stand and often include areas of lower canopy cover (e.g., 40 to 70 percent, Call et al. 1992; 30 to 50 percent, Tempel et al. 2014) and a wider range of forest structure classes, including shrub/sapling patches and especially habitat patch edges (Eyes 2014, Tempel et al. 2014). This habitat heterogeneity can promote increased prey diversity, abundance, and population stability throughout the long owl breeding and juvenile dependency period (March through September) (Roberts et al. 2015). Studies of northern spotted owls suggest reproductive success is positively associated with foraging habitat quality, and fledging success improves with increasing prey abundance (Carey et al. 1992, Rosenberg et al. 2003). However, it is difficult to determine a threshold of heterogeneity and find a balance between habitat heterogeneity and minimal fragmentation. California spotted owl reproductive success is negatively correlated with the proportion of nonforested areas and forest types not used for nesting or foraging within the 203-ha (500-ac) core areas (Blakesley et al. 2005). Spotted owls may need a connected matrix of high canopy cover/closure throughout their core area to maintain protection from predators because they have to return to their nest or roost after foraging. Having to cross large, open areas could expose them to predation, especially if those open areas are connected to areas inhabited by great horned owls (*Bubo virginianus*), known predators of spotted owls (Verner et al. 1992b).

Foraging Habitat Characteristics

Spotted owl foraging habitat is characterized by a mosaic of vegetation types and seral stages infused within mature forest (fig. 3-2). This juxtaposition of mature closed-canopy forest and open-canopy patches may promote higher prey diversity and abundance by increasing habitat diversity across the forest landscape (Franklin et al. 2000, Tempel et al. 2014, Ward et al. 1998, Zabel et al. 1995). This habitat mosaic is correlated with higher reproductive output and survival in northern spotted owls (*Strix occidentalis caurina*) (Franklin et al. 2000). Northern and California

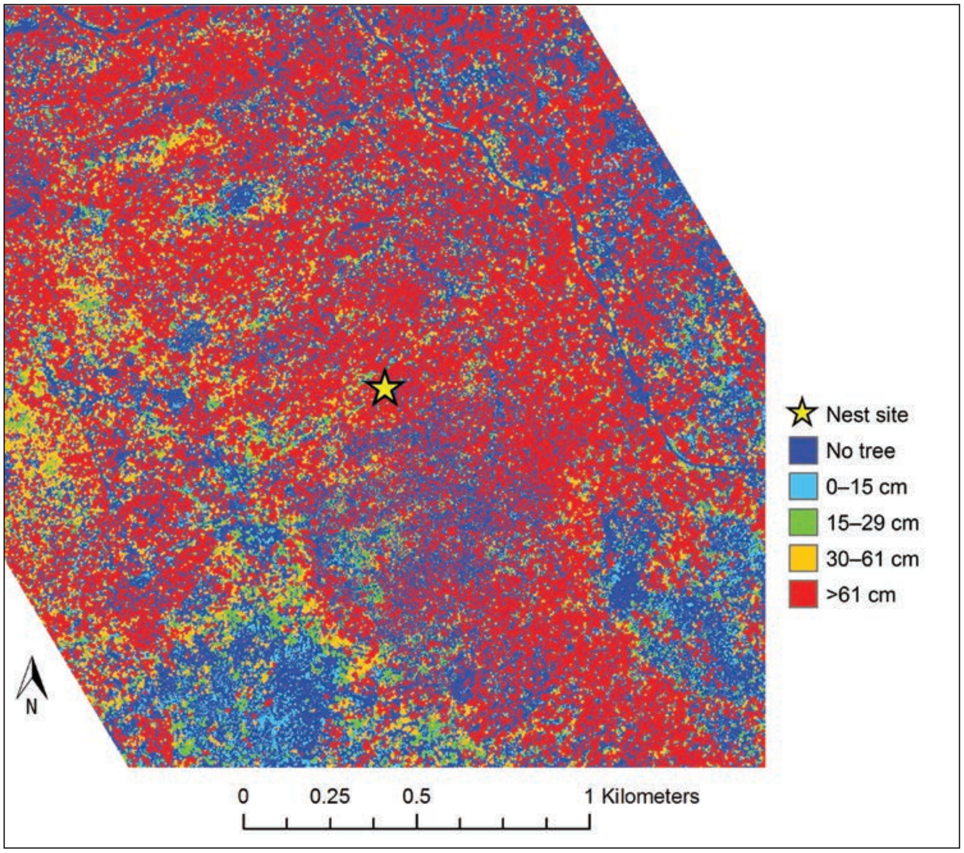

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Figure 3-2—Light detection and ranging (LiDAR) data illustrats canopy height modeling of an area equivalent to a spotted owl "Protected Activity Center" 121 ha (300 ac) in Yosemite National Park, California. The legend displays the modeled tree size classes in diameter at breast height for individual trees. The "cropped" corners are due to the confinement of the LiDAR data collection (the collection footprint) and have nothing to do with habitat structure or connectivity.

spotted owls forage in high-contrast edges more often than in interior patches (i.e., non-edges) characterized by greater structural homogeneity (Clark 2007, Eyes 2014, Folliard et al. 2000, Ward et al. 1998). In the Sierra Nevada, California spotted owls select edge habitat for foraging (Eyes 2014, Williams et al. 2011) suggesting that foraging owls exploit a heterogeneous forest matrix when foraging. These results are consistent with prey studies in the Sierra Nevada, suggesting small mammal diversity is enhanced by increased structural heterogeneity at large spatial scales and greater development of mature forest structure (Kelt et al. 2014, Roberts et al. 2015).

Within the larger mosaic of vegetation types, contiguous patches of mature closed-canopy forests are an important characteristic of spotted owl foraging habitat. Williams et al. (2011) found foraging owls selected mature forests with higher canopy cover (≥40 percent) in greater proportion relative to its availability in the landscape. Mature forests with an abundance of large trees and patches of greater canopy cover and closure (generally >50 percent) provide both important roosting habitat for spotted owls and foraging habitat for northern flying squirrels (*Glaucomys sabrinus*), a principal prey species of spotted owls in Sierra Nevada forests (Meyer et al. 2007a, 2007b; Roberts et al. 2011, 2015; Waters and Zabel 1995). The inclusion of larger California black oaks (*Quercus kelloggii* Newberry) in these forests may also benefit dusky-footed woodrats (*Neotoma fuscipes*) (Innes et al. 2007), another important spotted owl prey species.

The enhancement of habitat heterogeneity without fragmenting existing mature closed-canopy forest represents a significant challenge in forest management (Stephens et al. 2010, 2014). One approach, based on retrospective analysis of fire effects, suggests creation of a dynamic mosaic of tree clumps and openings (≥0.3 ha [0.7 ac]) of variable sizes, shapes, spatial configurations, and seral stages (Kane et al. 2013). This approach can enhance forest resilience to fire and other disturbances and protect existing stands of mature, multicanopied forest that is preferred spotted owl habitat. However, fuel and restoration treatments designed to increase ecological resilience should strive to balance the short-term impacts of fuel reduction on habitat quality with the long-term benefits of these treatments (Stephens et al. 2010, 2014). Of the number of forest treatments executed within owl foraging areas to reduce fuels, Gallagher (2010) showed foraging spotted owls avoided recently treated Defensible Fuel Profile Zones where the mechanical treatments create stands with widely and regularly spaced trees to reduce fire spread. Gallagher's results were less clear for other fuel treatments (e.g., understory thinning), possibly due to a lack of statistical power to detect a treatment effect. These and other fuel treatments may fragment spotted owl habitat, especially when applied uniformly across the forest landscape or in sensitive habitat areas (e.g., nest sites). Nest stands and owl core areas are especially important because California spotted owls forage close to the nest or roost (Eyes 2014, Gallagher 2010, Irwin et al. 2007). Moreover, Stephens et al. (2014) showed that landscape-level strategy of applying fuels treatments reduced the number of owl territories. Therefore, improving or maintaining forest structure in nest stands and core areas for both survival and reproduction (e.g., unfragmented, high canopy cover with some structural heterogeneity) could greatly benefit California spotted owls. Forest openings and habitat edges created by mechanical treatments or fire may enhance oak (*Quercus* spp.) and pine (*Pinus* spp.) regeneration and growth (Bigelow et al. 2011, York and Battles 2008). These forest openings are also associated with increased densities of woodrats, a large-bodied prey species, and other spotted owl prey species (Innes et al. 2007, Kelt et al. 2014, Roberts et al. 2015), and owl fitness may be positively linked to woodrat abundance (Smith et al. 1999). Clearly, there is a key uncertainty in Sierra Nevada spotted owl biology concerning a balance of connectivity between forest patches with high canopy cover and adjacent forest openings and habitat edges.

Prey Habitat Characteristics

Habitat characteristics of most spotted owl prey remains largely unstudied in the Sierra Nevada, with limited additional information published since Williams et al. (1992). However, several recent studies have contributed to a better understanding of prey habitat characteristics, especially for northern flying squirrels, dusky-footed and big-eared (*N. macrotis*) woodrats, and deer (*Peromyscus maniculatus*) and brush mice (*P. boylii*). These combined species represent the primary prey of California spotted owls in the Sierra Nevada and elsewhere (e.g., southern California) (Williams et al. 1992).

In the mid-elevation forests of the Sierra Nevada, northern flying squirrels are associated with mature forest stands with patches of moderate to high canopy closure (often exceeding 70 percent), large (>75 cm [30 in] d.b.h.) live or dead trees, thick (≥3 cm [1 in]) and extensively distributed litter layers, and sparsely distributed coarse woody debris or understory cover (e.g., shrubs and tall herbaceous plants) (Kelt et al. 2014; Meyer et al. 2005a, 2007; Pyare and Longland 2002; Roberts et al. 2015; Waters and Zabel 1995). Northern flying squirrels may select nesting or foraging sites in proximity to riparian habitat (Meyer et al. 2005a, 2007a, 2007b) or in moist mixed-conifer stands (Meyer et al. 2005a, Wilson et al. 2008). Riparian habitat is also associated with increased truffle (i.e., the fruiting bodies of ectomychorrizal fungi) (Meyer and North 2005) and tree hair lichen (*Bryoria fremontii*) (Rambo 2010) abundance, which compose the primary diet of northern flying squirrels (Meyer et al. 2005b, Smith et al. 2007). Truffle diversity is also positively associated with proximity to riparian areas, which are generally characterized by wetter soils with denser vegetation (Meyer and North 2005). Although flying squirrel foraging habitat may be associated with coarse woody debris cover in many parts of its geographic range (Smith 2007), most studies in the Sierra Nevada find either no association (e.g., Meyer et al. 2007a, Pyare and Longland 2002) or a weak association between flying squirrel occurrence and coarse woody debris abundance (e.g., Kelt et al. 2014). Excessive or widespread woody debris and understory vegetation (e.g., saplings) may hinder movements of this volant species during foraging bouts or predator evasion (Kelt et al. 2014, Roberts et al. 2015), but sparse and spatially variable patches of woody debris (within the natural range of variation) may benefit flying squirrels by providing protective cover or foraging cues for truffles (e.g., Pyare and Longland 2001). Fire that occurs under the natural range of variation for the region will remove rotten down woody material, but much of the large, sound logs will remain after fire, providing sparse, spatially variable patches of woody debris (Knapp et al. 2005).

In lower elevation forests, woodlands, and shrublands of the west-side Sierra Nevada, the dusky-footed woodrat (located in the northern Sierra Nevada), big-eared woodrat (located in the central and southern Sierra Nevada), and brush mouse are positively associated with oak cover or large oak (>33 cm [13 in] d.b.h.) density (Innes et al. 2007, Kelt et al. 2014, Roberts et al. 2008). Oaks (especially, California black oak) provide woodrats and brush mice with valuable food resources, especially acorns (Carraway and Verts 1991, Innes et al. 2007). Brush mice also tend to favor sites with greater herbaceous plant or shrub cover (Kelt et al. 2014, Laudenslayer and Fargo 2002) and may also be associated with riparian areas or dense clumps of tanoak (*Lithocarpus densiflorus*) (Amacher et al. 2008). Dusky-footed woodrats and brush mice exhibit moderate avoidance of areas with greater canopy cover, tree basal area, and large snag densities, especially at broader spatial scales; although woodrats may favor these habitat features at finer scales (Kelt et al. 2014) as well as logs and steep slopes (Innes et al. 2007). These scale-dependent habitat features emphasize the importance of promoting broad-scale structural heterogeneity and habitat complexity for small-mammal communities (Kelt et al. 2014, Roberts et al. 2008).

The deer mouse occupies a diverse array of habitats in lower and upper montane forest, woodland, and shrubland habitats of the Sierra Nevada (Verner and Boss 1980). This habitat generalist species is also one of the most numerous and widespread of all small mammals in North America with highly variable habitat associations across the Sierra Nevada (e.g., Amacher et al. 2008; Coppeto et al.

2006; Kelt et al. 2014; Monroe and Converse 2006; Roberts et al. 2008, 2015). Studies of the short-term effects of mechanical thinning or fire on deer mice are also varied in the Sierra Nevada, with posttreatment responses ranging from positive to negative to inconsequential. However, most studies agree that the effects of mechanical and prescribed fire treatments on deer mouse populations are either negligible or short lived, both in the Sierra Nevada (Stephens et al. 2014) and across the larger United States (Converse et al. 2006).

A few recent studies provide insights in the habitat use patterns of flying squirrels and deer mice in burned landscapes of the Sierra Nevada. Roberts et al. (2015) found unburned refugia (i.e., unburned patches within fire perimeters) were positively associated with northern flying squirrels in mid-elevation forests of Yosemite National Park. Unburned patches and low- to moderate-severity fire may also promote truffle diversity across these forest landscapes in Yosemite (Meyer et al. 2008). In contrast, greater fire severity (and mechanical thinning intensity) eliminates suitable habitat for flying squirrels by removing tree canopy cover, overall biomass, and litter depth below thresholds generally suitable for this species (e.g., ≤55 percent canopy cover) (Lehmkuhl et al. 2006, Meyer et al. 2007a, Roberts et al. 2015). In contrast to flying squirrels, deer mice occupy a variety of burned and unburned habitats in lower and upper montane habitats of the Sierra Nevada, but respond negatively to increased fire severity in mid-elevation forests of Yosemite (Roberts et al. 2008, 2015). Information pertaining to fire effects on woodrats is currently lacking in the Sierra Nevada, although Lee and Tietje (2005) found virtually no effect of prescribed fire on dusky-footed woodrat demography in the Central Coast Range of California.

Home Range Characteristics

A home range is defined as the area used by an individual to meet its requirements for survival and reproduction (to distinguish from “territory” see chapter 2) and understanding home range requirements is essential for the conservation of a species. Theoretically, smaller home ranges should be of greater habitat quality because individuals expend less energy to satisfy their needs (McNab 1963). For higher level trophic predators such as spotted owls, large home ranges are typical for a variety of reasons (see chapter 2 for details).

California spotted owls establish and defend large, year-round home ranges that contain higher habitat diversity than their northern subspecies (Forsman et al. 1984, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Verner et al. 1992b). Home range size estimates vary among studies (634 to 2195 ha [1,567 to 5,423 ac]), study area (latitude), and individual owls (table 3-1). Generally, California spotted owl home ranges are largest in the northern Sierra Nevada and smallest in the southern Sierra Nevada. In the southern Sierra Nevada, specifically Sierra National Forest, where oaks are the dominant tree, owl home ranges are significantly smaller (Zabel et al. 1992). Home range size is similar between years, sexes (Eyes 2014, Gallagher 2010, Williams et al. 2011, Zabel et al. 1992), and seasons, but there are often seasonal shifts in territorial delineations among neighboring pairs (Zabel et al. 1992). Owl home ranges frequently include heterogeneity and habitat edges; however, increases in heterogeneity lead to increases in home range size, suggesting a negative correlation of too much heterogeneity on habitat quality (Eyes 2014, Williams et al. 2011).

Consistently across studies and study areas, owl home ranges contain a greater abundance of large trees and greater proportion of mature forest than is randomly available across the landscape (Call et al. 1992, Moen and Gutiérrez 1997, Williams et al. 2011). Owls will forage in patches of smaller sized trees ("pole-sized" 15 to 28 cm [6 to 11 in] d.b.h.), but the presence of residual, large (super-canopy) trees greatly influenced owl use (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997, Williams et al. 2011). Although there is substantial variation among individual owls, Williams et al. (2011) found that the average home range in their study was comprised of patches of low canopy cover (11.8 percent), hardwood forest (3.5 percent), pole-size conifer forest with ≥40 percent canopy cover (6.3 percent), medium-sized (28.1 to 61 cm [11.1 to 24 in] d.b.h.) conifer forest with >70 percent canopy cover (47.1 percent), mature (>61 cm d.b.h.) forest with >70 percent canopy cover (10.7 percent) and mature forest with 40 to 70 percent canopy cover (1.6 percent). However, their study reflects an area with limited availability of patches of mature forest >30 ha (74 ac) owing to timber harvesting, and this forest type may have been underrepresented in terms of owl selection (Williams et al. 2011). Further, when investigating the habitat type composition of owl home ranges in heavily managed forests, the results are confounded by what habitat types are available to the owl and do not truly reflect spotted owl preferences.

Delineating the proportions and configuration of habitat patches in owl home ranges is nearly impossible using ground-based data because of the large-scale, landscape-level habitat metrics necessary for the analyses. Therefore, researchers typically use remotely sensed data, most commonly derived from satellites (see chapter 6 for details on remote sensing). However, vegetation maps available at this scale are often inaccurate, especially for residual trees (Moen and Gutiérrez 1997, Williams et al. 2011). Further research is needed to determine the size, composition, and configuration of habitat patches contained in an owl's average home range. The use of light detection and range (LiDAR) technology can greatly assist this research (see chapter 6). For example, important forest characteristics such as canopy cover and tree heights (fig. 3-1) can be quantified within spotted owl home ranges (e.g., fig. 3-2).

Effects of Fire on Spotted Owl Habitat

Fire is a dynamic ecological process in Sierra Nevada forests that varies greatly over space and time (Sugihara et al. 2006, van Wagtendonk and Lutz 2007). The effects of fire on spotted owl habitat are complex because fire burns heterogeneously across the landscape, resulting in a mosaic of variable fire severities (please refer to chapter 5 for more details on the regime and natural range of variation for fire frequency and severity for the Sierra Nevada). In low-fire-severity patches, fire consumed the surface fuels (e.g., low vegetation, coarse woody debris, and litter) and many shrubs and some small trees, but in these patches, nearly all canopy trees survived (Key and Benson 2005). In moderate-severity patches, fire consumed most of the surface fuels and small trees, as well as removed up to 75 percent of the canopy trees. In high-severity patches, all of the surface fuels were consumed by fire as well as nearly all mature plants, including >75 percent of canopy trees as determined from ground-based measurements (Composite Burn Index) (Key and Benson 2005) or >95-percent reduction in tree basal area or canopy cover as determined from remotely sensed data (Relative Differenced Normalized Burn Ratio) (Miller et al. 2009). In Yosemite National Park (central Sierra Nevada), where forests have a very minimal history of mechanical treatments, managers have allowed fires (prescribed and wild) to burn since the 1970s. Under the natural fire regime for mixed-conifer forests in Yosemite, with fires burning every 2 to 14 years that resulted in a mosaic of low to moderate fire severities, fire had no effect on spotted owl occupancy (Roberts et al. 2011). Further, although their study did not differentiate the fire-severity proportions within their burned areas, Bond et al. (2002) found that fire did not negatively affect spotted owl pair bonds, site fidelity, or reproductive success. High-severity patches, however, affected colonization on two territories in another area in the central Sierra Nevada, but did not affect territory extinction (Tempel et al. 2014), although it is unknown how their results may or may not be confounded by postfire salvage logging of their study area. Fires that result in large patches of high-severity fire significantly reduce owl colonization, occupancy, and use of these forest types (Eyes 2014, Roberts et al. 2011, Tempel et al. 2014). In southern California, Lee et al. (2013) found that owl extinction probability increased as high-fire-severity patches exceeded 50 ha (123.5 ac). In Yosemite National Park, the largest high-severity patch size foraging owls used more than once was 36.0 ha (89.0 ac), and the mean high-severity patch size used by foraging owls was 6.5 ha (16.1 ac) (SE = 10.5 ha [25.9 ac]) (Eyes 2104). Ideally, fire-resilient landscapes that contain contiguous patches of closed-canopy mature forest embedded with smaller forest openings and variable forest structure and composition (e.g., presence of large oaks) may sustain long-term foraging opportunities for spotted owls. A landscape with this forest structure would be largely consistent with the currently understood forest structure under a natural fire regime for this region (van Wagtendonk and Lutz 2007). Indeed, fires that burn within the natural range of variation for the Sierra Nevada, such as frequent low to moderate fires, tend to maintain habitat characteristics (e.g., retention of large trees and higher canopy closure) essential for spotted owl occupancy (Roberts et al. 2011).

Restoring and maintaining forest resilience to fire is currently a major concern for forest managers, especially when considering the needs of sensitive species such as the California spotted owl. The closed-canopy forests that are important to spotted owl occupancy and nesting, tend to have spatially contiguous high fuel volumes that increase the vulnerability of these forests to uncharacteristically large and severe fires (Agee and Skinner 2005, Agee et al. 2000, Weatherspoon et al. 1992). The impacts of climate change, longer fire seasons, and extended droughts, compounded by a century of fire suppression, have led to larger and more severe fires across the range of the California spotted owl, most notably in mixed-conifer forests (Mallek et al. 2013, Miller and Safford 2012). These trends are critical, because while California and northern spotted owls will forage throughout burned forests, they tend to avoid large high-severity patches (Clark 2007, Eyes 2014). Additionally, the abundances of many owl prey species (e.g., northern flying squirrel, deer mouse) are negatively correlated with fire severity (Roberts et al. 2008, 2015). In contrast, Bond et al. (2009) reported that owls frequently used high-severity patches for foraging, but based their conclusion on a limited owl sample size and a single year (4 years after the fire) of postfire data, which may fail to account for potential time-lag responses of a territorial species with high site fidelity. Since the completion of their brief study, anecdotal observations indicate that at least one of their four study owls abandoned their territory within the burn, switched mates, and shifted their habitat use away from high-severity patches.[2] However, while owls may be avoiding the interior of these high-severity patches, they will forage in the high-contrast edges created by high-severity fire (Eyes 2014), further suggesting that habitat heterogeneity may be important to owls. The

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[2] **Galloway, R. 2015.** Personal communication. Wildlife biologist, Sequoia National Forest, 1839 S Newcomb St., Porterville, CA 93257.

balance between enough habitat heterogeneity for successful owl foraging and too much heterogeneity leading to owl habitat fragmentation remains elusive. Importantly, there may need to be an essential connection between the juxtaposition of those edges to forest with dense canopy for spotted owls to avoid depredation. The only two cases of observed spotted owl depredation in Yosemite National Park occurred along high-contrast edges created by recent (<5 years) high-severity fire (Roberts pers. obs.).

New Findings Relative to Management Guidelines

The current standards and guidelines used by the U.S. Forest Service (USFS) to manage California spotted owl (USDA FS 2004) are founded on the core area concept, as described in the California spotted owl report (Verner et al. 1992b). Based on the recommendations of Verner et al. (1992b), the Sierra Nevada Forest Plan Amendment (i.e., Sierra Framework; USDA FS 2004) formally established the 121-ha (300-ac) protected activity centers (PACs) that USFS biologists delineate around a spotted owl activity center, such as a nest (fig. 3-2). These PACs were designed to include either the observed or the suspected nest stands and the best available habitat in a contiguous and compact arrangement. These designated areas are managed to contain:

- ≥ two layers of tree canopy
- ≥ 60 percent canopy cover
- An average d.b.h. ≥61 cm (24 in) for the dominant and codominant trees
- Some snags ≥114 cm (45 in) d.b.h.
- Higher than average volume of snags and down woody debris

Biologists designate a home range core area (HRCA) around each PAC, and the sizes of HRCAs are based on the average breeding pair home range of spotted owls (USDA FS 2004). Because spotted owl home range sizes increase with latitude, managers vary sizes of HRCAs as follows: 243 ha (600 ac) on the Sequoia and Sierra National Forests; 405 ha (1,000 ac) on the Modoc, Inyo, Humboldt-Toiyabe, Plumas, Tahoe, Eldorado, and Stanislaus National Forests, and the southern district of the Lassen National Forest; and 971 ha (2,400 ac) on the northern two districts of the Lassen National Forest. Managers attempt to maintain or develop desired conditions within HCRAs using five criteria:

- ≥ two layers of tree canopy
- ≥50 percent canopy cover
- ≥61 cm (24 in) d.b.h. for the dominant and codominant trees
- A “number” of live trees >114 cm (45 in) d.b.h.
- Higher than average volume of snags and down woody debris

These are the areas USFS managers must consider, as defined by the existing forest plan standards and guidelines, when developing forest treatment prescriptions, especially for mechanical treatments. Unless exempted for specific reasons, the USFS generally avoids mechanical treatments inside PACs, but prescribed fire can be used inside a PAC, and any management activity (though typically limited) can occur in HRCAs.

Research investigating the efficacy of USFS spotted owl PACs in protecting essential habitat around owl activity centers (i.e., nests or roosts) is limited. Berigan et al. (2012) found that PACs, as estimated and updated by USFS staff following the directives established in the Sierra Framework (USFS 2004), protected essential high-use habitat for California spotted owls. They showed that the mean PAC area (116.3 ± 3.4 ha [287.5 ± 8.4 ac]) for 29 owls was similar to the mean size of their estimated core areas actually used by those same 29 owls (135.4 ± 31.9 ha [334.7 ± 78.8 ac]) over 24 years of observations. They also found 70 percent spatial overlap between delineated PACs and observed use areas using 90 percent of the locations for each individual of a pair.

Research has yet to provide an estimate of the threshold value for the amount of mature or late-successional conifer forests that is required to support a pair of spotted owls. However, habitat alteration (e.g., mechanical tree removal) involving ≥20 ha (49 ac) of a 121-ha PAC was negatively correlated with site colonization and occupancy (Seamans and Gutiérrez 2007). Seamans and Gutiérrez (2007) also suggested that this human-caused habitat alteration was correlated with either decreased owl survival or increased emigration from their study population. These researchers did not use radiotelemetry to follow their study owls, thereby making it difficult to know the fate (i.e., survival) of an owl that abandoned its territory. Regardless of their true fate, it is concerning when owls disappear from their long-established territories after mechanical treatments of ≥20 ha (49 ac) occurred within their PAC.

Chapter Summary

- Fuel and forest restoration treatments, including the use of fire, could attempt to balance the short-term impacts of these treatments on habitat quality with the long-term benefits to the ecosystem.
- Although one study showed that the current size for spotted owl PACs (121 ha [300 ac]) may be adequate to protect current core use areas, there is insufficient evidence (i.e., large-scale experimental research) to ascertain whether PACs provide long-term spotted owl persistence on national forest lands.

- All of the research strongly indicates that large, old trees are important aspects of spotted owl habitat, providing complex vertical structure and canopy layering as well as potential nesting cavities. Although the presence of large trees alone is insufficient for the persistence of spotted owls, restoration treatments that prioritize the retention of large and old trees, even in marginal habitat, can form the foundation for future high-quality habitat where the site potential is adequate.
- Conservation efforts would be enhanced by prioritizing areas on the landscape that may enable the protection of spotted owl habitat from stand-replacing fire. This could include the strategic identification of areas targeted for (1) fuel treatments to reduce wildfire risk to occupied forest landscapes and (2) protection objectives during incident management to minimize the impacts of wildfire and fire management operations to critical habitat. To begin this landscape prioritization, there is a need for accurate, landscape-level vegetation maps and a better understanding of the importance of vegetation types (and their patch sizes) to spotted owl occupancy, reproduction, and long-term population persistence and viability. Using accurate vegetation maps to identify important habitat needs to be coupled with our understanding of fire behavior across the landscape. It may be important to incorporate in our forest restoration planning how topography will affect fire behavior and how fire and topography will interact with the vegetation to influence the fire effects in an area. There are tools available (e.g., ArcFuels; http://www.arcfuels.org/) that could act as a place to start for managers to assess wildfire risk and aid in fuels management planning.
- Forest restoration treatments may increase the abundance of spotted owl prey by promoting late-seral forest conditions, vegetation heterogeneity, and shrub and oak patches. In addition, managing fires for a mosaic of burn severities (dominated by low- and moderate-severity patches), including contiguous patches of unburned refugia, promotes suitable habitat for diverse small-mammal assemblages including northern flying squirrels, deer mice, and woodrats.
- Wildland fires (prescribed fire and wildfire) that burn primarily at low to moderate severity (including unburned patches) likely maintain spotted owl occupancy while increasing resilience of the forest landscape in the long term. Although high-severity (i.e., stand-replacing) fires may also benefit spotted owls in smaller patches and proportions more consistent with the natural range of variation, large high-severity-burn patches may significantly

curtail habitat use and occupancy and long-term persistence of suitable nesting and roosting habitat. There is insufficient information available to allow a determination of the potential threshold responses of spotted owls to high-severity fire.

- Managers focusing forest treatments on enhancing spotted owl habitat may wish to juxtapose nesting or roosting habitat structures in some stands (or larger habitat patches) and foraging habitat in others, keeping in mind that it is important to maintain a balance to minimize habitat fragmentation. Consider using the biophysical environment (e.g., topography, soils, and climate water deficit) as well as fire behavior and crew safety to guide the treatment placement and prescriptions.
- For stands where the enhancement of nesting or roosting habitat is the objective, the research reviewed above suggests increasing or maintaining the abundance of large live trees and snags and canopy cover with complex layering. In stands where the promotion of foraging habitat is the objective, the research reviewed above suggests facilitating shrub or hardwood patches, large oaks, and small canopy gaps that provide sufficient edge habitat and foraging opportunities. Forest landscapes that contain a greater proportion of mature forest with old and large trees will provide more suitable habitat for spotted owls.

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Chapter 4: Population Distribution and Trends of California Spotted Owls

Douglas J. Tempel, R.J. Gutiérrez, and M. Zachariah Peery[1]

Distribution

Geographic Range

Following Verner et al.'s (1992) technical assessment of the California spotted owl (CASPO), we divided the range of the California spotted owl (*Strix occidentalis occidentalis*) into two major physiographic provinces: the Sierra Nevada and the mountains of southern California (Tehachapi Pass was the demarcation between the regions). Verner et al. (1992) noted that these provinces are geographically distinct and that movement of owls between them is probably rare, which remains true today (see "Population and Conservation Genetics of California Spotted Owls" section below). The California spotted owl is also found in the coastal mountains north to Monterey Bay, but much less is known about owl numbers and locations along the coast (see figs. 4-1 and 4-2). That portion of the southern Cascade Range that abuts the Sierra Nevada has been considered to encompass the range of the California spotted owl on the east side of California (see chapter 2). Where the ranges of the northern (*S. o. caurina*) and California spotted owls meet, a hybrid zone occurs in the area of contact near the Pit River (Barrowclough et al. 2011; see chapter 2). Hereafter, we refer to owls occurring south of the Pit River as belonging to the Sierra Nevada population of California spotted owls.

Within the Sierra Nevada population, the distribution of owls is relatively contiguous. The majority of owls occur within the mid-elevation, mixed-conifer forests on the west slope of the Sierra Nevada. Some owls also occur at lower elevations in the oak woodlands of the western foothills in the southern Sierra Nevada, at higher elevations in red-fir forests, and in conifer forests on the eastern slope of the mountains (Verner et al. 1992). In contrast, the owl population in central and southern California is more fragmented because owls inhabit major mountain ranges and mountain complexes that are isolated to varying degrees, which limits movement of individuals among these mountain ranges. In this chapter, we focus almost solely on the Sierra Nevada population of owls while deferring discussion of southern California to chapter 9. However, when discussing general properties of

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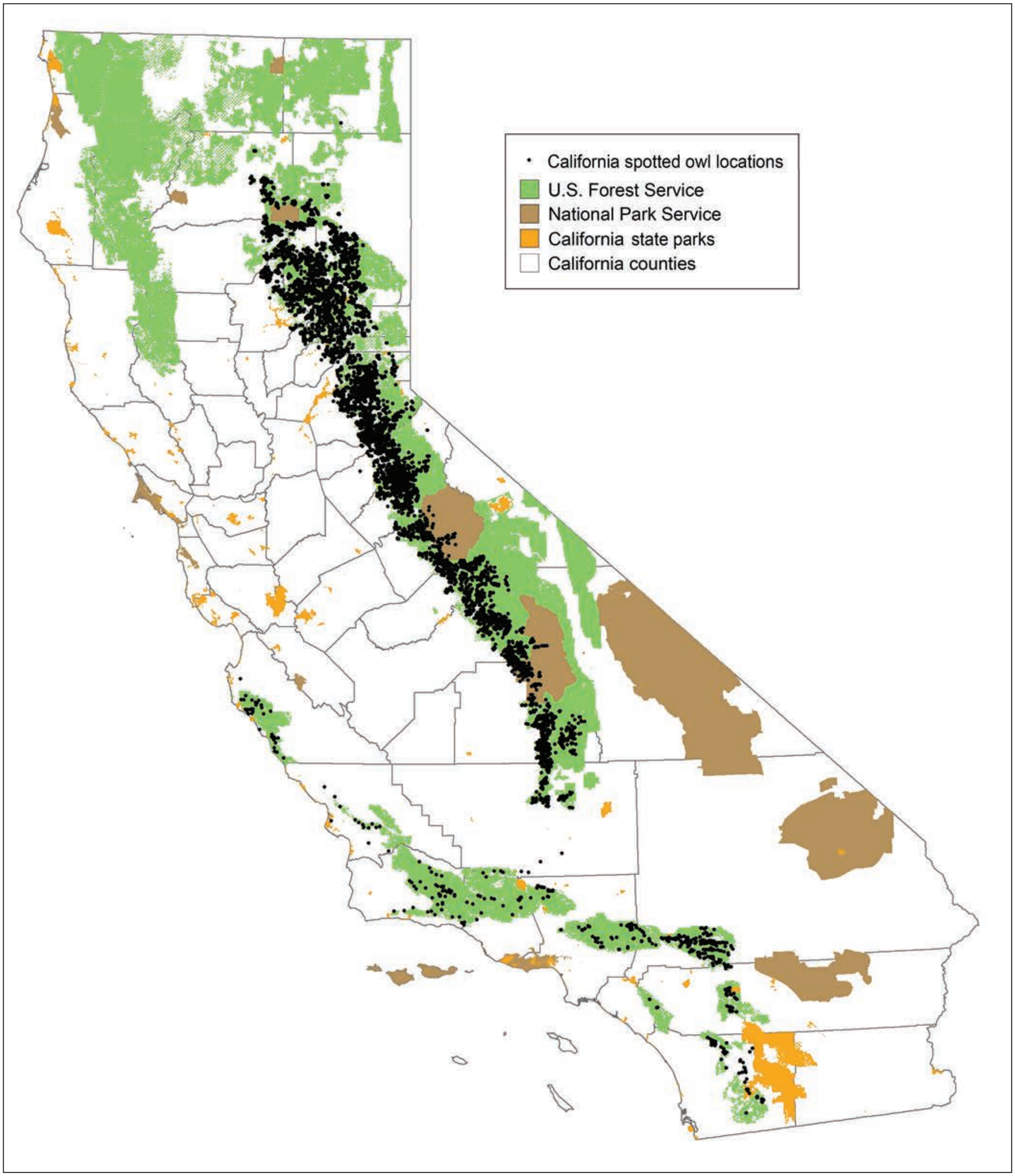

Figure 4-1—Unique detections of California spotted owls from 1900 through 1992 using databases provided by the California Department of Fish and Wildlife and Pacific Southwest Region of the U.S. Forest Service.

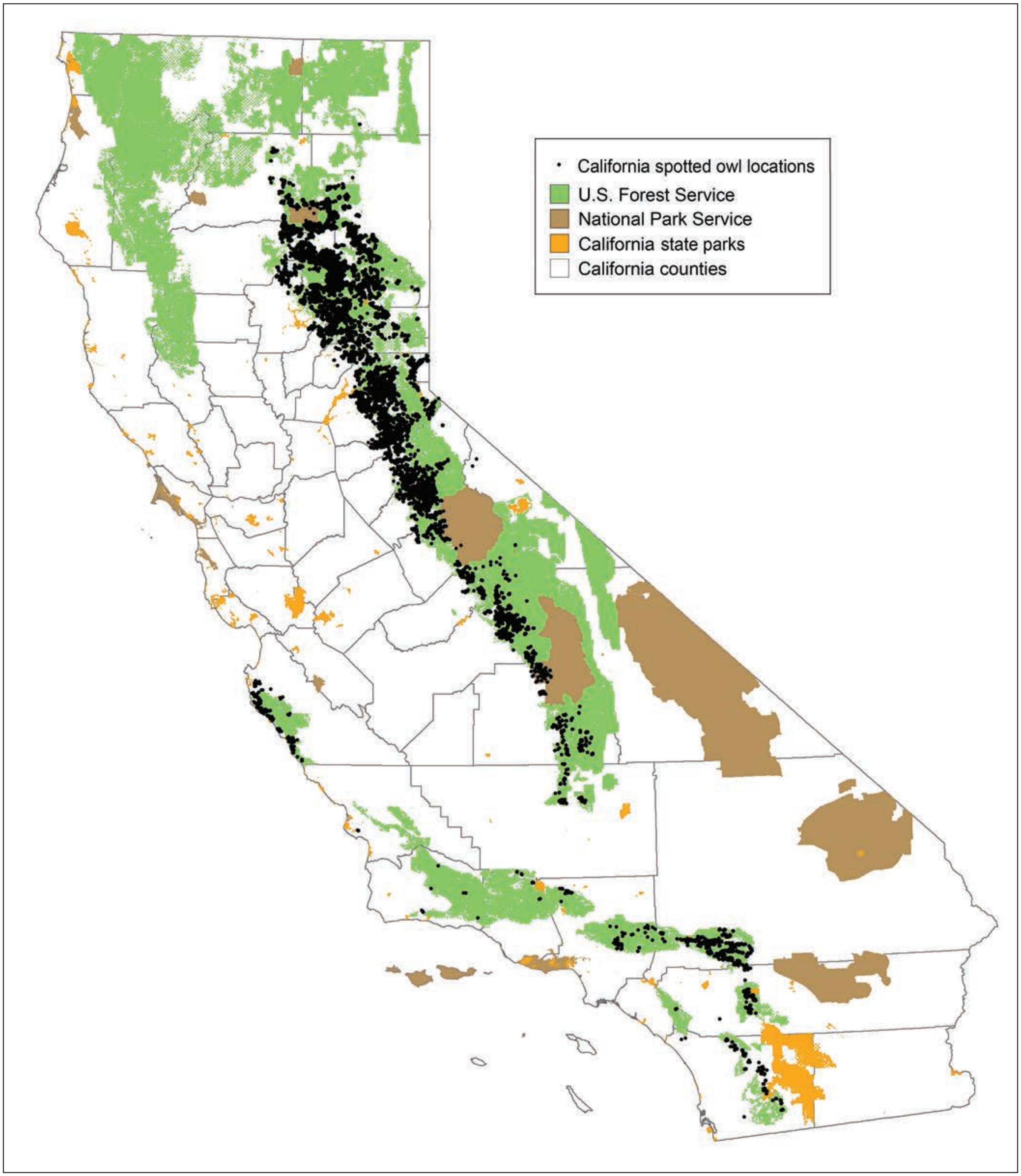

Figure 4-2—Unique detections of California spotted owls from 1993 through 2013 using databases provided by the California Department of Fish and Wildlife and Pacific Southwest Region of the U.S. Forest Service.

spotted owl population dynamics, we may also refer to other subspecies as well as southern California owl populations.

Distribution of Owls and Gaps in Distribution

Verner et al. (1992) noted that unlike the northern spotted owl, there were no obvious gaps in the distribution of the California spotted owl. This observation led them to recommend a conservation strategy based upon identification of habitat, protection of key habitat areas or activity centers around nests and roosts (i.e., protected activity centers PACs), and specific guidelines for timber harvest (restrictions on size of trees harvested, standards for tree basal area retention, and restrictions on canopy cover reductions; see chapter 1). To evaluate the CASPO premise of no gaps in the distribution, we obtained the California spotted owl databases from the California Department of Fish and Wildlife (CDFW) and the Pacific Southwest Region of the U.S. Forest Service (USFS). Both databases primarily included information for owl detections (i.e., mark-recapture or reproductive data were not consistently recorded), and many physical locations were represented by a large number of detections obtained over many years. Because we could not establish individual identities for most of the detections or, in many cases, even reliably assign detections to a specific owl territory, these databases cannot be used to infer trends in population size. However, they do provide a general, rangewide distribution of California spotted owls and some indication of the proportion of owls found on public versus private lands. Further examination of these databases showed that the CDFW database was missing many owl detections on USFS land, particularly after 1993. Therefore, we combined the databases and attempted to eliminate duplicate detections (i.e., detections in the same geographic location on the same date).

We estimated that there were 15,322 spotted owl detections prior to 1992 (CASPO) and 34,365 detections from 1993 through 2013 (post-CASPO) (figs. 4-1 and 4-2). The increase in the number of detections after 1992 was largely due to increased survey effort on national forest lands. The overall distribution of owls was largely similar for the two time periods (pre-1993 and 1993–2013), but there were noticeably fewer detections after 1992 within the Transverse Range north of Santa Barbara on the Los Padres National Forest. As noted above, there appeared to be a significant gap in the owl's distribution between the Sierra Nevada and the mountains of southern and central California. In addition, there appeared to be gaps in the owl's distribution between the major mountain ranges of southern and central California, particularly along the central coast. Most spotted owl detections were on public lands (88 percent prior to 1993, 87 percent from 1993 through 2013), and for both time periods >90 percent of the detections on public lands were within U.S.

national forests. Although there were clearly more California spotted owls on public lands, we could not determine how much of the observed difference in detections on public versus private lands was due to greater survey effort on public lands, particularly around proposed timber sales within U.S. national forests. Private lands may constitute an important component of California spotted owl habitat throughout its range, and owl conservation would benefit from the effective management of habitat on private lands.

Demographic Rates

History of Demographic Research in the Sierra Nevada

Spotted owls exhibit high adult survival rates with low temporal variation, whereas their reproductive rates are low and vary greatly from year to year (Franklin et al. 2000, Seamans and Gutiérrez 2007). Franklin et al. (2000) invoked these patterns as a "bet-hedging" life history strategy (Stearns 1976) where natural selection has favored the evolution of long lifespans to increase the likelihood that individuals will experience years that are favorable for reproduction (see also chapter 2).

Data collected on five long-term California spotted owl study areas have provided substantial empirical data on demographic rates and population trends subsequent to CASPO (Verner et al. 1992). Of these five study areas, four were in the Sierra Nevada (see fig. 4-3)—three on national forests (Lassen, Eldorado, and Sierra) and one within Sequoia and Kings Canyon National Parks. Data collection began in 1986 on the Eldorado and in 1990 on the other three study areas; all of these studies continued through 2014. The fifth study area was located on the San Bernardino National Forest in southern California where data were collected from 1987 through 2000 (see fig. 4-3). Two meta-analysis workshops have been conducted to analyze demographic rates and population trends on the Sierra Nevada study areas (Blakesley et al. 2010, Franklin et al. 2004), but more recent studies have provided updated analyses that included additional data collected after the second meta-analysis (Conner et al. 2013, Tempel and Gutiérrez 2013, Tempel et al. 2014b).

Additionally, Sierra Pacific Industries (SPI) recently initiated systematic surveys on five study areas throughout the Sierra Nevada where the company owned significant amounts of land (proportion of land owned by SPI ranged from 34 to 69 percent).[2] Although Roberts et al. (see footnote 2) concluded that populations on

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[2] **Roberts, K.; Hall, W.E.; Shufelberger, A.J.; Reno, M.A.; Schroeder, M.M. 2015.** The occurrence and occupancy status of the California spotted owl on Sierra Pacific Industries' lands in the Sierra Nevada of California. 11 p. Unpublished document: On file with: Sierra Pacific Industries, 3950 Carson Rd., Camino, CA 95709.

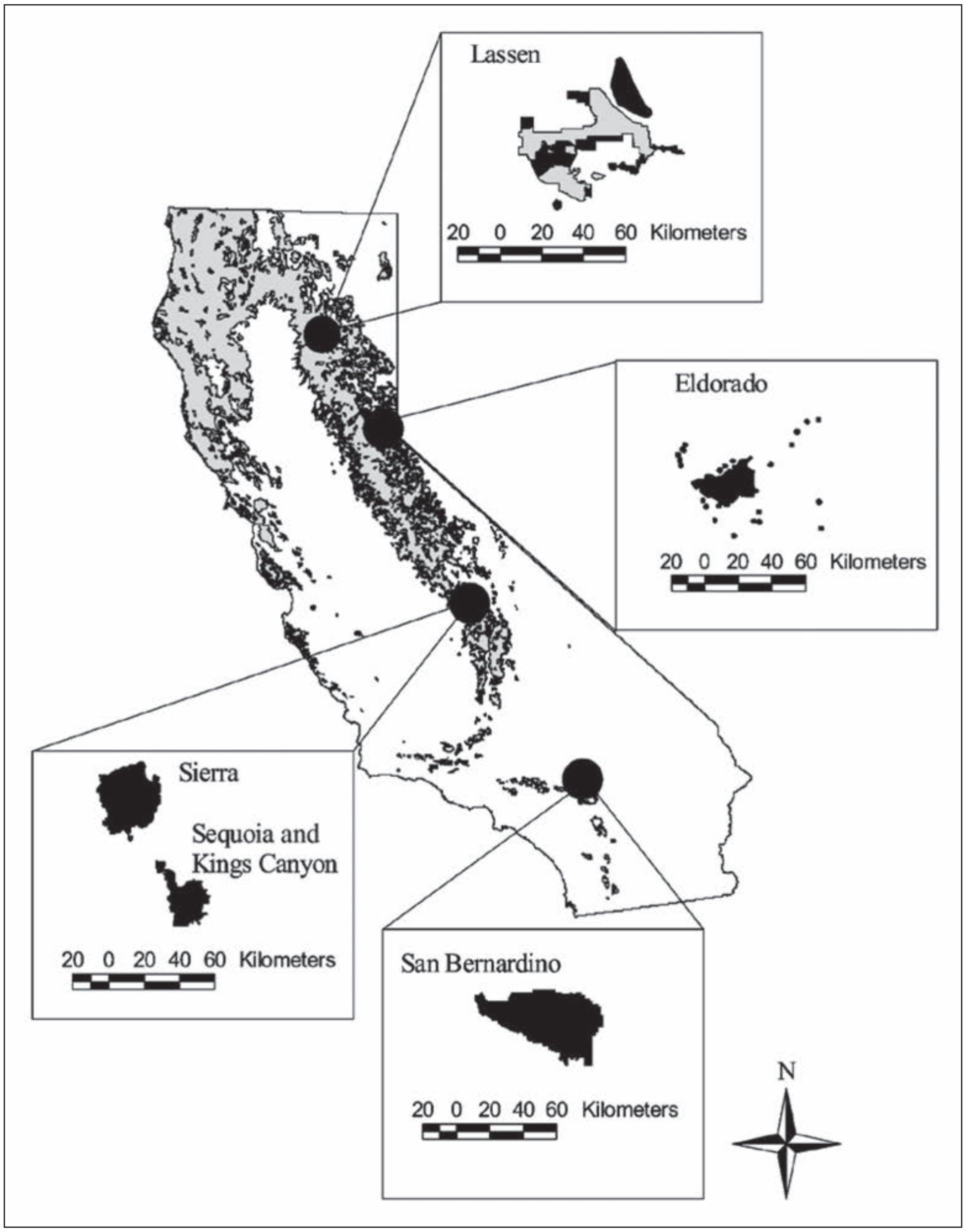

Figure 4-3—Locations of California spotted owl demography studies in relation to forested habitat (shaded gray) throughout California. (Franklin et al. 2004; reproduced with permission of © American Ornithological Union).

their study areas were stable or increasing, we contend that their survey data are currently insufficient to assess population trends for several reasons:

- Detection probabilities were not modeled.
- Surveys were conducted over a limited number of years (2012–2014), whereas trends on the study areas discussed above took more than 10 years to detect because spotted owls show high site fidelity and are long lived.
- Survey effort increased over time.
- There typically is a "learning curve" associated with initiation of occupancy studies that yields an increase of occupied sites solely related to accumulated knowledge of field technicians.
- Most of the owls were unmarked and thus could not be individually identified.

Roberts et al. (2015) also reported higher owl densities on their study areas than the Lassen and Eldorado National Forest study areas. However, we caution that density is not always a reliable indicator of habitat quality because large numbers of owls may be maintained in "sink" habitats (i.e., within-habitat reproduction is insufficient to balance local mortality) by continued immigration from more productive, nearby areas of "source" habitat (Pulliam 1988). Moreover, they sampled relatively small study areas, and there is often an "edge effect" associated with areas that are small relative to the home range size of the species being monitored. Although it is possible that the areas surveyed by Roberts et al. (see footnote 2) contain stable populations, additional years of data, including data on individual identification, reproduction, and survival, would be needed to make this determination.

Reproduction

Blakesley et al. (2010) reported substantial variation in reproductive rates (number of young fledged per territorial female for which reproduction was assessed) among the four Sierra Nevada study areas, ranging from 0.48 on the Sierra to 0.99 on the Eldorado. Because different studies sometimes use different units of measurement, we have used caution when comparing reproductive rates among studies. For example, Franklin et al. (2004) used the number of female young fledged per territorial female (assuming a 50:50 sex ratio among offspring), whereas Blakesley et al. (2010) used the total number of young fledged per territorial female. In addition, Seamans (2005) found that differences in field protocols used by researchers on different study areas affected estimates of annual reproductive rates, particularly whether one or two nonreproduction protocols were needed to infer nonreproduction. Therefore, in contrast to Franklin et al. (2004), Blakesley et al.

(2010) standardized field protocols among the four study areas such that the criteria for inferring nonreproduction had to be met on at least two surveys in a given year. However, this stricter requirement (i.e., two surveys vs. one) eliminated many data observations from the Eldorado because there were many instances when only one nonreproduction protocol was available; in most of these instances, it was likely that owls did not reproduce. This removal of observations where reproduction likely equaled zero could bias reproductive analyses that incorporate covariates for territories or individual owls. MacKenzie et al. (2009) recommended analyses using multistate occupancy models that distinguished between surveys where reproduction was detected or not detected to make more efficient use of reproductive data.

Blakesley et al. (2010) reported that reproduction declined over time on the Eldorado National Forest but was relatively constant on the other study areas. Furthermore, they found support for an even-odd (EO) year effect on reproductive rates for all four study areas (see chapter 2 for a discussion of this even-odd pattern) with the strongest pattern occurring for the Eldorado and Lassen National Forests; this pattern has also been reported for northern spotted owls (e.g., Forsman et al. 2011). Thus, spotted owl reproduction in much of the Sierra Nevada appeared to follow an alternating pattern where years of relatively high reproduction were followed by years of relatively low reproduction, although there remained much variation not explained by the even-odd pattern. In addition, Stoelting et al. (2015) could not simulate the even-odd cycle in California spotted owls using a cost of reproduction estimated for the Eldorado (see chapter 2).

Adult female California spotted owls (≥3 years old) have higher reproductive rates than subadult females (1 or 2 years old). For example, Blakesley et al. (2010) found that the annual proportion of subadult females among all territorial females had a strong negative correlation with reproductive rates on the Eldorado and Sierra National Forests. In addition, reproductive rates for adult females were much higher than those for subadult females on the Eldorado (Seamans and Gutiérrez 2007, Seamans et al. 2001, Tempel et al. 2014a) and Lassen Nationa Forests (Blakesley et al. 2001) in analyses that were independent of the two California spotted owl meta-analyses (Blakesley et al. 2010, Franklin et al. 2004).

Reproductive rates have been correlated with climatic conditions, either during the previous winter or the early nesting period. Seamans and Gutiérrez (2007) reported that reproductive rates on the Eldorado were negatively correlated with El Niño events, which in California typically result in winters with greater precipitation and warmer temperatures than average. Additionally, they found that reproduction was negatively correlated with colder temperatures and greater precipitation during incubation (April). Similarly, North et al. (2000) reported that colder temperatures and greater precipitation during the early breeding season (March to May) on the Sierra National Forest and Sequoia and Kings Canyon National Parks were negatively correlated with reproduction. Similar patterns have been observed for northern spotted owls (Franklin et al. 2000). These results have led to the hypothesis that colder temperatures and increased precipitation during the early nesting season negatively affect reproduction either by increasing the energetic requirements of owls, increasing the risk of egg exposure during incubation, or interfering with foraging (Franklin et al. 2000, Rockweit et al. 2012).

Finally, reproductive rates have been correlated with habitat characteristics, both within owl territories and at nest sites. When assessing the relationship between demographic rates (e.g., reproduction, survival, or occupancy) and habitat, scientists have considered various spatial scales as reference points. For example, at least four spatial scales have been used:

- The home range, which has been estimated from radiotelemetry locations
- The territory (the area actively defended by resident owls), which has typically been assumed to be approximately half the mean nearest neighbor distance between territory centers
- The core area of use within an animal’s home range, which is an area that receives concentrated use and is thought to encompass critical components such as nest sites, refugia, and foraging areas (Samuel et al. 1985)
- The area immediately surrounding the nest site

On the Lassen National Forest, Blakesley et al. (2005) assessed the relationship between reproductive output and the surrounding habitat within owl territories (estimated as 203 ha [508 ac] using half the mean nearest neighbor distance, which they referred to as the “nest area”). They found that reproduction was negatively correlated with the amount of nonforest or forests dominated by small trees (<30 cm [12 in] diameter at breast height [d.b.h.]) and positively correlated with the amount of nesting habitat, which were forests dominated by medium (30 to 61 cm [12 to 24 in] d.b.h.) or large trees (>61 cm [24 in] d.b.h.) and having high canopy cover (>70 percent). Two different studies on the Eldorado National Forest found strong support for a negative correlation between reproduction and the amount of oak woodlands within owl territories (estimated as 150 ha [400 ac] using half the mean nearest neighbor distance) (Seamans 2005, Tempel et al. 2014a). On the Sierra National Forest, Hunsaker et al. (2002) reported a positive correlation between “productivity” and forests with >50 percent canopy cover at each of three different spatial scales (72 ha [178 ac], 168 ha [415 ac], and 430 ha [1,063 ac]) that roughly corresponded to the home range, territory, and core area of use as defined above. The authors defined productivity as an index of reproductive output where productivity values at a territory ranged from zero to nine (0 = no owls present, 9 = nesting pair that produced three fledglings; see Hunsaker et al. [2002] for more details). At the spatial scale of the immediate nest area (0.05 ha [0.12 ac]), North et al. (2000) reported that reproduction was positively correlated with the foliage volume above the nest site.

Survival

Blakesley et al. (2010) reported high apparent survival of adult California spotted owls on the four Sierra Nevada study areas, ranging from 0.810 to 0.891. They also found that adults had higher annual survival rates than first- or second-year subadults and males have slightly higher survival rates than females. Higher survival rates for males (Seamans 2005, Seamans and Gutiérrez 2007, Tempel et al. 2014a) and adults (Tempel et al. 2014a) were also reported for the Eldorado National Forest in analyses independent from Blakesley et al. (2010). Data analyses for the Sierra Nevada studies have generally avoided estimation of juvenile survival rates because of potentially significant biases caused by undetected emigration of juveniles from the study areas (Burnham et al. 1996, Zimmerman et al. 2007). Estimates of nonjuvenile spotted owl survival have also been criticized as potentially biased because of undetected emigration of nonjuveniles (Boyce et al. 2005, Loehle et al. 2005), but this bias has been shown to be negligible because nonjuvenile owls (in contrast to juveniles) rarely disperse from study areas as large as those in the Sierra Nevada (Zimmerman et al. 2007). LaHaye et al. (2004) estimated that apparent juvenile survival rates in an insular population in the San Bernardino Mountains (i.e., juvenile emigration rates from this mountain range were negligible) was 0.368, which was similar to that reported on the Lassen National Forest (0.333) (Blakesley et al. 2001). Of note was that Blakesley et al. (2001) designed their study to improve estimation of juvenile survival.

Like reproduction, apparent survival has been correlated with habitat conditions within an owl territory. Blakesley et al. (2005) found that nonjuvenile survival was positively correlated with the amount of nesting habitat (see above) on the Lassen National Forest. In addition, Seamans (2005) and Tempel et al. (2014a) both reported that nonjuvenile survival rates on the Eldorado National Forest were positively correlated with the amount of forest dominated by medium (30 to 61 cm [12 to 24 in] d.b.h.) or large trees (>61 cm [24 in] d.b.h.) and having high canopy cover (≥70 percent). Tempel et al. (2014a) also found a positive correlation between survival and the amount of edge between shrubs/saplings and forest, but the 95 percent confidence interval on the beta coefficient overlapped zero.

Seamans and Gutiérrez (2007) conducted the only study that assessed climate effects on survival of California spotted owls in the Sierra Nevada. They found that survival was positively correlated with snow depth, which was opposite of their a priori prediction. Their results further suggested a quadratic relationship between survival and the Southern Oscillation Index, such that survival was greatest in years that were not dominated by either El Niño or La Niña weather patterns. The Southern Oscillation Index is a measure of atmospheric pressure differences in the southern Pacific Ocean that provides an indication of the development and intensity of El Niño or La Niña events. In the Sierra Nevada, El Niño events typically result in warmer, wetter winters and La Niña events typically result in colder winters; thus the quadratic relationship suggested that survival was highest when winters were not too wet or too cold. Furthermore, their weather models explained less temporal variation in survival than they did in reproduction (60 vs. 84 percent); reproduction also exhibited much greater temporal variation than survival.

Population Size and Trends

Population Size

To our knowledge, there has never been a formal attempt to estimate rangewide population sizes of the California spotted owl. We have provided summaries of the number of known California spotted owl sites obtained from the CDFW and the USFS (see above; figs. 4-1 and 4-2), but these data were not collected as part of a scientifically rigorous sampling scheme throughout the owl's geographic range. Therefore, to assess whether the overall population is declining, we must rely upon population trends estimated from individual, long-term study populations. Fortunately, the four study areas in the Sierra Nevada from which estimates have been derived were large and spanned the extent of the mountain range, and thus likely provided a representative estimate of trends throughout the Sierra Nevada.

Population Trends

Population trends of spotted owls are typically reported as the annual rate of population change (λ_t) where λ_t indicates the population size in year $t + 1$ relative to the population size in year t. Thus, $\lambda = 1.0$ for a stationary population, $\lambda_t > 1.0$ for an increasing population, and $\lambda_t < 1.0$ for a declining population. Furthermore, the overall change in population size during a defined period of time is expressed as realized population change (Δ_t) where Δ_t indicates the population size in year t

relative to the population size at the beginning of the study period (Franklin et al. 2004). The realized population change is equivalent to the product of the annual rates of population change over the study period ($1 \times \lambda_1 \times \lambda_2 \times \lambda_3 \times \ldots \lambda_{t-1}$). When assessing population trends, the processes affecting population change depend upon the scale of the population under consideration. Within the overall, rangewide population, changes in population size are due to a combination of reproduction and survival. However, within finite study areas, changes in population size are due to a combination of reproduction, survival, immigration, and emigration. Therefore, the estimates we report below for finite sampling areas will incorporate immigration and emigration of owls across study area boundaries, although the immigration and emigration rates are typically unknown.

Estimated population trends for spotted owls have benefitted from advances in analytical methods since the first northern spotted owl meta-analysis in 1993 (Gutiérrez 2008). Researchers first used stage-based population projection matrices and estimates of demographic rates to determine changes in abundance within specified age classes during annual time increments (Blakesley et al. 2001, LaHaye et al. 2004, Noon et al. 1992, Seamans et al. 2001). Using this approach, the annual rate of population change was obtained by finding the dominant eigenvalue for a defined population matrix. From the perspective of spotted owl studies, the "rate of population change" provided by projection matrices may be biased low because the estimated juvenile survival rates implicitly incorporate emigration (i.e., juvenile dispersal) from a study area, but the matrices do not account for immigration onto a study area. To accommodate this fact, Seamans and Gutiérrez (2007) and Seamans et al. (2001) used the estimated juvenile survival rate derived from an analysis of an insular spotted owl population in the San Bernardino Mountains as a surrogate for juvenile survival in the Eldorado National Forest under the assumption that the values would be similar between the Eldorado and southern California. From 1990 through 1999, population trends estimated using projection matrices suggested that both the Lassen (= 0.910, SE = 0.025; Blakesley et al. 2001) and Eldorado National Forests (= 0.948, SE = 0.026; Seamans et al. 2001) populations experienced significant declines.

However, Pradel (1996) developed a new method to estimate λ_t using mark-recapture data, which was motivated by a desire to obtain unbiased estimates of λ_t for northern spotted owl study areas (Gutiérrez 2008). This statistical method, referred to as a temporal symmetry model, estimated recruitment, nonjuvenile survival, and population change directly from the mark-recapture data. This approach implicitly incorporated both emigration and immigration because new recruits can be individuals that were either born on or immigrated onto a study area and apparent survival rates reflected either true mortality or emigration off a study area. The first two and the last estimates of λ_t were not used in any analysis because the first and last estimates were confounded with recapture probability and the second estimate had a potential bias from "trap response" or a "learning curve" for field crews at the beginning of studies (Hines and Nichols 2002). "Trap responses" have occurred when observers preferentially sampled known owl sites or when owls either avoided or preferentially responded to human presence by virtue of behavioral conditioning. "Learning curves" have been a function of personnel becoming familiar with a new study area and accomplishing work objectives more efficiently as they gained experience (i.e., if the same number of observers detected more owls because of greater experience, the population could falsely be assumed to be growing when it is not). The Pradel method was used in the two California spotted owl meta-analyses (Blakesley et al. 2010, Franklin et al. 2004). Franklin et al. (2004) reported that the Pradel estimates of mean λ_t from 1992 through 1999 for the Sierra Nevada studies (except the Eldorado) were < 1.0, but all of the 95 percent confidence intervals overlapped 1.0, which meant that it was uncertain if declines had actually occurred. Subsequently, Blakesley et al. 2010 reported that the Pradel estimates of mean λ_t from 1992 through 2002 were <1.0 for the Sierra and Lassen National Forest and slightly >1.0 for the Eldorado National Forest and Sequoia and Kings Canyon National Parks, but again all of the 95 percent confidence intervals overlapped 1.0. However, the estimate of Δ_t for the Lassen National Forest suggested that this population declined over the study period.

Population trends have been recently reanalyzed for all four study areas using new statistical techniques and incorporating additional data collected after the second meta-analysis (Conner et al. 2013, Tempel and Gutiérrez 2013, Tempel et al. 2014b). Conner et al. (2013) used the Pradel model within both maximum-likelihood and Bayesian frameworks to conclude that the Lassen and Sierra study populations had median λ_t less than 1.0. In addition, their Bayesian analysis showed that the Lassen and Sierra study areas had 0.69 and 0.40 probabilities, respectively, of declining by ≥15 percent over the study period. In contrast, the Sequoia and Kings Canyon National Parks study population had a median λ_t >1.0 and only a 0.04 probability of a ≥15-percent decline. The authors recently updated their analyses to include additional data collected in 2012 and 2013, which suggests it is even more likely that the Lassen and Sierra National Forests study populations have declined (fig. 4). Bayesian methods will allow generation of a posterior distribution for Δ_t, which allows the estimation of probabilities of specified declines of interest rather than the classic statistical approach of rejecting or accepting the null hypothesis that $\hat{\Delta} = 1.0$ at a specified probability level (typically $p = 0.05$). Thus, Conner et al. (2013) suggested that Bayesian methods were more informative for managing species of conservation interest than traditional statistical methods.

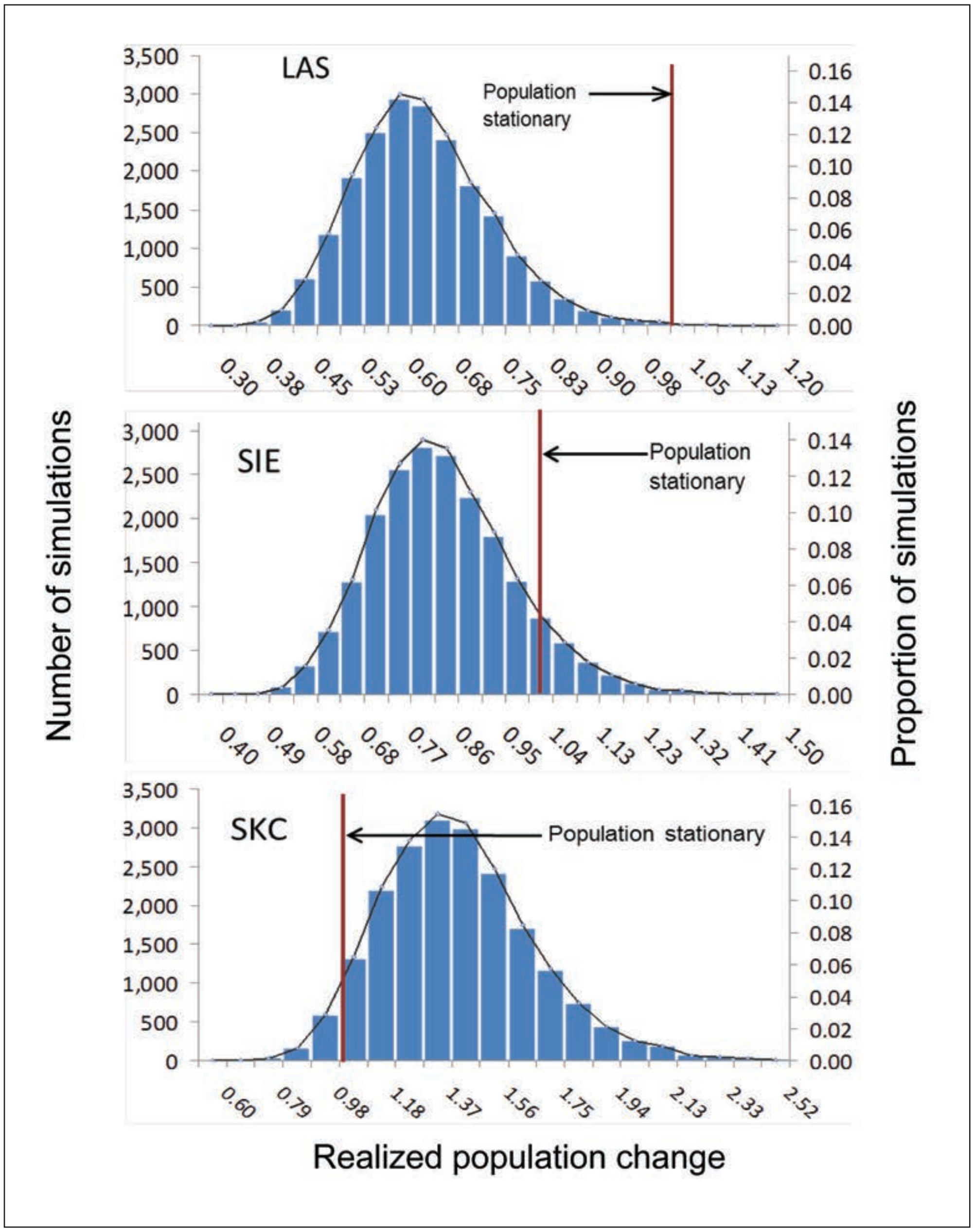

Figure 4-4—Estimated posterior distributions of overall realized population change (Δ_t) of California spotted owls based on posterior distributions of λ_t from 10,000 Markov chain Monte Carlo simulations. Data are from three Sierra Nevada study areas (Lassen [LAS], Sierra [SIE], and Sequoia and Kings Canyon [SKC]), 1990–2013 (used with permission of John Keane).

Tempel and Gutiérrez (2013) used the Pradel model to estimate $\hat{\Delta}$ = 0.725 (95 percent confidence interval = 0.445 to 1.004) for the Eldorado study population from 1993 through 2010; this result closely matched the estimated trends in territory occupancy. They also noted that the Eldorado "density" study area was not surveyed entirely prior to 1993 because of funding constraints, which resulted in a gradual expansion of their study area size from 1990 through 1993 until funding was adequate to survey the entire study area, and that the initial λ_t estimates would have been biased had they included mark-recapture data collected prior to 1993.

Tempel et al. (2014b) then developed an integrated population model (IPM) for the Eldorado National Forest study population that used all data collected on the Eldorado (occupancy, reproductive, and mark-recapture histories for juveniles and nonjuveniles) in a unified analysis. They first used a multistate occupancy model that accounted for imperfect detection to obtain annual counts of the number of young produced and the number of nonjuvenile territorial birds. These counts were then used as input data to the IPM, along with the mark-recapture histories. The IPMs offer several advantages over the traditional analysis of individual datasets, including greater precision in parameter estimates and the ability to estimate demographic parameters (e.g., immigration rates) for which no explicit data are available. They found that mean λ was <1.0 ($\hat{\bar{\Delta}}$ = 0.969, 95 percent credible interval = 0.957 to 0.980), which resulted in a 50 percent decline in population size from 1990 through 2012 ($\hat{\bar{\Delta}}$ = 0.501, 95 percent CRI 0.383 to 0.641; see fig. 4-5). Tempel et al. (2014b) were able to use data from 1990 through 1992 because the multistate occupancy model imputed the count values at territories that were not surveyed in a given year and the mark-recapture data were used solely to estimate apparent survival rates.

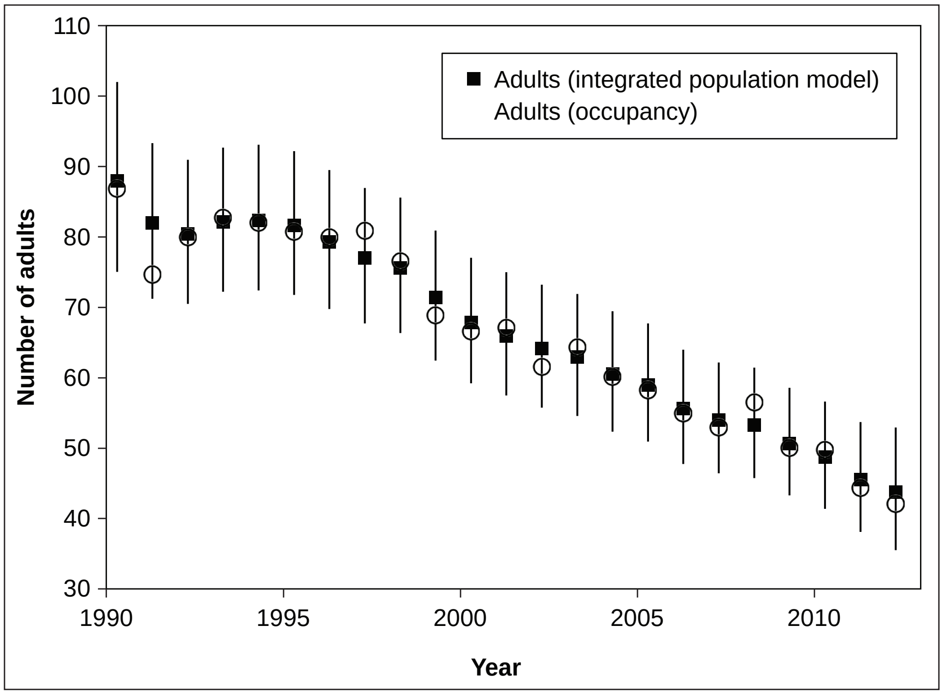

Figure 4-5—Posterior means (95 percent CRI [credible interval]) of realized population change from a Bayesian integrated population model for California spotted owls in the central Sierra Nevada, 1990–2012 (Tempel et al. 2014a; reproduced with permission of Elsevier Inc.©).

They attributed the larger observed decline (cf. Tempel and Gutiérrez [2013]) to the use of additional data and an increase in the number of territories occupied by single owls during the study. They also found that changes in λ were more highly correlated with immigration rate than any other demographic rate (reproductive rate, juvenile survival, and nonjuvenile survival), which suggested that changes in population size were also influenced by processes occurring outside of the study area.

Blakesley et al. (2001) and Seamans and Gutiérrez (2007) performed sensitivity analyses to assess which demographic rates had the most influence on changes in λ. Blakesley et al. (2001) reported that λ was most sensitive to changes in adult female survival on the Lassen National Forest, but fecundity contributed more to observed variation in λ because fecundity varied more than survival. Similarly, Seamans and Gutiérrez (2007) found that λ was most sensitive to changes in survival of nonjuvenile owls on the Eldorado National Forest, but that reproductive output and survival made similar contributions to changes in λ because reproductive output varied more than survival. The authors of both of these studies, as well as Tempel et al. (2014b), observed that juvenile survival made the least contribution of any demographic rate to changes in λ.

Thus far, despite its obvious relevance, researchers have attempted only one comprehensive assessment of how changes in habitat conditions within California spotted owl territories are correlated with changes in λ. Tempel et al. (2014a) created annual vegetation maps for owl territories on the Eldorado National Forest that differed over time because of timber harvest, wildfire, and forest succession. They found that reproduction was negatively correlated with medium-intensity timber harvests and the amount of hardwood forest within territories, where "medium-intensity harvests" encompassed a range of harvest types (group selection, single-tree selection, thinning for hazardous fuels reduction, fuel break, commercial thin). In addition, they found that nonjuvenile survival was positively correlated with the amount of high canopy cover (≥70 percent) forest dominated by medium or large trees (see above). However, life-stage simulations showed that changes in λ at the territory scale were more correlated with changes in the amount of high canopy cover forest than with the other variables they measured ($R^2 = 0.74$ for a logarithmic regression; see fig. 4-6).

Site Occupancy

A growing number of studies have assessed site occupancy for California spotted owls, where the site has typically been defined as a unique owl territory based on the presence of roosting or nesting owls. Occupancy studies can be one or more years in length, but only multiseason studies provide information on changes in

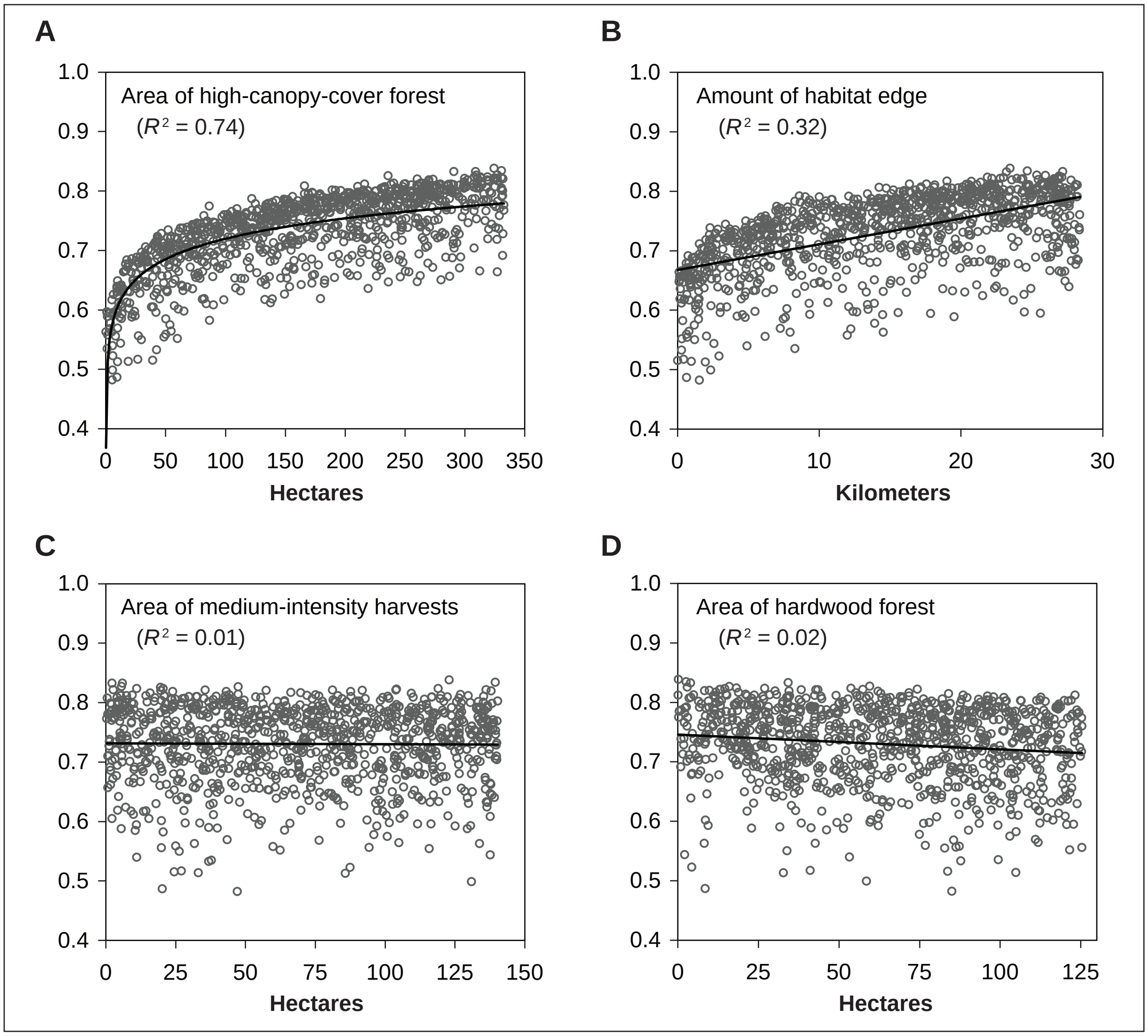

Figure 4-6—Results of a life-stage simulation analysis to assess the sensitivity of annual population growth rate (λ) of California spotted owls to changes in forest vegetation conditions within owl territories. One thousand values of λ were generated by drawing the following habitat variables from a uniform distribution: (a) area (ha) of high canopy cover (≥70 percent) forest dominated by trees ≥30.5 cm (≥12 in) diameter at breast height; (b) amount (km) of habitat edge; (c) area (ha) of medium-intensity timber harvests; and (d) area (ha) of hardwood forest (Tempel et al. 2014b; reproduced with permission of 2014 Ecological Society of America ©).

occupancy status over time and what factors (e.g., habitat conditions, timber harvest, wildfire) are correlated with these changes. Changes in occupancy status are the combined effect of two processes:

- Local colonization, which is the probability that a previously unoccupied site becomes occupied.
- Local extinction, which is the probability that a previously occupied site becomes unoccupied (MacKenzie et al. 2003).

Refer to chapter 3 for a review of how habitat and habitat disturbances such as wildfire and logging affect spotted owl territory occupancy dynamics.

Because spotted owl territories can only be occupied by one or two individuals, occupancy-based studies may be a cost-effective alternative to mark-recapture studies for assessing owl population trends. Indeed, as we previously noted, Tempel and Gutiérrez (2013) found that trends in territory occupancy on the Eldorado National Forest from 1993 through 2010 closely matched population trends estimated from mark-recapture data using the Pradel model. However, Tempel et al. (2014a) analyzed data on the Eldorado from 1990 through 2012 using an integrated population model and found a larger population decline than Tempel and Gutiérrez (2013), partly owing to an increase over time in the number of territories occupied by single owls. Thus, multistate occupancy models that distinguish between territories occupied by single owls from those occupied by owl pairs may be preferable when inferring demographic trends from spotted owl occupancy data. Furthermore, occupancy studies are ideally suited to assess owl responses to management activities (e.g., timber harvest or prescribed burns), wildfire, climate, and other factors.

Population and Conservation Genetics of California Spotted Owls

Genetic methods and principles can provide valuable insights into the population status and management of species of conservation concern in many ways (Allendorf and Luikart 2007). These include (1) identifying conservation units, (2) estimating connectivity (i.e., gene flow and dispersal) among fragmented populations, (3) quantifying the level of genetic variation present within populations, and (4) characterizing demographic history. Genetic information can be applied to several other aspects of species conservation, but we limit our review to the four topics listed above, which in our opinion are the most relevant to the conservation of California spotted owls. We also note that issues associated with spotted owl-barred owl (*Strix varia*) hybridization are discussed in detail in chapter 6. For each of the conservation genetic issues we discuss, we first provide a brief overview of relevant population genetics principles to help interpret previous genetic studies on spotted owls and inform future management and research directions.

Conservation Units

A conservation unit is typically defined as a group of individuals that merits conservation attention independent of other such groups (Ryder 1986). Conservation units have been defined in several ways and applied to species with a variety of objectives. Typically, “evolutionary significant units” (ESUs) refer to populations that are reproductively isolated from other populations and, as a result, have evolved unique adaptations through natural selection (Moritz 1994, Ryder 1986). The ESUs are conserved because the adaptations that differentiate them from other groups of conspecifics may be important for the persistence of the entire species in light of rapid environmental change. In contrast, a "management unit" (MU) generally represents a demographically independent population that receives little immigration from other populations (Moritz 1994, Palsbøll et al. 2007). The MUs are managed independently of other units because they are not expected to be "rescued" via immigration. From a legal perspective, two roughly parallel types of conservation units can be listed as "threatened" or "endangered" under the Endangered Species Act (ESA 1973): a taxon (species or subspecies) and a distinct population segment (DPS). The subspecies concept was defined in chapter 2, and as described therein can be listed under the ESA with the objective of preserving the evolutionary potential of the species, similar to the rationale behind delineating ESUs. The DPS status can be assigned to a population based on its evolutionary, ecological, or geopolitical discreteness, significance to the entire range of the species, and conservation status. In practice, the delineation of all types of conservation units is frequently informed using genetic data given the genetic underpinnings of adaptive traits (Crandall et al. 2000, Moritz 1994, Palsbøll et al. 2007).

As described in chapter 2, spotted owls are clearly divided into three well-delineated subspecies based on phylogeographic patterns in the mitochondrial DNA (Barrowclough et al. 1999, 2005; Haig et al. 2004) as well as differences in microsatellite allele frequencies among populations (Funk et al. 2008a). With the exception of a small number of California spotted owl haplotypes detected within the geographic range of northern spotted owls, the three subspecies appear to be "reciprocally monophyletic" based on the control region of the mitochondrial genome (i.e., all sampled haplotypes were more closely related to other haplotypes in the same subspecies than to those of the other subspecies) (Haig et al. 2004). Thus, these three groups could be also be considered as discrete ESUs, each of which is important to conserve in order to maintain the evolutionary potential of the species, at least according to one commonly used definition for ESUs (Moritz 1994).

Within the range of the California subspecies, genetic data appears to support the designation of multiple MUs. Owls in the Sierra Nevada are clearly genetically distinct from owls in the mountains of southern California (Barrowclough et al 1999, 2005; Funk et al. 2008a; Haig 2004). Large areas of unsuitable lowland habitat between the Sierra Nevada and southern California mountains certainly impede dispersal to the point that owls in these two regions are demographically independent. Indeed, Barrowclough et al. (2005) estimated that approximately zero to one female migrant was exchanged between these two regions per generation. Some mountain ranges within southern California may also be demographically independent, and thus could be treated as discrete MUs, given limited gene flow (Barrowclough et al. 2005; see also below) and that little dispersal by marked individuals has been observed as part of mark-recapture studies (LaHaye et al. 2001). However, additional genetic analyses that include nuclear DNA would be needed to define MUs within southern California.

Connectivity in Fragmented Populations

Understanding the level of connectivity among populations that are isolated to some degree by habitat fragmentation or physiographic barriers (e.g., nonforested habitat between mountain ranges) has several important implications for the conservation of species, where connectivity can refer to gene flow (the movement of genes) or dispersal (movement of individuals). The isolation of formerly contiguously distributed populations into remnant habitat patches can impede gene flow and dispersal, thereby hastening extinction through a variety of genetic and demographic processes symptomatic of small populations (Keller and Waller 2002). As a result, a daunting array of genetic approaches has been developed to quantify gene flow and dispersal and assess whether habitat fragmentation has affected these processes to the point where management intervention is required (Lowe and Allendorf 2010). It is important to recognize that different genetic methods often yield inferences about gene flow and dispersal that apply to different time scales (i.e., a single generation to thousands of generations) and have a range of limitations, including the assumption of genetic drift-migration equilibrium (stable gene flow and effective population size) and difficulty at estimating dispersal when it is high enough to affect local population dynamics (Paetkau et al. 2004, Palsbøll et al. 2007, Peery et al. 2008). Moreover, maintaining the distinction between gene flow and individual dispersal is important because the dispersal of individuals does not necessarily translate to gene flow (Nosil et al. 2005, Peery et al. 2010).

Although spotted owl habitat within the Sierra Nevada has been extensively modified over the past approximately 150 years, we expect relatively little effect of historical habitat fragmentation on gene flow or dispersal in California spotted owls in this region. Spotted owls and their habitat remain reasonably well-distributed across the Sierra Nevada and the species is a strong disperser (Forsman et al. 2002). In the only genetic-based study of connectivity within the Sierra Nevada, Barrowclough et al. (2005) estimated gene flow among spotted owl populations sampled in the northern, central, and southern Sierra Nevada using coalescent approaches applied to patterns of mitochondrial sequence variation. Their estimates of the effective number of female migrants ranged from zero (northern to central) to 25 (central to northern) per generation. An estimate of 25 migrants per generation is considered reasonably high from a population genetics perspective, whereas zero is clearly low. Gene flow estimates using this method, however, represent long-term averages (i.e., over evolutionary time scales) and do not necessarily reflect current rates of gene flow (or dispersal). Further study using nuclear genetic markers (e.g., microsatellites) and landscape-scale sampling could provide additional insights into current rates of gene flow and dispersal within the Sierra Nevada, as well as the environmental factors that influence these processes. Funk et al. (2008b) conducted such a "landscape genetics" study for northern spotted owls using 10 microsatellites to understand how landscape-scale topographic features such as major mountain ranges, valleys, and rivers impeded gene flow. In this study, gene flow was impeded by natural barriers such as mountain ranges without suitable owl habitat at higher elevations and, paradoxically, smaller and relatively undeveloped valleys, but not the large and extensively modified Willamette Valley.

As described above, Barrowclough et al. (2005) estimated low levels of gene flow among California spotted owl populations occurring in the mountains of southern California. Clearly, the natural isolation of these mountain ranges by unsuitable habitats such as deserts has acted as a barrier to gene flow over long time scales. However, urbanization and habitat development over the past century could have increased the isolation of these populations and further reduced gene flow and dispersal (LaHaye and Gutiérrez 2005, Verner et al. 1992). Additional genetic-based studies of connectivity using nuclear genetic markers could provide insight into the extent to which habitat fragmentation currently threatens southern California populations.

Genetic Variation Within Populations

Conserving adaptive genetic variation within populations is important for maintaining the evolutionary potential of species (Frankel and Soulé 1981). Loss of alleles occurs at a relatively rapid rate in small (e.g., bottlenecked) populations because of the enhanced effects of genetic drift, and the resultant loss of alleles with adaptive significance can compromise the ability of the species to adapt to future environmental change (Frankham et al. 1999, Lande and Shannon 1996, O'Brien and Evermann 1988). Inbreeding, the mating of close kin, is also more likely to occur in bottlenecked populations because remaining individuals tend to be related. Rare deleterious alleles are more likely to be expressed in inbred populations owing to high levels of homozygosity, which can result in declines in individual fitness (i.e., inbreeding depression) and increase the likelihood of extinction (Keller and Waller

2002). Thresholds for effective population sizes below which species will become vulnerable to the loss of adaptive genetic variation and inbreeding have been the subjective debate among scientists and are likely species-specific traits. Nevertheless, consensus exists that preventing the loss of adaptive genetic variation and inbreeding depression is best accomplished by maintaining large, well-connected populations.

California spotted owls exhibit relatively little sequence variation in the mitochondrial DNA control region compared to northern and Mexican (*S. o. lucida*) spotted owls (Barrowclough et al. 1999, 2005; Haig et al. 2004). Because the control region is a nonprotein coding sequence, it likely reflects the evolutionary history of mitochondrial genes given that the mitochondrial DNA represents a single nonrecombining genome. Indeed, nucleotide diversity, which represents the average number of nucleotide differences per site across pairs of randomly selected DNA sequences, is several times lower in California spotted owls sampled in the Sierra Nevada than in populations of the other two subspecies (Barrowclough et al. 1999, 2005). Moreover, no sequence variation was detected in the mitochondrial control region of owls sampled in southern California, either in an initial screening of 10 individuals in the San Bernardino and San Jacinto Mountains (Barrowclough et al. 1999), or in an expanded sample of 38 individuals that included owls from Mount Palomar (Barrowclough et al. 2005). Barrowclough et al. (1999, 2005) offered three possible explanations for relatively low observed mitochondrial diversity in California spotted owls:

- Small historical and current effective population sizes
- Historical population expansion (i.e., a colonization event or in situ recovery from a historical bottleneck)
- A beneficial mutation followed by a “selective sweep.”

Of these possibilities, clearly a population bottleneck would have the most detrimental impacts on the evolutionary potential of California spotted owls.

Genetic variation has also been assessed in a rangewide study of spotted owls using a panel of 10 microsatellite loci (tandemly repeating nuclear DNA sequences; Funk et al. 2008a). Although Funk et al. (2008a) did not directly report heterozygosity or allelic diversity for each sampled population, they stated that minimum expected heterozygosity across sampling sites was 0.685, which included two localities in the Sierra Nevada. This level of heterozygosity is typical of wild populations and, at face value, does not seem symptomatic of a severe population bottleneck. Caution, however, should be exercised when interpreting levels of genetic variation present in microsatellite markers because of “ascertainment bias,” which results from researchers selecting the most polymorphic loci from a larger panel of candidate loci for use in population genetic studies. Highly polymorphic loci are useful for characterizing population genetic structure, understanding introgression, and estimating dispersal, but may be subject to high mutation rates and, therefore, yield an optimistic perspective of effective population size. Clearly, additional work is needed to fully characterize understanding of the demographic and microevolutionary factors that have shaped present-day genetic variation in spotted owls (see "Characterizing Demographic History" section below).

To date, tests of inbreeding or inbreeding depression have not been conducted for California spotted owls. However, several lines of evidence suggest that inbreeding does not currently threaten California spotted owls in the Sierra Nevada. First, Funk et al. (2008a) reported that observed heterozygosity did not deviate from expected heterozygosity for any of their sampled populations (inbred populations are expected to have lower observed than expected heterozygosity) across their panel of microsatellite loci. Second, natal dispersal is strong in spotted owls (Forsman et al. 2002) and, as a result, incestuous matings are rarely observed in this species (Carlson et al. 1998, Forsman et al. 2002). Third, in the Sierra Nevada, California spotted owls remain well-distributed and occur at higher abundances than typically observed in populations experiencing noticeable impacts of inbreeding depression. By contrast, spotted owls in the mountains of southern California are distributed among relatively small and insular populations that are likely connected by low levels of gene flow and are likely to be more susceptible to inbreeding. Nevertheless, even in the Sierra Nevada, future reductions in owl habitat from timber harvesting, fire, and climate change could result in smaller, more isolated owl populations that are more susceptible to the detrimental effects of inbreeding.

Characterizing Demographic History

Changes in effective population size, such as bottlenecks, often register signals in the DNA of the individuals that make up the population. Thus, the demographic history of a population of interest can be studied by examining relevant aspects of genetic variability in present-day populations. Genetic methods provide an appealing means for understanding changes in effective population because they only require a population sample taken at a single point in time, as opposed to long-term population monitoring (although historical samples can strengthen inferences). Consequently, many population genetic methods have been developed that can be used to characterize the demographic history of species of conservation concern such as California spotted owls (e.g., Beaumont 1999, 2003; Cornuet and Luikart

1996; Garza and Williamson 2001). However, as with genetic estimators of connectivity, caution must be exercised when interpreting the results of genetic-based assessments of demographic history as they often require making assumptions (e.g., about the way genes mutate) that are difficult to test, and results can be sensitive to violations of assumptions (Peery et al. 2012).

Applications of genetic data to questions of demographic history in California spotted owls are few, but as discussed above, this subspecies has depauperate mitochondrial DNA variation compared to northern and Mexican spotted owls (Barrowclough 1999, 2005; Haig 2004). Demographic explanations for relatively low genetic variation in California spotted owls, both in the Sierra Nevada and southern California, are uncertain but include persistently small populations, population bottlenecks, and recent colonization followed by population expansion (Barrowclough et al. 1999, 2005). These three competing hypotheses could be tested using coalescent methods applied to a panel of nuclear markers (e.g., microsatellites) or mitochondrial DNA (Beaumont 1999, 2003; Drummond and Rambaut 2007; Wu and Drummond 2011), as well as based on differences in microsatellite diversity statistics (Cornuet and Luikart 1996, Garza and Williamson 2001, Luikart and Cornuet 1998). Indeed, Funk et al. (2010) used genetic bottleneck tests based on microsatellite diversity statistics to test for declines in effective population size in northern spotted owls and demonstrated that bottlenecks were generally apparent in populations that demographic studies indicated were declining. Again, although such methods are sensitive to several potentially important assumptions, careful application of bottleneck tests and associated methods could provide important and novel insights into the demographic history of California spotted owls. Moreover, these genetic methods have the potential for reconstructing demographic history on longer time scales than spanned by California spotted owl demography studies (about 25 years), which could provide insights into how historical changes in forest extent and structure and climate have affected this subspecies. Finally, emerging genomic methods now provide increasing opportunities for more detailed reconstructions of the demographic history of California spotted owls (Hung et al. 2014).

Chapter Summary

Population data gathered subsequent to CASPO demonstrates that owl populations have declined over the past 20 years on three of the four long-term demographic study areas in the Sierra Nevada, which removes one of the key uncertainties of CASPO. Because these study areas were not selected at random, it cannot be inferred unequivocally that they represent the status of spotted owls in the entire Sierra Nevada. However, these study areas are large, span the entire length of the

Sierra Nevada, occur primarily in the mid-elevation forests that have the highest densities of owls, and exhibit no obvious special selection criteria that would likely result in the bias of derived information. Therefore, we infer that spotted owl populations in the Sierra Nevada are declining on most landscapes. We note that the populations that have declined are all located on national forests, and the only stationary population is located within Sequoia and Kings Canyon National Parks. The differences among study areas may have been related to differences in forest management, the presence of giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) groves in Sequoia and Kings Canyon National Parks, differences in the proportion of oak woodlands, or some combination of these factors (Blakesley et al. 2010). We further note that whereas barred owls have negatively affected northern spotted owl populations, barred owls have appeared on the study areas in the Sierra Nevada only within the past 10 years and are either uncommon (Lassen) or extremely rare (Eldorado and Sierra National Forests, Sequoia and Kings Canyon National Parks). Thus, the observed population declines on the Eldorado and Sierra cannot be attributed to barred owls, and these declines may intensify if barred owls continue their southern range expansion in the future. Finally, these studies highlight the importance of long-term monitoring studies of long-lived species where small annual population declines are difficult to detect but result in large cumulative declines over long time periods.

Reproductive output and nonjuvenile survival contribute more to variation in spotted owl population size than juvenile survival. It is now well established that California spotted owl survival (and reproduction, to a lesser degree) is dependent upon having a sufficient amount of high canopy cover forest containing larger trees within breeding territories. This forest cover type has been positively correlated with survival rates at all four of the long-term demographic study areas and with reproductive rates at two of the study areas (Lassen and Sierra). Furthermore, Tempel et al. (2014a) noted that population growth rate (λ, which is determined by reproduction and survival) at the territory scale was strongly dependent upon the amount of high canopy cover ($\geq$70 percent) forest within owl territories. Their results also suggested that maintaining between 100 and 150 ha (247 and 370 ac) of high canopy cover forest within owl territories would be sound conservation practice because small changes in annual population growth rate can translate into large changes in realized population size over extended periods of time, and populations in the Sierra Nevada have already declined by as much as 50 percent over the past two decades. In addition, 100 to 150 ha is a more realistic target than managing for amounts of high canopy cover forest (e.g., 200 ha) that maximized population growth in Tempel et al. (2014a). This amount of habitat also coincides with the size of spotted owl PACs, which have been consistently used for nesting and roosting over a 24-year period on the Eldorado (Berigan et al. 2012). Finally, some evidence exists that northern and California spotted owls may benefit from some habitat heterogeneity and edge between forest types (Franklin et al. 2000, Tempel et al. 2014a), but the best available data indicate that sufficient high canopy cover forest is needed within owl territories.

A key remaining uncertainty is the degree to which changes in demographic rates and population abundance are related to various types of habitat disturbance such as high-severity wildfire and timber harvest. Thus far, the evidence for how disturbance may affect spotted owls has been mixed. Tempel et al. (2014a) reported that local colonization was negatively correlated with wildfire, but that timber harvest had relatively minor effects on reproduction, nonjuvenile survival, and territory occupancy. However, they found that territory fitness and occupancy were highly correlated with the amount of high canopy cover forest within owl territories, so disturbances that reduce this cover type could negatively affect spotted owl populations. Other studies that focused specifically on site occupancy and wildfire suggested that owls were resilient to low- and moderate-severity fire, but vacated territories when large areas were burned at high severity. Because of the remaining uncertainty on how timber harvest and wildfire affect spotted owls, the apparent benefits that closed-canopy forests provide owls, and the substantial recent population declines in some regions, landscape-scale fuel treatments implemented to reduce fire risk within owl habitat cannot be adequately assessed for their efficacy without an accompanying rigorous monitoring program.

Ideally, future research would be conducted within an experimental context, but experimental studies are likely to be impractical because of logistical difficulties and the large home ranges of spotted owls. Therefore, researchers and managers will likely need to continue to rely on correlative, quasi-experimental approaches that account for logging and wildfire effects in a rigorous manner. In addition, simulation modeling of owl populations at larger spatial scales where the model parameter values are based on empirical results from smaller study areas may provide insights into regional population dynamics. For example, recent modeling for the northern spotted owl suggested that the demographic performances of regional metapopulations were more affected by complex source-sink dynamics among the metapopulations than by metapopulation specific habitat values (Schumaker et al 2014).

Genetic investigations support treating California spotted owls in the Sierra Nevada and southern California, collectively, as a discrete ESU in light of their genetic divergence from the northern and Mexican subspecies. Further, genetic exchange and dispersal between southern California and Sierra Nevada owl populations appears to be very low, suggesting that owls in these two regions should be treated as independent management units. Genetic variation is low and may constrain the ability of California spotted owls to adapt to inevitable future environmental change, and further population declines could result in even lower levels of genetic variation and greater constraints on evolutionary potential. Evidence for historical (long-term) population declines from genetic data is equivocal but could be tested with additional analyses. In general, rapidly emerging technologies and analytical frameworks within the field of "conservation genomics" provide exciting new opportunities for characterizing the population structure and demographic history of California spotted owls.

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Chapter 5: Current and Projected Condition of Mid-Elevation Sierra Nevada Forests

Malcolm P. North, Mark W. Schwartz, Brandon M. Collins,
and John J. Keane[1]

Introduction

Most of the California spotted owl's (*Strix occidentalis occidentalis*) habitat is concentrated in mid-elevation forests of the Sierra Nevada (see chapter 9 for a discussion of southern California spotted owls and their habitat), which are made up primarily of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), mixed-conifer, white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and mixed-evergreen forest types. These forests have undergone substantial change since the arrival of Europeans and are projected to dynamically respond to ongoing factors affecting ecosystem conditions. In this chapter, we summarize some of the historical changes in mid-elevation forests that have most extensively altered ecosystem conditions. We also explore sources and spatial distribution of the more extant changes in forest condition. We then discuss likely trends in forest response to projected stressors, particularly climate change, drought, and fire. Finally, we examine recent research and resulting changes in management practices that might affect future forest conditions in an effort to increase ecosystem resilience.

Forest Management

Management practices, including fire suppression, over the past century have largely shaped current forest conditions in the Sierra Nevada. These conditions significantly vary with land ownership because owners have different incentives and constraints that influence their management practices. We examine the three main ownerships in the Sierra Nevada, their historical management practices, and current conditions of the different forests.

Ownerships

The U.S. Forest Service (USFS) is the largest steward of public lands in the Sierra Nevada. About 2.93 million ha (7.24 million ac; 47 percent of the 6.24 million ha

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[15.42 million ac]) in the Sierra Nevada bioregion are under USFS management (Davis and Stoms 1996). The USFS has a broad mandate of managing national forests for multiple use and providing sustainable ecosystem services (NFMA 1976). About 2.34 million ha (5.77 million ac; about 37 percent) of conifer forests in the Sierra Nevada are in private ownership (Davis and Stoms 1996), and their management is governed by California's Forest Practice Regulations, which promotes "achiev[ing] a balance between growth and harvest over time consistent with the harvesting methods within the rules of the Board, maintain functional wildlife habitat…, retain or recruit late and diverse seral stage habitat components…, and maintain growing stock, genetic diversity, and soil productivity" (CA FPR Section 897, USDA FS 2012). There are five national parks in the Sierra Nevada and southern Cascades: Devil's Postpile, Lassen, Sequoia and Kings Canyon, and Yosemite covering 696 000 ha (1.73 million ac). The National Park Service (NPS) serves as steward of these parks and is under a mandate to provide recreational opportunities for people, and to protect and showcase natural resources without exploitation.

Historical Management Practices

Until about 1990, similar management objectives and silvicultural prescriptions were used on both public and private lands (McKelvey and Johnston 1992). Therefore, we combined our synopsis of management practices during this period for both ownerships.

Early logging prior to 1900 occurred mainly near mining operations and associated communities at low elevations in the southern and central Sierra Nevada, with most logging occurring below national forest lands. Logging extended to mid and high elevations in the northern Sierra Nevada to support mining at higher elevations and lands adjacent to the Southern Pacific Railroad line (McKelvey and Johnston 1992). The Lake Tahoe and Truckee River basins were exceptions to these general patterns as they were extensively logged to support the Comstock silver mines in western Nevada. Away from railroad lines, log removal was limited to wagons and short-haul skidding with animals and steam "donkeys." Because of these transportation limitations, most logging consisted of high-grading of large and valuable trees. With improvements in transportation, timber harvest increased steadily after 1900, although it declined for about a decade during the Great Depression. Timber harvest in the Sierra Nevada peaked in the post-World War II years, and then stabilized generally ranging between about 1.3 and 1.7 million board feet (mmbf) (1960 through 1990), with a short decline during the 1980s recession (McKelvey and Johnston 1992).

Prior to the 1980s, most silvicultural prescriptions were selection harvests of commercially valuable trees, leaving those with marginal value standing. Clearcutting prescriptions were incorporated in the 1970s, and clearcuts accounted for most of the volume in the mid-1980s. In the late 1980s, most volume was harvested using salvage prescriptions, following mortality principally from fire and insect events. In general, similar harvest prescriptions tended to be implemented on public and private lands prior to 1990 (McKelvey and Johnston 1992).

A legacy of management practices during this period is a reduction in "defect" trees (Bouldin 1999). Over many decades, stand improvement practices often involved removing "defects" such as trees with broken tops, missing limbs, rot and large cavities (see Walsh and North 2012 for examples). Such defect trees typically require many years to develop and thus decades of this practice have probably resulted in a significant decline in these structures often used by wildlife for nesting, resting, and roosting habitat (Bull et al. 1997, Carey 2002, Carey et al. 1997, Cockle et al. 2011, Hunter and Bond 2001, Wiebe 2011).

McKelvey and Johnston (1992) summarized four key changes in forest conditions that occurred from 1850 through 1992: (1) the loss of old, large-diameter trees and associated large downed logs; (2) a shift in species composition toward shade-tolerant, fire-sensitive tree species (i.e., from pines to fir and cedar); (3) increases in fuel loads associated with the mortality of small-diameter trees; and (4) the presence of fuel ladders that facilitate crown fire. Further, they indicated that management direction identified in land management plans (LMPs) for Sierra Nevada national forests current at that time would likely not alleviate these concerns and trends in forest dynamics. The LMPs projected that national forest lands in the western Sierra Nevada would be converted to even-age systems using clearcut, seed tree, and shelterwood prescriptions at a rate of 91 600 ha (226,350 ac) per decade and that selection logging would occur on 32 000 ha (80,000 ac) per decade. This management direction provided no guarantees that old, large trees and their derivatives (e.g., large snags and logs) would be maintained. Rather, it suggested large proportions of future forest would trend toward areas of even-aged plantations with stands of dense, smaller diameter trees (McKelvey and Johnston 1992).

Forest Management Since 1990

Concern for the conservation of California spotted owls began in the mid-1980s with awareness first raised over the status of the related subspecies, the northern spotted owl (*Strix occidentalis caurina*). With the adoption of the California spotted owl guidelines following the California spotted owl technical assessment (CASPO) in 1992 (Verner et al. 1992), national forest and private ownership management practices significantly diverged in the mid-1990s. Timber harvest dramatically decreased on USFS lands. Overall, 83.4 percent of the timber volume harvested between 1994 and 2013 was generated from private lands with public lands contributing from 10 to 24 percent (fig. 5-1).

National Forest System lands—
About 490 000 ha (1.2 million ac) of treatments occurred on National Forest System (NFS) lands in the Sierra Nevada between 1990 and 2014 (table 5-1; see appendix p. 155 for more detailed information). The number of treated acres has declined over time, from highs of 40 000 to 48 000 ha (100,000 to 120,000 ac) per year in 1990–1992 to a low of around 8000 ha (20,000 ac) per year in 2011–2013 (table 5-1, fig. 5-2). The highest proportion of total treated acres from 1990 through 2014 occurred on the Lassen (113 966 ha [284,916 ac]) and Plumas National Forests (101 764 ha [254,411 ac]), with intermediate amounts on the Stanislaus (63 802 ha [159,804 ac]), Tahoe (62 683 ha [156,708 ac]), and Eldorado (58 098 ha [145,244 ac]) National Forests (fig. 5-3).

Concurrent with a decline in the number of acres treated has been a change in the predominant silvicultural prescriptions used on NFS lands (table 5-1, fig. 5-2). From 1990 through 1994, the predominant silvicultural prescriptions were sanitation and salvage cuts, followed by lower amounts of clearcuts and overstory removal. Adoption of CASPO guidelines in 1993 led to an increase in commercial thinning following CASPO guidelines that maintained all trees >30 in diameter at breast height (d.b.h.), maintained overstory canopy cover >40 percent, and removed

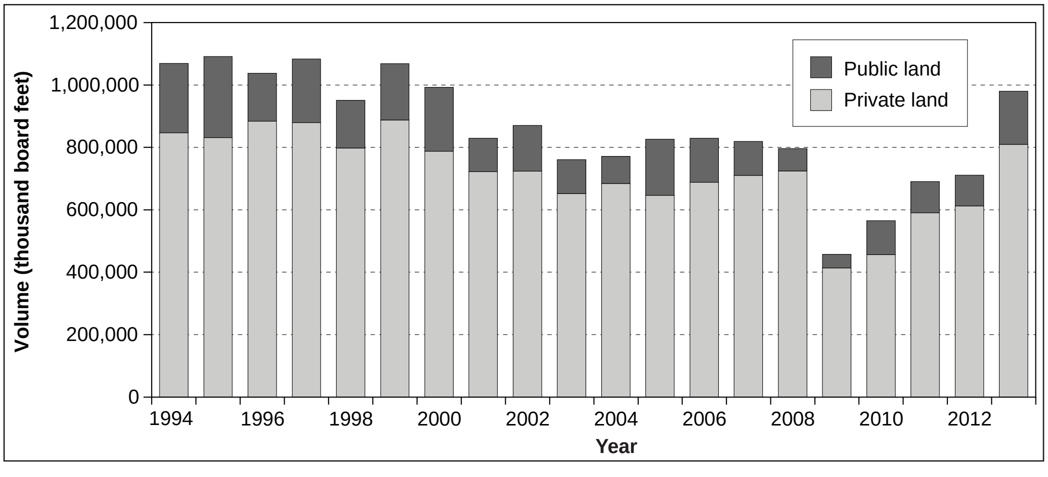

Figure 5-1—Annual timber volume harvested (thousand board feet [mmbf]) by year on public and private lands from counties in the Sierra Nevada 1994–2013. See text for further details. Source: Timber Yield Tax program, California State Board of Equalization.

Table 5-1— Treatment hectares accomplished on National Forest in the Sierra Nevada by silvicultural prescription and year during 1990–2014

Year	Clear-cut	Commercial thin	Group selection	Other	Overstory removal cut	Salvage cut	Sanitation cut	Seed tree cut	Single tree selection cut	Total
1990	5,390	4,113	109	134	4,023	16,052	15,017	970	1,625	47,434
1991	4,000	1,746	49	67	2,086	14,004	14,831	999	1,951	39,733
1992	3,770	855	33	16	2,121	11,714	29,853	341	929	49,631
1993	2,425	2,052	90	22	1,799	10,620	18,011	552	686	36,258
1994	2,063	1,131	36	56	1,506	3,278	8,924	283	152	17,428
1995	3,120	5,082	33	143	2,636	674	7,529	369	437	20,022
1996	7,389	7,905	148	79	582	576	9,764	511	2,581	29,535
1997	2,191	10,199	120	207	135	688	9,815	146	658	24,159
1998	689	12,573	25	142	559	2,335	12,910	74	620	29,927
1999	346	13,617	449	423	45	2,622	948	21	826	19,296
2000	31	10,940	93	929	0	183	1,728	17	248	14,169
2001	28	7,635	280	632	8	126	1,094	48	96	9,947
2002	263	8,864	400	370	43	160	256	0	330	10,686
2003	2,451	7,611	100	186	0	9,893	1,010	0	91	21,342
2004	13	13,611	273	0	0	1,414	1,402	5	1,250	17,969
2005	3	5,067	108	0	1	669	1,245	2	900	7,995
2006	1,714	12,755	410	29	3	3,648	617	0	454	19,630
2007	201	11,331	252	17	0	297	388	0	31	12,516
2008	0	3,743	26	8	0	1,047	315	0	77	5,216
2009	103	6,668	157	42	0	6,632	452	0	307	14,360
2010	238	7,546	399	97	0	1,046	176	0	320	9,822
2011	110	6,086	184	96	0	690	24	0	1	7,190
2012	0	7,924	203	44	0	216	0	0	90	8,477
2013	0	5,046	39	1	0	3,675	84	0	0	8,844
2014	194	1,931	45	3	0	5,437	0	0	91	7,701
Total	36,732	176,028	4,063	3,740	15,547	97,694	136,393	4,339	14,751	489,287

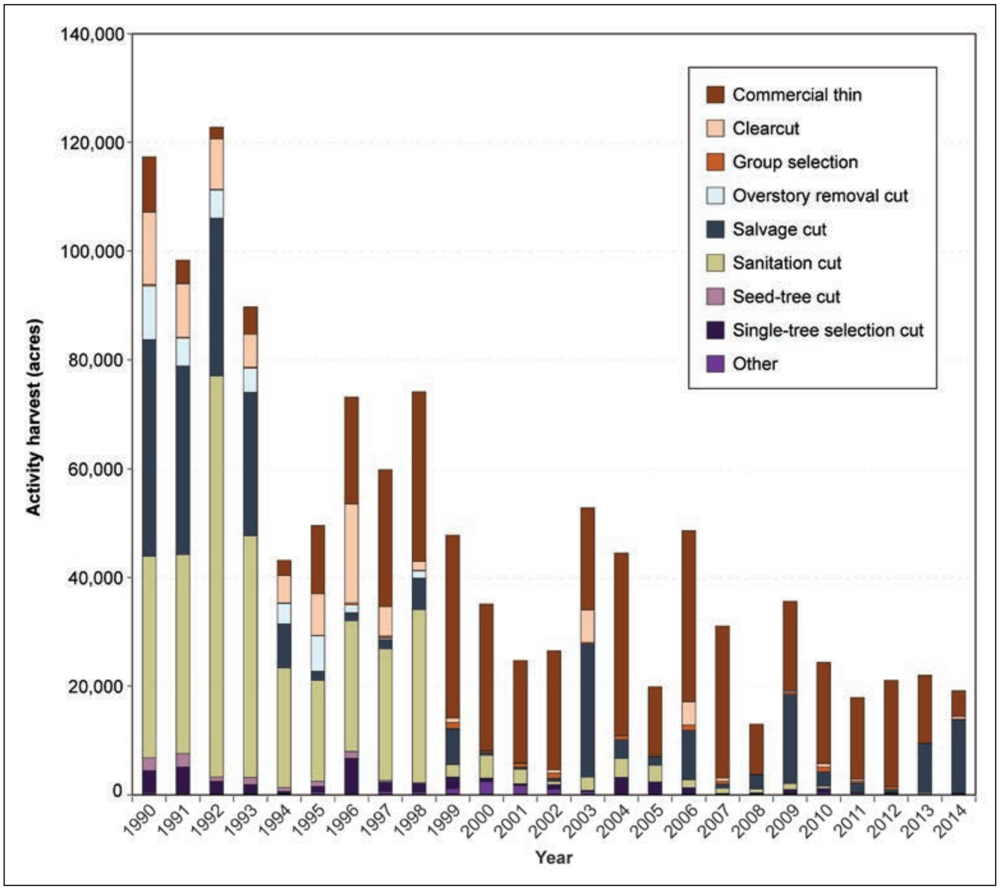

Figure 5-2—Treatment acres accomplished on national forests in the Sierra Nevada by silvicultural prescription and year, 1990–2014. Source: Taken from USFS Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Research Region silviculturist).

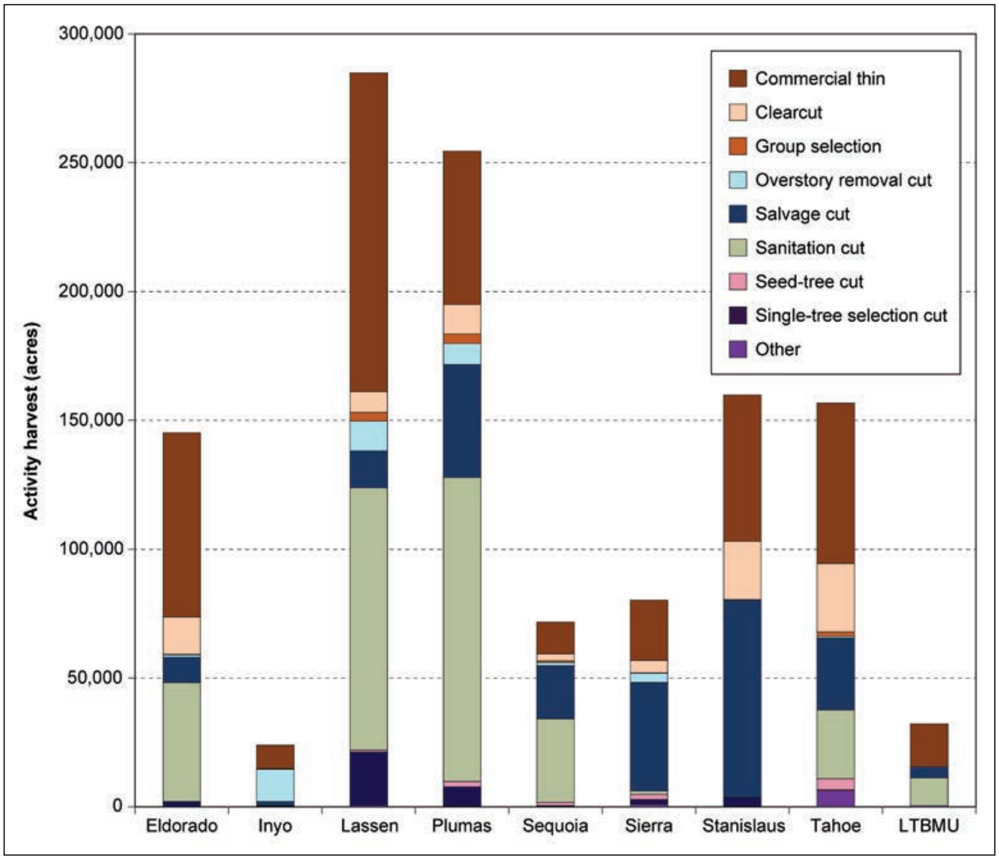

Figure 5-3—Treatment acres accomplished on national forests in the Sierra Nevada by silvicultural prescription and national forest, 1990–2014. LTBMU = Lake Tahoe Basin Management Unit. Source: Taken from USFS Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Research Region silviculturist).

small trees to an upper diameter limit. The proportion of sanitation cuts dropped in 1999 as existing contracts established before CASPO were completed and CASPO prescriptions became the predominant silvicultural prescription. Commercial thinning associated with CASPO guidelines, a focus on forest thinning to meet fuels reduction objectives, and postfire salvage logging have been the dominant prescriptions on NFS lands in the Sierra Nevada between 1999 and 2014 (fig. 5-2).

About 255 143 ha [665,357 ac] of silvicultural treatments occurred within the range of the California spotted owl in the Sierra Nevada (see appendix p. 155 for details), of which about 199 600 ha (299,000 ac; 45 percent) were treated from 2002 through 2014 when NFS spatial data on treatments was complete (table 5-2, fig. 5-4). Sanitation cuts were the predominant silvicultural prescription used during 1990–1994. Commercial thin was the predominant prescription used during 1996–2013, followed by episodic salvage events and smaller amounts of clearcutting (table 5.2).

Table 5-2—Treatment hectares accomplished on National Forest lands within the range of the California spotted owl in the Sierra Nevada by silvicultural prescription and year during 1990–2014

Year	Clear Cut	Commercial Thin	Group Selection	Other	Overstory Removal Cut	Salvage Cut	Sanitation Cut	Seed-tree Cut	Single Tree Selection Cut	Total
1990	4,123	1,246	109	121	3,213	1,467	10,348	899	1,577	23,104
1991	3,262	1,486	49	67	1,864	5,803	6,599	986	1,936	22,051
1992	3,488	609	11	16	973	4,888	7,257	305	834	18,380
1993	1,790	1,228	89	22	417	4,268	733	424	641	9,613
1994	1,746	851	36	56	551	166	4,164	253	152	7,975
1995	1,341	2,852	11	143	559	24	747	348	137	6,163
1996	742	3,655	78	40	89	0	5,316	139	286	10,344
1997	2,146	4,396	66	180	135	47	746	146	459	8,322
1998	418	8,151	20	90	29	2,298	1,088	57	83	12,235
1999	250	8,555	282	286	45	2,469	670	6	811	13,375
2000	4	6,837	43	470	0	168	1,340	17	214	9,094
2001	28	5,925	127	632	8	111	439	48	94	7,412
2002	263	4,847	28	370	43	93	79	0	329	6,051
2003	2,450	5,032	3	186	0	9,480	814	0	45	18,010
2004	13	9,255	94	0	0	824	1,284	5	643	12,119
2005	3	4,359	50	0	1	576	650	2	209	5,850
2006	1,724	11,012	408	29	3	2,187	568	0	454	16,386
2007	115	9,448	231	7	0	281	319	0	28	10,428
2008	0	3,203	8	8	0	1,041	313	0	66	4,639
2009	4	5,295	96	38	0	6,343	411	0	43	12,230
2010	7	7,971	343	89	0	1,045	174	0	314	9,942
2011	12	5,431	172	77	0	201	20	0	0	5,912
2012	0	6,734	183	37	0	75	0	0	90	7,119
2013	0	5,632	14	1	0	3,574	82	0	0	9,303
2014	0	760	14	0	0	2,339	0	0	91	3,203
Total	23,928	124,768	2,565	2,964	7,929	49,770	44,162	3,637	9,538	269,261

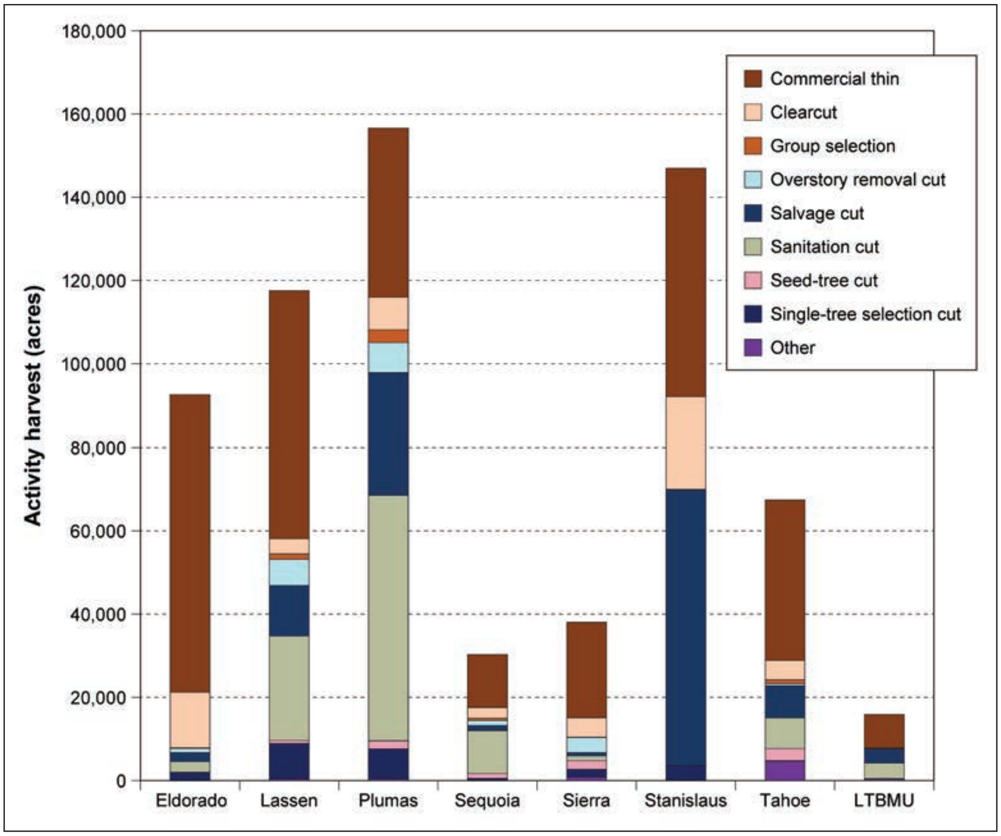

Figure 5-4—Treatment acres accomplished on national forest lands within the range of the California spotted owl in the Sierra Nevada by silvicultural prescription and national forest, 1990–2014. Sources: Taken from USFS Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Research Region silviculturist); owl range from California Department of Fish and Wildlife.

Current USFS practices often focus on two metrics when implementing management treatments; maximum tree diameter removed (“diameter limits”) and residual canopy cover. Although trees up to 75 cm (30 in) d.b.h can be marked for removal, in many forests that have been previously thinned, the maximum diameter limit is set to a lower size because removing larger trees would drop the residual canopy cover below the target. Canopy cover is usually indirectly estimated using the Forest Vegetation Simulator or FVS model based upon the number, size, and species of the leave trees. As an indirect estimate, FVS assumes a certain amount of crown overlap (Crookston and Stage 1999) and does not account for spatial variability in tree locations (Christopher and Goodburn 2008). Nor does the FVS-generated canopy cover target consider canopy closure patterns or distinguish between clumped or regular distributions, differences that appear to be important functional and structural attributes of fire-adapted forests (Churchill et al. 2013, Larson and Churchill 2012, Lydersen et al. 2013).

Canopy cover targets are a featured objective in recent management guidance documents (e.g., Sierra Nevada Forest Plan Amendments of 2001 and 2004; USDA FS 2001, 2004) and are set to be no lower than an average of 40 percent in the larger “home range core area” (HRCA), and no lower than an average of 50 percent in the “protected activity center” (PAC). Treatment in owl PACs is intended to be limited (see the 2004 Sierra Nevada Forest Plan Amendment; USDA FS 2004), but canopy cover targets are still widely used when fuels reduction treatments are implemented within the HRCA on NFS lands. The cumulative area of PACs and HRCAs affects a fairly large proportion of a landscape. See chapter 3 for more details on these management designations and their detailed definitions.

On national forests, some aspects of spotted owl habitat have likely improved since the 1992 release of the CASPO guidelines. Average tree diameter in many forests has increased because of growth and the removal of smaller trees in treated stands while retaining all trees ≥75 cm (30 in) d.b.h. In general, the amount of forest dominated by large trees is probably gradually increasing, although some studies suggest climate change or drought mortality may be disproportionately higher in larger than smaller trees (Lutz et al. 2009, van Mantgem et al. 2009). Likewise, forest growth increases canopy cover and, even in treated stands, cover is retained at 40 percent or greater.

However, in three of the four owl demographic areas, populations are declining. It is uncertain to what degree some of this decline is due to legacy effects (e.g., loss of large tree and defect structure removal and reduction in canopy cover) before CASPO guidelines took hold after 1992. Compounding the uncertainty is the increased role of high-severity wildfire in changing forest conditions. More owl habitat is now affected by wildfire than by mechanical treatment each year (North et al. 2012), and its effects on habitat conditions likely vary with severity and patch size effects of fire behavior.

Private industrial forest lands—

About 1.2 million ha (2.9 million ac) of silvicultural treatments were approved or completed on private industrial forestlands between 1990 and 2013 (table 5-3; see appendix p. 155 for detailed information). Of the majority of acres attributed with a specific silvicultural prescription, the predominant treatments were selection cuts (322 652 ha [806,630 ac]), shelterwood cuts (201 622 ha [504,054 ac]), commercial thins (114 460 ha [286,152 ac]), clearcuts (105 493 ha [263,733 ac]), and sanitation salvage cuts (82 541 ha [206,352 ac]) across the 1990-2013 assessment period (table 5-3). The highest numbers of treated acres were recorded for Shasta, Lassen, Plumas and Tehama Counties (table 5-4). At least 403 876 ha (998,000 ac) of treatment are recorded to have occurred within the range of the California spotted owl in the Sierra Nevada during 1997–2013 (table 5-5).

On average, forests on private land are younger (71 years) than those on public land (104 to 115 years) (Stewart et al. 2016) and often lack the stand structural features associated with old forests such as "defect" trees and large snags and logs. Most commercial harvest is concentrated on the large ownerships predominantly in the southern Cascades and northern Sierra Nevada. Almost 60 percent of commercial harvest on private lands comes from five northern California counties (Humboldt, Shasta, Siskiyou, Mendocino, and Plumas), and collectively, private ownership forests produce about 85 percent of California forests' lumber, pulp and bioenergy products (Morgan et al. 2012).

National parks—

The NPS maintenance of mid-elevation forest conditions faces three challenges. A primary constraint to NPS resource management is that much of these parks is within federally designated wilderness areas, and mechanical manipulation is restricted in these areas. The NPS does not generally mechanically manipulate vegetation but will for human safety or park infrastructure. Hence, managing tree density can only be accomplished with fire; both prescribed fire and managed wildland fire. The NPS is further constrained by a limited capacity to deploy prescribed fire. Limited staffing and air quality restrictions generally result in a relatively small fraction of the national parks being treated with prescribed fire (North et al. 2012). The prescribed fire that has been deployed is typically limited to areas of high

Table 5-3—Treatment hectares completed or approved in timber harvest plans on private industrial forest lands in the Sierra Nevada by silvicultural prescription and year during 1990–2013

Year	Clear cut	Commercial thin	Conversion	Damaged timber-land	Fuel break	Group selection	Other	Rehabilitation	Sanitation salvage	Seed-tree cut	Selection cut	Shelter-wood cut	Transition	Total
1990	1,595	1,265	0	0	0	0	21,271	679	1,811	2,024	6,643	8,673	8,026	51,986
1991	3,852	6,909	0	0	0	0	11,041	229	2,827	1,171	6,206	12,483	9,014	53,732
1992	478	4,677	0	0	0	0	9,180	568	1,382	795	7,620	4,622	9,909	39,231
1993	956	1,945	6	0	0	0	10,056	826	1,813	1,061	12,410	7,303	7,129	43,504
1994	998	3,826	16	0	0	0	8,105	634	2,044	1,659	7,708	3,498	9,750	38,236
1995	1,075	4,689	8	0	0	0	9,710	623	2,446	1,205	12,767	5,354	8,864	46,741
1996	1,132	6,789	177	0	0	5	12,130	585	4,567	1,395	13,860	7,073	10,374	58,087
1997	711	5,887	0	0	0	96	7,513	773	3,309	833	20,285	3,369	5,021	47,798
1998	735	5,763	220	0	0	18	6,869	1,957	11,368	419	10,976	3,809	4,024	46,159
1999	1,977	6,480	2	0	32	407	6,384	1,635	2,781	864	27,269	5,931	4,041	57,803
2000	2,099	7,733	600	0	193	1,404	1,412	559	4,214	1,162	19,386	10,665	713	50,139
2001	4,274	9,477	27	2	274	1,316	2,819	1,252	3,272	2,519	11,973	12,582	348	50,136
2002	2,618	6,679	164	17	380	2,463	307	806	2,691	1,019	14,041	10,079	91	41,356
2003	4,325	4,920	334	75	254	1,239	876	1,581	4,991	2,951	17,619	10,361	465	49,990
2004	4,730	6,692	149	104	902	1,294	344	743	4,015	921	14,841	11,297	459	46,490
2005	5,990	3,997	436	107	243	2,053	22	688	2,852	1,861	11,713	14,582	166	44,709
2006	4,901	1,663	382	15	160	2,110	45	933	1,120	1,076	12,160	5,095	59	29,719
2007	4,066	4,460	576	0	203	3,086	47	703	3,639	2,965	9,821	14,357	170	44,092
2008	6,768	4,813	107	3	1,049	3,185	133	402	2,649	1,013	16,403	8,625	90	45,240
2009	4,963	1,591	85	192	181	1,962	0	327	767	454	13,150	10,238	49	33,959
2010	3,674	328	46	239	179	2,772	0	122	1,049	196	4,614	4,210	0	17,428
2011	3,755	881	193	405	1,068	4,509	0	158	639	187	7,093	3,122	27	22,038
2012	7,678	2,311	139	377	433	2,566	0	104	4,443	347	9,625	5,567	93	33,684
2013	6,552	1,124	238	1,390	408	10,996	0	153	436	194	5,058	4,317	186	31,053
Approved (no completion date)	26,829	10,900	794	1,803	2,505	42,383	1,716	1,181	12,384	2,091	33,189	16,773	817	153,366
Total	106,729	115,801	4,699	4,730	8,464	83,866	109,980	18,221	83,508	30,380	326,432	203,983	79,884	1,176,677

Table 5-4—Treatment hectares completed or approved in timber harvest plans on private industrial forest lands in the Sierra Nevada by silvicultural prescription and county during 1990–2013

County	Clear-cut	Commercial thin	Conversion	Damaged timber-land	Fuel break	Group selection	Other	Rehabilitation	Sanitation salvage	Seed-tree cut	Selection cut	Shelter-wood cut	Transition	Total
Alpine	55	44	8	0	0	0	246	0	181	25	92	38	0	688
Amador	2,262	449	341	0	873	630	5,021	737	312	1,535	5,684	3,575	3,209	24,629
Butte	9,384	6,254	35	656	258	2,362	7,598	3,909	2,724	2,910	13,516	13,282	2,056	64,945
Calaveras	5,788	3,391	84	0	1,192	1,721	9,709	1,237	747	2,071	16,909	3,991	4,659	51,500
El Dorado	12,968	6,170	237	0	619	1,321	13,020	1,732	7,975	5,962	9,651	19,576	6,937	86,169
Fresno	117	490	326	0	0	457	1,153	157	214	116	20,655	15	352	24,053
Kern	0	12	0	0	0	0	258	97	652	0	3,383	0	0	4,403
Lassen	12,610	20,689	37	55	457	15,660	10,313	1,891	12,162	167	66,747	18,695	8,200	167,682
Madera	0	0	0	0	0	0	165	81	77	7	905	151	466	1,852
Mariposa	38	81	0	0	124	343	682	642	208	330	3,766	399	812	7,426
Nevada	2,897	2,545	1,021	5	321	8,107	3,017	704	5,377	1,386	11,709	13,926	3,886	54,902
Placer	2,831	2,688	1,023	0	203	3,815	10,000	1,325	8,454	1,729	10,019	17,115	4,075	63,276
Plumas	6,003	13,664	1,267	2,266	1,438	15,356	3,780	732	5,761	2,021	45,186	19,998	12,413	129,887
Shasta	34,379	40,782	283	1,410	1,785	19,590	29,586	2,434	28,402	4,692	63,212	47,773	15,069	289,396
Sierra	1,406	4,902	2	0	42	6,794	1,522	202	3,498	719	7,546	6,886	1,067	34,586
Tehama	9,674	8,639	7	297	565	3,994	9,255	873	3,910	3,259	22,219	29,974	8,559	101,224
Tulare	0	91	0	0	122	2	334	42	453	40	2,111	0	164	3,359
Tuolumne	4,222	3,860	7	26	404	133	1,932	551	1,368	2,709	20,139	1,479	6,663	43,493
Yuba	2,095	1,050	21	15	61	3,583	2,391	874	1,031	703	2,983	7,108	1,294	23,209
Total	106,729	115,801	4,699	4,730	8,464	83,866	109,980	18,221	83,508	30,380	326,432	203,983	79,884	1,176,677

Table 5-5—Treatment hectares completed in timber harvest plans on private industrial forest lands within the range of the California spotted owl in the Sierra Nevada by silvicultural prescription during 1997–2013

Silvicultural Prescription	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Totals
Clearcut	14	55	449	896	1,873	1,901	3,321	3,467	4,642	2,762	2,748	5,195	3,240	2,252	1,768	4,423	3,112	42,118
Commercial thin	42	22	295	416	1,115	1,606	2,770	2,646	2,360	696	1,066	3,478	1,418	265	805	1,221	1,020	21,241
Conversion	0	1	2	31	1	17	201	93	29	188	388	89	59	46	177	119	236	1,679
Fuelbreak/defensible space	0	0	32	173	165	304	250	889	141	143	203	583	181	105	954	387	408	4,917
Group selection	7	8	394	601	514	1,895	1,096	1,167	2,038	2,022	2,886	3,101	1,724	1,381	4,381	1,861	8,900	33,976
Rehabilitation—understocking	113	30	32	124	215	165	912	354	450	286	382	197	233	74	11	46	116	3,742
Sanitation salvage	44	21	313	163	594	1,235	1,715	2,296	2,402	821	2,089	2,431	640	622	246	2,633	318	18,582
Seed tree removal cut	157	21	212	694	173	300	958	136	264	437	489	97	28	40	55	172	92	4,326
Seed tree seed cut	30	3	22	36	157	297	603	467	681	483	2,023	430	426	147	132	159	94	6,189
Selection	127	547	3,047	7,253	2,647	6,415	12,218	9,617	8,749	7,029	7,321	13,049	11,803	4,133	3,257	4,401	3,741	105,355
Shelterwood prep cut	0	0	0	0	0	94	71	1	752	58	53	0	0	13	0	5	0	1,047
Shelterwood rem/commercial thin	0	93	0	0	5	239	0	358	829	32	935	874	505	668	60	1,091	0	5,688
Shelterwood removal cut	123	461	1,316	1,595	2,718	2,688	5,425	5,885	7,184	3,498	6,230	5,826	4,523	1,598	1,641	2,769	2,342	55,821
Substantially damaged timberland	0	0	0	0	0	17	31	103	0	15	0	3	192	1	405	135	511	1,413
Transition	87	48	38	225	50	45	83	87	58	59	101	86	49	0	26	52	44	1,137
Totals	743	1,311	6,152	12,207	10,228	17,219	29,653	27,566	30,581	18,528	26,914	35,440	25,020	11,345	13,917	19,474	20,934	307,230

human use (e.g., sequoia groves, Yosemite Valley). Consequently, the NPS uses wildfire to the extent possible to accomplish forest management objectives (van Wagtendonk and Lutz 2007). Managing to retain and restore resilient forest ecosystems has been more aggressive on NPS lands than other areas because NPS policy enables wildfires in appropriate locations to run their course when feasible.

There has been a recent untethering of the NPS resource stewardship from directives of striving for historical representation (USDI NPS 2012) with growing recognition that this is an unattainable and undesirable goal (USDI NPS 2012). In response, NPS has taken on management planning to build ecosystem resilience for coping with changing climates. "National Park Natural Condition Assessments" are designed to identify key indicators of natural condition (http://www.nature.nps.gov/water/nrca/). "Resource Stewardship Strategies" (http://www.nature.nps.gov/water/planning/resourcestewardshipstrategies.cfm) are attempts to plan for future management, including climate change (http://www.nps.gov/subjects/climatechange/response.htm). Parks units are now compelled to consider climate change adaptation and how to manage for climate-resilient forests. This new management directive is likely to include incentives to foster forested ecosystems that are resilient to a range of future stressors.

Current Status of Forests With Potential California Spotted Owl Habitat

Focusing solely on lands included within the California wildlife habitat relations (CWHR)-defined California spotted owl range map for the Sierra Nevada, existing vegetation classification and mapping (EVEG) estimates that there are about 1.98 million ha (4.9 million ac) of CWHR class 4M or greater habitat (4M, 4D, 5M, 5D, 6) (>30 cm [12in] d.b.h., >40 percent canopy cover), with approximately 75, 7, and 18 percent occurring on NFS, NPS, and private/other government (POG) lands, respectively (table 5-6). About 53 percent of the 4M and greater classes are classified as Sierra Nevada mixed conifer (SMC), with the majority of SMC occurring on NFS lands. About 1.2 million ha (2.9 million ac) of 4D and greater classes (4D, 5D, 6) (>30 cm [12 in] d.b.h., >60 percent canopy cover) are estimated to be present, with 73, 9, and 18 percent distributed across NFS, NPS, and POG lands, respectively (table 5-7). The 4D and greater class habitat is predominantly classified as white fir (53 percent). For CWHR class 5M and above (5M, 5D, 6) (>60 cm [24 in] d.b.h., >40 percent canopy cover), about 607 029 ha (1.5 million ac) are estimated with 80, 10, and 10 percent distributed on NFS, NPS, and POG lands, respectively (table 5-8). The 5M and above class is classified primarily as SMC (63 percent).

Table 5-6—Distribution (hectares) of California wildlife habitat relationships class 4M or greater (4M, 4D, 5M, 5D, 6) by vegetation type and land ownership within the range of the California spotted owl in the Sierra Nevada

Agency	Blue oak woodland	Douglas-fir	Eastside pine	Jeffrey pine	Lodgepole pine	Montane hardwood/conifer	Montane hardwood	Ponderosa pine	Red fir	Sierran mixed/conifer	White fir	Other	Total
National forest:													
Eldorado	76	0	3	1,147	1,371	5,361	6,836	12,492	31,045	110,115	9,708	545	178,698
Inyo	0	0	128	130	1,760	14	108	0	581	1,943	134	1,648	6,448
Lassen	61	0	2,443	3,053	3,014	2,101	1,628	7,276	9,733	109,522	26,607	395	165,834
LTBMU	0	0	14	5,985	2,041	8	0	0	3,928	13,671	2,083	925	28,655
Plumas	63	10,817	5,736	277	218	19,422	7,505	6,450	7,725	189,595	40,043	172	288,024
Sequoia	3,014	0	918	8,259	3,818	11,508	20,575	9,744	27,643	71,187	950	3,282	160,898
Sierra	1,317	0	0	2,311	8,833	21,699	26,239	25,945	36,208	89,457	934	21,977	234,921
Stanislaus	798	0	0	2,475	1,263	14,242	17,660	21,667	25,933	108,734	6,086	569	199,427
Tahoe	262	20,594	1,004	446	2,689	11,322	7,865	5,411	22,943	130,935	17,331	488	221,291
National park:													
Lassen Volcanic National Park	0	0	0	45	91	83	0	0	1,475	5,772	1,464	162	9,092
Sequoia and Kings Canyon National Parks	0	0	0	4,605	1,299	3	707	1	10,185	29,100	3,876	3,204	52,980
Yosemite National Park	51	124	0	6,379	3,577	151	2,560	2,594	15,873	51,009	2,055	2,417	86,791
Private/other government	7,676	32,841	5,453	266	433	50,934	44,103	58,134	357	146,686	2,961	3,090	352,934
Total	13,319	64,376	15,699	35,381	30,407	136,851	135,786	149,714	193,629	1,057,726	114,232	38,873	1,985,993

Table 5-7—Distribution (hectares) of California wildlife habitat relationships class 4D or greater (4D, 5D, 6) by vegetation type and land ownership within the range of the California spotted owl in the Sierra Nevada

Agency	Blue oak woodland	Douglas-fir	Eastside pine	Jeffrey pine	Lodgepole pine	Montane hardwood/ conifer	Montane hardwood	Ponderosa pine	Red fir	Sierran mixed/ conifer	White fir	Other	Total
National forest:													
Eldorado	43	0	1	276	279	4,559	6,733	171	10,348	7,191	78,489	4,506	112,597
Inyo	0	0	9	16	552	10	72	210	0	98	285	14	1,267
Lassen	18	0	367	1,221	801	1,558	1,335	188	3,262	4,568	41,096	10,967	65,381
LTBMU	0	0	0	255	184	6	0	22	0	95	540	289	1,391
Plumas	22	9,520	943	56	4	15,993	5,160	164	4,164	2,038	82,963	12,766	133,793
Sequoia	728	0	27	1,347	573	9,011	19,073	1,105	7,657	8,982	40,907	249	89,658
Sierra	796	0	0	719	5,505	14,989	23,848	9,956	23,198	21,436	65,164	707	166,318
Stanislaus	461	0	0	329	320	12,539	16,982	155	16,148	10,150	80,245	4,823	142,153
Tahoe	127	16,881	239	189	1,644	7,434	5,426	182	2,704	8,826	97,631	8,270	149,552
National park:													
Lassen Volcanic National Park	0	0	0	41	2	50	0	21	0	124	1,920	282	2,440
Sequoia and Kings Canyon National Parks	0	0	0	1,590	517	3	615	848	1	8,150	24,686	3,106	39,516
Yosemite National Park	4	118	0	1,386	3,178	59	1,557	1,794	623	13,786	41,346	1,990	65,841
Private/other government	3,274	25,002	881	41	228	41,461	31,520	1,612	39,692	112	74,863	1,148	219,833
Total	5,473	51,520	2,468	7,465	13,786	107,674	112,320	16,426	107,797	85,555	630,137	49,117	1,189,740

Table 5-8—Distribution (hectares) of California wildlife habitat relationships class 5M or greater (5M, 5D, 6) by vegetation type and land ownership within the range of the California spotted owl in the Sierra Nevada

Agency	Blue oak woodland	Douglas-fir	Eastside pine	Jeffrey pine	Lodgepole pine	Montane hardwood/ conifer	Montane hardwood	Ponderosa pine	Red fir	Sierran mixed/ conifer	White fir	Other	Total
National forest:													
Eldorado	0	0	1	113	247	53	10	356	3 494	19 255	1 862	45	25 436
Inyo	0	0	1	4	170	2	0	0	156	74	10	81	497
Lassen	12	0	39	196	96	468	56	978	1 754	26 684	5 423	96	35 803
LTBMU	0	0	0	931	467	2	0	0	774	1 865	46	260	4 346
Plumas	18	7 349	767	57	25	7 588	1 332	2 915	2 823	86 033	14 335	3	123 244
Sequoia	186	0	211	4 563	798	1 575	1 880	2 033	6 064	25 406	329	565	43 611
Sierra	188	0	0	41	1 953	2 902	1 607	9 108	12 169	40 341	490	2 542	71 340
Stanislaus	12	0	0	352	273	1 035	64	1 155	7 298	26 106	2 738	86	39 120
Tahoe	89	15 545	378	279	1 661	6 383	757	1 661	16 704	95 909	12 072	290	151 729
National park:													
Lassen Volcanic National Park	0	0	0	36	18	6	0	0	478	2 997	445	104	4 085
Sequoia and Kings Canyon National Parks	0	0	0	0	0	2	0	0	1	4 397	0	0	4 400
Yosemite National Park	7	46	0	1 389	1 686	20	82	1 074	10 750	33 991	1 708	984	51 737
Private/other government	456	15 202	416	16	5	4 505	1 115	13 596	67	27 765	349	355	63 847
Total	968	38 141	1 813	7 978	7 402	24 542	6 902	32 876	62 532	390 825	39 807	5 412	619 196

LTBMU = Lake Tahoe Basin Management Unit.

Most acres of important California spotted owl habitat classes occur on NFS lands. Between about 133 547 and 166 326 ha (330,000 and 411,000 ac) of 4D and greater habitat is estimated to occur on the Sierra, Tahoe, Stanislaus, and Plumas National Forests, while between 65 155 and 112 503 ha (161,000 and 278,000 ac) are estimated to occur on the Eldorado, Sequoia, and Lassen National Forests (tables 5-6 to 5-8). The Inyo National Forest and Lake Tahoe Basin Management Unit support fewer habitat acres, as the Inyo overlaps minimally with the range of the California spotted owl in the Sierra Nevada, while habitat is generally limited to the western half of the Lake Tahoe basin. Although inferences about amounts and distributional patterns of California spotted owl habitat may be tempered given the uncertainty regarding the accuracy and consistency of the base vegetation maps, results highlight the importance of NFS lands for providing spotted owl habitat in the Sierra Nevada. About 73 to 80 percent of the CWHR habitat classes most often used by owls are estimated to currently occur on NFS lands.

Historical Fire Effects on Mid-Elevation Forests

Fire is a critical ecosystem process throughout Sierra Nevada mid-elevation forests. This is particularly the case for yellow and Jeffrey pine (*P. jeffreyi* Balf.) and mixed-conifer forest types within the Sierra Nevada, where fire historically (i.e., pre-Euro-American settlement) occurred frequently, with generally low- to moderate-severity effects (Skinner and Taylor 2006, van Wagtendonk and Fites-Kaufman 2006). Numerous studies demonstrate that this fire frequency (5 to 15 years) maintained low-density stands across much of the landscape, composed of primarily large, fire-resistant trees. Reconstructed conifer densities (trees >15 cm [6 in] d.b.h.) in these forest types ranged from 60 to 82 trees/ha (24 to 41 trees/ac) (Collins et al. 2011; Scholl and Taylor 2010; Taylor 2004, 2010). Collins et al. (2011) estimated the average canopy cover for historical forest conditions was 22 percent, with a range of 8 to 37 percent. Interestingly, these canopy cover estimates are similar to those measured in a contemporary Jeffrey pine-mixed-conifer forest that has a more intact disturbance regime (i.e., no timber harvesting and limited fire suppression) in the Sierra San Pedro Martir, Baja, California (Stephens and Gill 2005). However, stand density, structure, and composition likely varied depending on topographic and edaphic conditions, as well as a result of the stochastic patchiness of fire effects.

The preponderance of evidence in the scientific literature currently supports the notion that contemporary forests that have not been subject to recent forest management (i.e., tree removal) are generally considerably denser than forests found prior to 100+ years of fire exclusion and selective logging. However, a few recent studies conducted in the Sierra Nevada challenge the prevailing understanding of historical forest structure and fire patterns (see Baker 2014, Odion et al. 2014). They indicate that stand-replacing fire effects were a greater component of historical fire regimes than the predominant body of research suggests, and that resulting tree densities were greater than those reported in previous studies (e.g., Ansley and Battles 1998, Bouldin 1999, Collins et al. 2011, Knapp et al. 2013, McKelvey and Johnson 1992, North et al. 2007, Parson and Debenedetti 1979, Scholl and Taylor 2010, Taylor 2004, Taylor et al. 2014, Vankat and Major 1978). Odion et al. (2014) used stand age estimates from Forest Inventory and Analysis data to infer past proportions of stand-replacing fire. From this they concluded that current "reference" conditions underrepresent early successional plant communities created by stand-replacing fire. Baker (2014) used historical tree data from land survey markers to reconstruct historical proportions and patch sizes of stand-replacing fire across large landscapes. He concluded that historical forests in the Sierra Nevada were generally much denser, hence supported much greater amounts of stand-replacing fire than other historical forest reconstructions have reported. The significance of his conclusions, and their applicability to restoration of mixed-conifer forests in the Sierra Nevada, merit careful consideration and vetting through the scientific community to reconcile the foundation of the discrepancies with existing published literature. Concerns about the source of the observed discrepancies include:

- Potential bias in plot/tree selections. Baker used General Land Office survey witness trees that have been shown to be biased toward trees that were less likely to be harvested—smaller trees or less commercially valuable species, hence higher likelihood that the trees would persist as markers for locating survey points (see Bouldin 2008, Manies and Mladenoff 2000). Odion et al. 2014 only included plot data from wilderness areas and national parks, which in the Sierra Nevada tend to be in higher elevations, hence a greater proportion of upper montane forest types. Upper montane forests are associated with longer intervals between fire and greater proportions of high-severity relative to the pine-mixed-conifer forests in the lower montane zone (Van de Water and Safford 2011). This limits the applicability of the study across the pine-mixed-conifer zone.
- Limited density of tree samples. Baker (2014) relied on sampling densities that are less than 1 tree per (80 ac) 32.3 ha.
- Misinterpretation of tree data. Odion et al. (2014) used composite stand-age estimates as evidence of postfire cohort initiation dates. These composite estimates have a high degree of error in capturing actual tree initiation dates, and as a result, are a poor representation of the time since last stand-replacing disturbance (Stevens et al. 2016).

These limitations and others (see Fulé et al. 2013) call into question the robustness of these studies and their applicability toward forest restoration efforts.

Several studies have demonstrated a high degree of spatial complexity across historical landscapes, which consisted of early seral vegetation (e.g., dense conifer regeneration, shrubs) and denser mature forest stands (e.g., Beaty and Taylor 2001, Collins et al. 2015, Nagel and Taylor 2005, Stephens et al. 2015, Taylor 2000), within a matrix of generally low-density stands. This complexity was likely a product of differential fire effects and timing, including some stand-replacing fire, driven by variability in multiple factors: vegetation/fuels, topography, site productivity/moisture availability, and climate. Estimates of historical stand-replacing fire in mixed-conifer and yellow pine forests range from 5 to 10 percent of the area within a burn at any given time (Mallek et al. 2013), which was likely aggregated in small patches (usually <2 ha [5 ac]) distributed across the landscape (Collins and Stephens 2010, Show and Kotok 1924). Drainage bottoms associated with larger perennial streams may have experienced less frequent fire than more upslope locations and thus were able to sustain more consistently dense and multilayered canopies (Collins and Skinner 2014). Another attribute associated with frequent fire in these forests is a complex spatial pattern of trees, consisting of isolated individuals, multiple tree clumps, and openings (Churchill et al. 2013, Fry et al. 2014, Knapp et al. 2012, Lydersen et al. 2013). This complexity was also most likely driven by fine-scale patchiness in fire effects and was yet another source of heterogeneity in historical forest conditions (Show and Kotok 1924).

Drivers of Forest Change

Current and Projected Fire Effects

Irrespective of any uncertainty about the historical role of fire in the Sierra Nevada, contemporary fire patterns in the Sierra Nevada differ from those that occurred historically. The differences are in both overall proportion and patch sizes of stand-replacing fire, which are in many cases greater for contemporary fires (Mallek et al. 2013; Stephens et al. 2013, 2014). The proportion of stand-replacing fires and burn patch sizes also have been increasing in the Sierra Nevada from 1984 through 2010 (Miller et al. 2009, Miller and Safford 2012, Steel et al. 2015). These changes in fire characteristics are driven by (1) fire suppression, which tends to constrain fire occurrence to burning primarily under the most extreme fire weather conditions because these are the conditions when a small minority of fires escape initial suppression efforts (Finney et al. 2011), allows an increase in surface and ladder fuels to accumulate, and fosters increased connectivity and homogeneity of vegetation patterns (Collins et al. 2011, Hessburg et al. 2005, Parsons and Debenedetti 1979, Taylor et al. 2014); and (2) climate change, which has and will increase the length of the dry season, which increases both the risk and scale for high-severity fires (Collins 2014, Westerling et al. 2011). Further, projected increases in temperature and decreases in snowpack for the Sierra Nevada (Safford et al. 2012) are likely to result not only in a continued increasing trend in both patch size and proportion of landscape with stand-replacing fire but also an increasing potential for repeated stand-replacing fire, which can lead to vegetation type conversion (Stephens et al. 2013). Current trajectories of fire size and impact, along with predicted doubling of predicted future fire likelihoods, suggest a future in which proportions of stand-replacing fire in the Sierra Nevada exceed levels interpreted from historical data, regardless of sources.

Postfire Forest Management

A recent assessment of land cover change in California demonstrated that fire now accounts for a greater proportion of live tree mortality or “loss” than any other activity (e.g., timber harvesting, development) (Sleeter et al. 2011). Recent research has also demonstrated an increasing proportion of stand-replacing fires and fire patch sizes since 1984 (Miller and Safford 2012, Miller et al. 2009), which has raised concerns about what type of forest, if any, will be reestablished following stand-replacing fire. Recent studies from the northern Sierra Nevada and southern Cascade Range found very low natural conifer regeneration in areas affected by stand-replacing fire up to 11 years following the burn (Collins and Roller 2013, Crotteau et al. 2013). The low conifer regeneration has been attributed mainly to the lack of direct mechanisms for seed persistence or dispersal into large stand-replacing patches (Barton 2002, Goforth and Minnich 2008, Keeley 2012). This suggests that frequent fire intervals for high-intensity fires result in slow and uncertain reforestation of conifer forests, which is particularly evident for pine species (Collins and Roller 2013). If the desired condition for mixed-conifer forests affected by stand-replacing fire is to have mixed-conifer forests return within several decades, then some management intervention may be necessary, particularly by planting pine species, to ensure greater future fire resilience.

Harvest of fire-killed trees (salvage) commonly accompanies reforestation efforts in burned areas. Salvage can have a range of ecological effects depending on the extent of burn area harvested and the removal method (i.e., whole tree harvest, cut to length, etc.). Management objectives for salvage-harvesting include recovering economic value of timber (Sessions et al. 2004), increasing personnel safety for reforestation efforts, and reducing large woody surface fuel accumulation (Peterson et al. 2015, Ritchie et al. 2013, Zhang et al. 2008), which can increase fire resilience. Although salvage-harvesting generally achieves these objectives, it has fewer short-term (<10 years) ecological benefits (Long et al. 2014, Peterson et al. 2009, Ritchie and Knapp 2014). In particular, there can be negative impacts on habitat, including the removal of snags, which also ultimately reduces coarse wood on the forest floor (Swanson et al. 2011). Over the long term (>30 years), the tradeoffs of salvage harvesting versus leaving fire-killed stands unaltered are less clear. A salvage-harvested and reforested area may return to mature conifer forest more quickly than an unaltered burned area, but could lead to a loss of habitat diversity over the landscape if large areas are planted using conventional techniques (i.e., equal spacing among planted trees).

However, stand-replacing fire facilitates development of alternate vegetation types (e.g., montane chaparral or California black oak forests [*Quercus kelloggii* Newberry]), which may be underrepresented in many contemporary landscapes (Cocking et al. 2012, 2014; Nagel and Taylor 2005). Spatial scale is a critical consideration when balancing these tradeoffs. For example, if patches of stand-replacing fire are large (e.g., >200 ha [500 ac]) and left unaltered, the potential for colonization by montane chaparral across the entire patch is high (Collins and Roller 2013, Conrad and Radosevich 1982, Crotteau et al. 2013, Goforth and Minnich 2008), resulting in a homogenization of landscape vegetation rather than increasing vegetation diversity.

Climate Change

General climate change model projections for the Sierra Nevada have temperatures increasing 3 to 6 °C (5.2 to 10.4 °F) during the 21st century (Cayan et al. 2013). Precipitation models differ, with some predicting increases and others decreases in net precipitation (Cayan et al. 2013). These models, however, mask consistent predictions of decreased winter snowpack and increased ecosystem moisture stress (Cayan et al. 2013), accompanied by an increase in the frequency of extreme climatic events (droughts as well as flooding) (Gershunov et al. 2013). These climate change models consistently suggest that by the late 21st century, the Sierra Nevada will experience (1) a decreasing fraction of its annual precipitation as snow, and hence loss of snowpack; (2) increasing temperatures that will increase dry season soil moisture stress (climate water deficit [CWD]); (3) a higher fraction of annual precipitation in fewer storm events; (4) an increased frequency of drought, and (5) a lengthening of the fire season because of earlier onset and later ending of warm, dry conditions.

There are several ways to project the potential consequences of a changing climate on the distribution of Sierra Nevada vegetation types. One approach to projecting future ecosystem composition as a consequence of climate change is to project the future distribution of forest types. Ecosystem models, such as the MC1 model (Lenihan et al. 2008), are used to project the distribution of ecosystems into the future. The results of these models suggest upward shifts in most vegetation types, loss of subalpine forests, and massive forest conversion from types that now dominate to those characteristic of warmer and drier environments.

Another approach uses simple climatic envelope modeling to identify locations where current forest cover is projected to fall outside historical climatic parameters for that forest type (Schwartz unpublished data). These models also predict significant reorganization of forested ecosystems during the next century as warmer and drier conditions prevail, driving upslope expansion of grassland, savannah, and shrub-dominated ecosystems. This approach identifies the climatic attributes that describe present occurrences of each ecosystem type, and then overlays climate projections for different periods into the future (e.g., 2040–2070) onto sites to identify when and where instances of an ecosystem type are projected to no longer be within a suitable climate space for that ecosystem.

Changing climates are relevant to risk of fire, and all projections of future fire conditions that consider climate models predict a near doubling of fire likelihoods (e.g., Westerling et al. 2011). With fire extent, severity, and frequency already increasing in many places (Miller and Safford 2012, Miller et al. 2009), fire is likely to influence changes in forest cover types. Site type change from repeated high-severity fire is already occurring (Stephens et al. 2013). Future changes may be driven by voluntary recruitment or as an active adaptation strategy by planting different species in an effort to create more resilient forests. Vegetation models suggest that many portions of the mid-elevation conifer zone will be vulnerable to such changes.

Upper montane forests will likely also undergo significant changes (North et al. 2016). Modeling of predicted conditions in the Lake Tahoe basin suggests that forested areas that would not have benefited greatly from fuels treatments in the 20th century owing to low fire activity may need significant fuels treatments by the end of this century because of projected increase in fire activity (Loudermilk et al. 2013, 2014). Modeling also suggests that fire activity will increase significantly because of longer fire seasons that will allow more widespread fire ignitions from lightning (Yang et al. 2015). An analysis of trends in the upper elevation of burn areas over the past several decades suggests that wildfires may already be increasing in frequency in upper montane forests (Schwartz et al. 2015).

Increasing frequency and intensity of drought result in increased tree stress and have been implicated in widespread increases in large tree mortality (Dolanc et al. 2014, McIntyre et al. 2015, van Mantgem et al. 2009). Climate change projections of forest ecosystems (Lenihan et al. 2003), forest communities (Schwartz, unpublished report) and tree species (McKenzie 2010) all suggest that existing mid-elevation coniferous forests are poised for conversion to other forest types over much of their current distribution, given drivers such as wildfire. Pests and pathogens as drivers of forest change may also be increasing (e.g., Smith et al. 2005). Collectively, these trends strongly suggest that, under current management practices, all mid-elevation coniferous forests are threatened with conversion to vegetation characteristic of warmer, drier, and more frequently burned types such as montane chaparral, mixed-hardwood forests, and even grasslands (Lenihan et al. 2008).

Putting these predictions into context, however, requires understanding of the spatial resolution of climate projections. Projecting future climate is done using one or more "general circulation models" (GCMs) (IPCC 2013). Although the list of GCMs continues to grow (>15), each GCM is a complex multivariate simulation of future climate on a global scale (IPCC 2013). The global nature of these models is such that they might not capture local processes well, even after downscaling (Gershunov et al. 2013). Although multiple models provide the opportunity to estimate variance in outcomes, they are likely to underestimate the true uncertainty with respect to climate futures. The variation among interrelated and nonindependent global models does not allow capturing the range of variability that might be expected in future climates. Further, microscale variation projections (e.g., cold air drainages) are locally downscaled under the general assumption that current patterns of local variation will be the same in the future. Hence, cold air drainages remain cold air drainages. Finally, we have a relatively poor understanding of forest soils in the Sierra Nevada and an equally poor understanding of the way that soils modify the extent to which changing climate will be expressed by changing forest composition, structure, and function. The consequence of this fine-scale uncertainty is that despite strong predictions of major forest changes in response to climate predictions at large spatial scales, there are likely to be refugia where cooler, moister forest types may persist. Identifying and conserving forests in these refugia might help provide long-term owl habitat even under accelerating changes in climate conditions.

Projections of forest change suggest that under warmer and drier future climate scenarios, all Sierra Nevada forest types are at risk of conversion to some other plant community over the majority of their current distributions. This includes the mid-elevation coniferous forests upon which California spotted owls currently depend. Many currently forested regions of the Sierra Nevada are predicted to be shrub or grassland dominated in the future. Models of late 21st century climate also suggest a future replete with unique combinations of species pools, climate, and disturbance regimes on the complex mixes of Sierra Nevada geologic substrates. The result is many regions may experience conditions that have no strict analogs in the past. This reduces our capacity to predict how they may respond. Forests in some geographic locations (e.g., drainage bottoms) may persist; others (e.g., south-facing slopes) may undergo pronounced shifts in environmental conditions and thus be more likely to change in structure and composition.

The forests of the Sierra Nevada are complex in composition, structure, and function. This complexity reflects wide variation in environmental conditions at both local and regional scales, rich floristic diversity, and a highly varied history of natural and human disturbances (Franklin and Fites-Kaufmann 1996). The role of geological and climatic diversity in creating this complex mosaic of vegetation is prominent. It is this very complexity that may provide an opportunity to ameliorate the potential for total conversion through forest management.

Future Management of Mid-Elevation Forests

> If owl habitat has improved as a result of fire suppression, such improvement may well be illusory and short-lived. Fire is inevitable in these forests, and the probability of catastrophic fire—certainly one of the greatest threats to owl habitat—increases as surface fuels and ladder fuels continue to accumulate. Overly dense stands are subject to extensive mortality from drought and insects, including loss of the most desirable large, old trees—a management policy characterized as 'hands-off plus fire exclusion' (allow forest succession to proceed uninterrupted by periodic natural disturbances) would likely lead to degraded and depauperate, rather than healthy and biologically diverse, ecosystems (Weatherspoon et al. 1992: 253).

Currently, mid-elevation forests in the Sierra Nevada are prone to high-severity fire, drought stress and loss of large trees, and climatically driven vegetation changes. Hands-off management is likely to perpetuate the compromised resilience of mid-elevation forests. Active management that decreases fuel loads and stand density can help reduce wildfire severity, water competition, and slow vegetation change. These active management choices may also affect forest conditions, particularly in dense stands with high canopy cover, that have been associated with preferred spotted owl habitat. New management practices are needed that can accommodate the multitude of management objectives that include fuels reduction, forest resilience, and some high canopy cover forest conditions (McKelvey and Weatherspoon 1992). Some studies have suggested this can be accomplished by increasing structural heterogeneity associated with ecosystem resilience in fire-dependent forests (Churchill et al. 2013, Lydersen and North 2012, North et al. 2009, Stephens and Gill 2005, Stephens et al. 2007). New management practices now attempt to realign forest conditions with their historical variability using existing stand structure (“what you’ve got to work with”) and topography to structure management actions. Topography is used because it is closely tied to two key processes that seem to strongly influence forest conditions: local productivity (associated with water availability) and fire regime.

Creating Forest Heterogeneity

Forest heterogeneity at the landscape level in the Sierra Nevada is strongly influenced by water availability (Tague et al. 2009) as measured by CWD (the difference between potential and actual plant evapotranspiration). Stephenson (1998) first proposed that topographic differences in plant water availability (actual evaporative transpiration [AET) and CWD determined forest type and productivity. Subsequent modeling found general agreement between predicted and actual forest conditions in the southern Sierra Nevada using just AET and CWD (Miller and Urban 1999a, 1999b). For example, fir-dominated forests are usually most abundant where water availability is high (such as on deep soils with their high water-holding capacities); whereas pine-dominated forests are most abundant where water availability is low (such as on shallow soils or in rain shadows) (Fites-Kaufman et al. 2007, Meyer et al. 2007, Stephenson 1998). Slope steepness and slope position (e.g., ridgetop, midslope, valley bottom) are also important factors, as they affect the reception and retention of both meteoric waters and water flowing above, within, and beneath the soil. Recent large-scale analysis of forests in Yosemite National Park using light detection and ranging found CWD to be the best predictor of forest conditions, including canopy cover (Kane et al. 2013, 2014, 2015a, 2015b).

Although overstory forest patterns seem to be associated with CWD, understory conditions are strongly shaped by fire. Lydersen and North (2012) assessed a wide topographic distribution of forests with restored fire regimes. They found that fire history had the strongest influence on understory stand structure. Small-tree density decreased and shrub cover increased with the increased fire severity and frequency that tend to occur on upper slope and ridgetop locations (Lydersen and North 2012). Consistent with other studies, they found that overstory forest conditions were associated with topographic differences in CWD (Lutz et al. 2010). The greatest densities of large, overstory trees, high total basal area and canopy cover, and an abundance of large snags and logs were in more mesic, productive sites such as lower slopes and riparian areas, which have lower CWD. This high biomass forest structure existed in these topographic positions regardless of fire history. These findings suggest that CWD and fire intensity strongly influence forest overstory and understory conditions, respectively. Topography's influence on these two factors appears to produce the heterogeneity characteristic of montane forest landscapes (Lydersen and North 2012, Taylor and Skinner 2003). It also provides a means to estimate which areas in the landscape had the high stem density and canopy closure conditions that might support species associated with these conditions (Taylor and Skinner 1998). Underwood et al. (2010) tested this idea using fisher and California spotted owl radiotelemetry locations. They found higher than expected use of topographic areas associated with higher productivity, forest biomass, and canopy cover such as found in canyon bottoms, lower slopes, and northeast aspect positions.

Heterogeneity within frequent-fire forest types across the Western United States has recently been examined using a meta-analysis of historical forest structure (Larson and Churchill 2012). The within-stand structure has been characterized as containing three main conditions: individual trees, clumps of trees, and openings or gaps (ICO) (Abella and Denton 2009, Churchill et al. 2013, Larson and Churchill 2012, Larson et al. 2012, Sánchez Meador et al. 2011). In this pattern, openings may inhibit crown-fire spread under most (less than severe) weather conditions (Agee et al. 2000, Agee and Skinner 2005, Stephens and Moghaddas 2005) and may be as effective as fuel breaks with regularly spaced trees with wide crown separations (Kennedy and Johnson 2014, Ritchie et al. 2007). The variable microclimate and vegetation conditions between the three conditions may also provide greater habitat diversity for both plants and animals (Roberts et al. 2015). Recent work in the Sierra Nevada using a rare stem map from 1929 has quantified an ICO pattern in mixed-conifer forest (Lydersen et al. 2013). This work provides measures of the relative proportions, sizes, and compositions of each of the three conditions, individual trees, clumps of trees, and openings within active-fire forests. Because stand conditions with an active fire regime vary with topography (Lydersen and North 2012) and different forest types, this single study with a small sample size might be used with caution until more research has been completed.

The openings in an ICO pattern may also increase forest drought resilience. Models suggest that openings could increase soil moisture (Bales et al. 2011) because more snow reaches the forest floor, melting into the soil instead of being intercepted in tree crowns where some of the snow directly sublimates back into the atmosphere (Molotch et al. 2007). Although montane forests are adapted to annual drought stress characteristic of Mediterranean climates, periods of multiple, consecutive dry years can have major impacts (e.g., Guarin and Taylor 2005). For example, there was substantial mortality of conifer trees in the San Bernardino Mountains after the drought of the late 1990s and early 2000s. In the absence of frequent fire, increases in forest density result in greater competition for scarce water (Dolph et al. 1995, Innes 1992). A major concern is potential increases in older tree mortality because large trees are often more prone to drought-induced mortality (Allen et al. 2010). Some studies have found higher than expected mortality rates in large trees (Dolph et al. 1995, Lutz et al. 2009, Ritchie et al. 2008 Smith et al. 2005). Research has not yet been conducted about whether ICOs reduce drought stress in adjacent tree groups. However, current large-tree mortality rates (van Mantgem and Stephenson 2007, van Mantgem et al. 2009) suggest that a ”leave-it-alone” forest management policy that does not reduce stand density could contribute to the loss of old-growth trees (Fettig et al. 2008, 2010a, 2010b; Ritchie et al. 2008).

There are many areas in the Sierra Nevada where mechanical treatment is currently infeasible (e.g., steep slopes, wilderness, roadless areas, etc.) (North et al. 2015). An alternative is the use of managed fire, which is one of the most effective and efficient means of promoting forest resilience (Collins et al. 2009, North et al. 2012). Although first-entry burns may actually increase fire hazard because of tree mortality and vigorous shrub regrowth (Schmidt et al. 2008, Skinner 2005), subsequent low-intensity burns can often produce greater heterogeneity and are more effective at reducing surface fuels than mechanical treatments. However, using fire in forests that have imbedded human development has significant risks. These risks include potential impacts to people and property from smoke production, reduced recreation opportunities, inadequate personnel to conduct and monitor fires, liability for fire escapes, and risk-adverse policies and institutions. Many of the issues relating to fuel treatment intensity and fire use are inherently social in nature (McCaffrey and Olsen 2012). In the future, managed fire may be more widely used but will probably be relegated to more remote areas where potential effects on rural communities are greatly reduced.

Chapter Summary

The processes that influence the distribution and dynamics of forests in the Sierra Nevada occur across large landscapes and multiple land ownerships. Yet, public land agencies struggle to coordinate management strategies and actions across management units, as well as ownership boundaries. A regional strategy to manage for the long-term viability of mid-elevation coniferous forests that accounts for climate change and fire-resilient forest ecosystems would be an important and valuable step toward these desired outcomes.

The mid-elevation coniferous forests of the Sierra Nevada, in their entirety, are highly threatened with conversion to warmer, drier adapted vegetation types. The drivers of this forecasted change are the synergy of warming and drying climate, unsustainable and unprecedented densities of trees, ensuing drought-induced stress, and increasingly severe wildfires. Large fires such as the Rim Fire in 2013 (100 000 ha [250,000 ac]) and the King Fire in 2014 (40 000 ha [100,000 ac]) have resulted in dead tree swaths (i.e., at or close to 100 percent mortality) of unprecedented size in the mid-elevation zone in just the past two years. Even larger fires have occurred in the Western United States in recent decades and are plausible for the Sierra Nevada. With climate change models predicting significant increases in fire probabilities (as much as double current probabilities) during this century, and increasing fuel loads, the prospect of large-scale, stand-replacing fire effects that affect significant portions of the lower and middle elevations of the Sierra Nevada over the next few decades is an increasing possibility. These conditions pose significant challenges to land managers because efforts to maintain current forest conditions are likely to fail. This represents a severe threat to sustaining old-growth habitat conditions associated with the spotted owl.

Our survey of forest change from historical to current conditions, and discussion of drivers of change, suggest there are significant management challenges in maintaining a well-connected network of closed-canopy mid-elevation conifer stands. We focus on five fundamental conclusions regarding the response of mid-elevation coniferous forests to contemporary and anticipated future drivers of change in the Sierra Nevada. First, based on our collective knowledge of pre-European forest structure and composition, the heterogeneity of historical forests likely provided a variety of conditions, including patches of forest vegetation that were suitable for species requiring high densities of large trees. However, the size and connectivity of high-density patches of medium to larger trees (i.e., 27 to 60 cm [11 to 24 in] d.b.h and >60 cm [24 in] d.b.h) in the Sierra Nevada under an active fire regime was likely much smaller than it is currently. These largely second-growth trees have grown and expanded on the landscape after most of the very large trees (i.e., >100 cm [40 in] d.b.h) were removed and fire suppression reduced young tree mortality.

Second, changing climate and increasing severity of wildfires threaten to decrease the current extent and connectivity of mature, dense stands. Third, management decisions predicated on reducing proximate threats to ecosystems (e.g., large-scale stand-replacing fire) by reducing fuels and tree density will result in some decreases in the concentration of high-density, mature-tree patches. Current management on NFS lands predominantly consists of protecting remaining high-priority pockets of suitable habitat while reducing fuels over broader landscapes. These fuel treatments have been applied on only small portions of the landscape (North et al. 2012, 2015) and have been inadequate in preventing large patches of stand-replacing fire. In contrast, the strategic and careful reduction of continuous high fuel loads in portions of high-density, mature forests by mechanical thinning and prescribed fire may reduce the risk of stand-replacing fire and forest type conversion. This fuel reduction effort would sustain larger forested landscapes that include suitable nesting, roosting, and foraging habitat. Ecosystem response models to changing climates suggest that stand-replacing fire will result in conversion of significant amounts of mid-elevation mixed-conifer forests to hardwood, scrub, and grassland vegetation. Based on modeling, conservation strategies for the fisher (*Martes pennanti*), another threatened species in the southern Sierra Nevada, project similar habitat loss because of climate- and disturbance-driven changes in forest conditions (Scheller et al. 2011, Spencer et al. 2010, Syphard et al. 2011). A calculated response to restore resiliency at a landscape scale is necessary to maintain a network of mature, closed-canopy coniferous forests in the Sierra Nevada.

Fourth, owing to different management priorities on private lands and constraints on mechanical thinning in national parks, the opportunities for meaningful long-term ecosystem management experiments may be largely limited to lands managed by the USFS. Evaluation of forest-restoration approaches will depend upon actually using adaptive management strategies and incorporating scientific support needed to monitor management effectiveness and inform changes to improve success (Gutiérrez et al. 2015). Further, all federal land managers are faced with demanding management objectives (e.g., clean air, water provisioning to lowlands, minimizing human risk, maintaining species diversity and ecosystem integrity) such that ecosystem-driven objectives that reduce specific attention to any individual species are favored.

Fifth, there is inadequate understanding of the degree to which California spotted owls would be affected by the predominant ecosystem-based approaches to managing for fire and adapting to climate change. A silvicultural strategy that creates a mosaic of different density patches (e.g., North et al. 2009) is currently viewed by some as the best opportunity to preserve some intact old-growth, legacy forests in the Sierra Nevada. An ecosystem-based forest restoration strategy that prioritizes resilience to fire and changing climates appears to offer a defensible approach to the dilemma that western coniferous forests face in the coming decades.

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Appendix 5-1: Information on Source and Data Quality Issues for Timber Harvest Volume, Silvicultural Prescriptions, and Habitat Data

Introduction

Assessing past trends and current status of timber harvest volume, number of treated acres, and predominant silvicultural prescriptions used, and the distribution and amounts of important California spotted owl (*Strix occidentalis occidentalis*) habitat types across the Sierra Nevada are a fundamental component for evaluating conservation status. This appendix identifies the data sources for the information summarized in chapter 5 for the above metrics. As described in the following sections, each data set has strengths and limitations as to completeness or accuracy of the data that must be considered when drawing inferences. Nevertheless, these data provide the sole sources of currently available data that provide valuable insight and information on trends and status of forest management treatments and habitat status.

Trends in Timber Volume Harvested From the Sierra Nevada: 1994–2013

Annual summaries of timber volume harvested from public and private lands by county in California are available from the California State Board of Equalization, Timber Tax Program, 2014. Annual summaries are available for 1994–2013, consisting of nonspatial, tabular data reporting annual timber volume harvested in thousands of board feet by county. Counties were filtered to include only those that intersect any portion of the California spotted owl range in the Sierra Nevada as determined using the species distribution map maintained by the California Wildlife Habitat Relationships Program, California Department of Fish and Wildlife. Because the timber volume data are nonspatial, some portion of the volume was harvested from county areas outside of the range of the California spotted owl.

Patterns in Silvicultural Prescriptions on National Forest Lands: 1990–2014

Prior to 2002, forest management treatments on national forest lands were tracked using the Stand Record (SRF) system. The SRF was a nonspatial, tabular database that recorded acres treated by silvicultural prescription by U.S. Department of Agriculture Forest Service (USFS) management unit (national forest and ranger district). Beginning in 2002, the USFS switched to use of the Forest Activity C Tracking System (FACTS) system for recording forest management treatments and activities. The FACTS is a spatial database that records the footprint of timber management activities as well as acres treated by silvicultural prescription by management unit. Efforts have been made to generate and incorporate spatial data for forest treatments conducted prior to 2002, but not all projects have been entered into the database, and some unquantified proportion of the total area treated prior to 2002 is not spatially mapped. Thus, available information on USFS treatments consists of a complete tabular, nonspatial summary of activities from 1990 through 2014 by national forest and ranger district (though October 2014). Spatial data on treatment type, amount, and location are complete from 2002 through 2014. Spatial data are incomplete for 1990–2001 and include some unquantified proportion of the actual activities.[1] The nonspatial data provides insight into the acres treated by silvicultural prescription and trends in the use of different silvicultural prescriptions over time during 1990–2014 on national forests that intersect any portion of the range of the California spotted owl in the Sierra Nevada (Sequoia, Sierra, Stanislaus, Inyo, Eldorado, Tahoe, Plumas, and Lassen National Forests, and the Lake Tahoe Basin Management Unit). Treated acres on some national forests are located outside of the range of the spotted owl so not all treatments occurred within the range of the owl. Numbers reported consist of the number of acres accomplished. The spatial data provide opportunity to assess treatment acres and silvicultural prescriptions used within the range of the California spotted owl in the Sierra Nevada as determined by using the species distribution map maintained by the California Wildlife Habitat Relationships Program, California Department of Fish and Wildlife. However, the spatial data are incomplete for 1990–2002, and thus summaries based on the spatial data do not include all acres treated during the 1990–2002 period.

Patterns in Silvicultural Prescriptions on Private Industrial Forest Lands: 1990–2013

Information on acres treated by silvicultural method on private industrial timberland and nonindustrial private lands is available in the CALFIRE Forest Practice Database managed by the California Department of Forestry and Fire Protection. Nonspatial, tabular data are available to assess acres by silvicultural prescription by county for the 1990–2013 time period. Counties were filtered to include only those that intersect any portion of the California spotted owl range in the Sierra Nevada as determined using the species distribution map maintained by the California

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Wildlife Habitat Relationships Program, California Department of Fish and Wildlife. Because the timber volume data are nonspatial, some portion of the volume was harvested from county areas outside of the range of the California spotted owl. Spatial data on private industrial forest land silvicultural treatments are available for the 1997–2013 period. This database includes all acres approved and completed for treatment under all timber harvest plans (THPs) approved beginning in 1997 and extending through 2013. However, this database does not include acres that were approved in THPs prior to 1997, yet the actual on-the-ground projects were conducted after 1997. A review of the 1997–2013 database indicates that most treatments are completed 4 to 6 years after approval, but that many acres are not reported as completed until 6 to 12 years after approval. Thus, the spatial data include all acres approved/or completed for 1997–2013 THPs, but more acres were actually treated then are shown because of pre-1997 THP acres not being included in the database.

Status and Trends in California Spotted Owl Habitat in the Sierra Nevada

The only source of information on the current distribution and abundance of California spotted owl habitat across the owl's range in the Sierra Nevada is provided by the existing vegetation classification and mapping (EVEG) map maintained by the Remote Sensing Laboratory, Pacific Southwest Region, USFS. The EVEG map stiches together map products developed using different imagery and methods at the national forest and national park scale to provide a bioregional-scale map product of habitat across the Sierra Nevada. No formal accuracy assessments have been conducted to validate the map across the bioregion or to resolve differences in habitat classifications resulting from different mapping approaches using different imagery at different spatial and temporal scales. Thus, inferences about habitat amounts and distributions should be tempered until formal accuracy assessments are completed to validate map accuracy and consistency across the Sierra Nevada. Nevertheless, these data provide the sole source of information on current amounts of California spotted owl habitat across the Sierra Nevada.

Chapter 6: Mapping Forest Conditions: Past, Present, and Future

Maggi Kelly[1]

Introduction

Mapping and mapped data have always been critical to public land managers and researchers for identifying and characterizing wildlife habitat across scales, monitoring species and habitat change, and predicting and planning future scenarios. Maps and mapping protocols are often incorporated into wildlife and habitat management plans, as is the case with the California spotted owl (*Strix occidentalis occidentalis*), a subspecies of management concern. Current spotted owl managers on all Sierra Nevada national forests use canopy cover and tree size guidelines designed to provide habitat for sensitive species (Chopping et al. 2012, Moghaddas et al. 2010) and to estimate accurately these important habitat metrics across scales from nest trees and the area surrounding them to broader scale characterization of core foraging and home ranges. These mapping tasks can be challenging in California forests, particularly in the Sierra Nevada because they exhibit great variability in composition, cover, and topography, and complex legacies of fire and logging (Hyde et al. 2005).

In this chapter, I have focused on mapping technology that can be used in the analysis of owl use of forested habitat. I reviewed and summarized 18 peer-reviewed papers published from 1992 through 2013 that described the use of remote sensing, aerial imagery, or other mapped products to assess forest structure used by California spotted owls across scales and that also were specific about mapping protocols. Because many of the newer papers used new remote sensing technologies such as light detection and ranging (LiDAR), I have presented a retrospective of mapping methods before the detailed summary of the literature on California spotted owl.

Owl Habitat Mapping Methods, Strengths, and Weaknesses

Historical Mapping Technology

Approaches to mapping wildlife habitat have been varied. They have included a range of remote sensing products and methods, manual delimitation and automated classifications, and mapping at many scales (Gottschalk et al. 2005, McDermid et al.

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2005). Data describing owl habitat have been gathered from field surveys (e.g., Bond et al. 2004), black and white or color air photos (e.g., Dugger et al. 2011, Ripple et al. 1997), or digital aerial imagery (e.g., Seamans and Gutiérrez 2007); and existing mapped products such as timber survey maps (e.g., Blakesley et al. 1992, Call et al. 1992), Landsat-derived vegetation maps (e.g., Bond et al. 2009, Hines et al. 2005), and fire-severity maps (e.g., Roberts et al. 2011). Remotely sensed imagery at fine spatial resolution (e.g., 1 m [3.3 ft]) and moderate resolution (e.g., 30 m [99 ft]) has also been used. Table 6-1 summarizes the types of remote sensing and mapping products commonly used for the mapping of spotted owl habitat.

Aerial Photography

Aerial photographs provide spatially detailed records of landscapes (Morgan et al. 2010). Despite the increase in the number and types of digital sensors available to managers and scientists, aerial photography remains a valuable tool for habitat

Table 6-1—Map products typically used to understand California spotted owl habitat

Type	Product	Data scale/resolution	Example reference
Aerial photography	Black and white imagery	1:12,000 to 1:40,000	Ripple et al. 1997
Aerial photography	Color photography	1:12,000 to 1:40,000	Blakesley et al. 2005, Dugger et al. 2011
Aerial photography	Color infrared photography	1:12,000 to 1:20,000; 1 m	Lee et al. 2013
Aerial photography	Digital orthophoto quadrangles	1:20,000 to 1:24,000; 1 m	Seamans and Gutiérrez 2007
Optical remote sensing	NAIP	1 m	Lee et al. 2013, Williams et al. 2011
Optical remote sensing	IKONOS (Satellite)	1 to 4 m	Moghaddas et al. 2010
Optical remote sensing	QuickBird	0.6 to 2.5 m	Chopping et al. 2012
Optical remote sensing	Landsat-5 Thematic Mapper	30 m	Hunter et al. 1995, Moen and Gutiérrez 1997
Optical remote sensing	Relative differenced normalized burn ratio	30 m	Roberts et al. 2011
Optical remote sensing	USFS EVEG	30 m	Bond et al. 2009, Hines et al. 2005
LiDAR	Airborne discrete return	10- to 50-cm footprint	García-Feced et al. 2011, Hyde et al. 2005
LiDAR	Airborne waveform	25- to 50-m footprint	Chopping et al. 2013
Existing mapped products	Timber strata maps	1:20,000; misc.	Blakesley et al. 1992, Irwin et al. 2007
Existing mapped products	FRAP fire perimeter maps		Bond et al. 2002

NAIP = National Agriculture Imagery, LiDAR = light detection and ranging, USFS EVEG = U.S. Forest Service existing vegetation, FRAP = Fire Resources and Assessment Program.

mapping for several reasons. First, aerial photographs predate satellite imagery; in California, imagery archives include images from the 1930s onward (Morgan et al. 2010). Second, the spatial detail provided by aerial photography is high, even when analog photographs are digitized. For example, a 1:20,000-scale photograph scanned at 200 dots per inch (dpi) will provide a digital image of 2.54-m (8.38-ft) resolution, and at 600 dpi yields 0.85-m (2.8-ft) resolution (Jensen 2000). This compares favorably to Landsat pixels, which are 30-m resolution and are similar to current high-resolution sensors such the QuickBird sensor. Third, when digitized, aerial photographs can be analyzed with powerful image analysis techniques. Although many of these techniques were originally developed for satellite imagery, they have also expanded upon the range of analysis techniques now available for aerial photographs (Cohen et al. 1996, Morgan et al. 2010).

The spatial scale of aerial photography influences how it is used. Large-scale (1:2,400 to 1:1,200) photographs can be used to map individual trees, stream reaches, and fine-scale habitat photographs at 1:20,000-to 1:4,800-scale are used to map forest stand polygons, vegetation communities, and habitat patches. Photographs of 1:40,000-scale-and-smaller are useful for general land cover with minimum mapping units (MMUs) of 2 to 4 ha (5 to 10 ac) (Wulder 1998). Aerial photographs are captured most commonly as panchromatic (black and white visible), color, or false-color infrared (CIR). These can be analyzed manually, with a trained analyst tracing boundaries between land cover patches (e.g., Chatfield 2005), and in more automated fashion, using similar algorithms pioneered in remote sensing (Cohen et al. 1996).

A standard format for digital aerial photographs is the digital orthophoto quadrangle (DOQ), which uses a standard image rectification procedure that aligns the image with longitude and latitude or other coordinate system. The U.S. Geological Survey (USGS) provides the largest catalog of DOQs, which may exist as far back as the early part of the 20th century. Typical spatial resolutions for DOQs are 1 m and less. More recently (since 2005 in California), the National Agriculture Imagery Program (NAIP) has been providing free periodic (usually every 5 years) digital CIR aerial imagery at 1-m resolution during the agricultural growing seasons in the continental United States. These images have proved useful for forest and habitat mapping (Cleve et al. 2008, Jakubowski et al. 2013a).

Landsat

The launch of the Earth Resources Technology Satellite 1, or ERTS-1 (ERTS-1) (later renamed Landsat-1) in 1972 (Lauer et al. 1997, Melesse et al. 2007) permanently changed the way remote sensing served resource management, although not immediately. From 1980 to 2000, there was nearly 20 years of increasing use of Landsat imagery by land managers and scientists for mapping forest vegetation (Franklin et al. 2000), particularly in California. Landsat-5 was launched in 1984 with the Thematic Mapper (TM) moderate resolution (30-m [99-ft]), six-band multispectral (typically broad spectral information in the visible to near-infrared light) sensor on board, and became the workhorse for remote sensing of land cover (Cohen and Goward 2004, Wulder et al. 2012). Throughout the 1980s and 1990s, the USDA Forest Service (USFS) and the California Department of Forestry and Fire Protection collaborated in California to produce a statewide Land Cover Mapping and Monitoring Program (LCMMP) to improve the quality and capability of monitoring data, and to minimize costs for statewide land cover monitoring (Levien et al. 2002). The mapping project aimed to support resource inventory, fire management, and habitat conservation goals, and an initial goal was to update these maps to quantify land cover changes every 6 years with the collaboration of the California Division of Forestry and Fire Protection (Franklin et al. 2000). Their initial method involved image segmentation into forest polygons (stands) using spectral and textural inputs, and either unsupervised classification or linear spectral mixed analysis. Results were calibrated with Forest Inventory and Analysis (FIA) data. Map attributes include a vegetation life-form class (e.g., conifer, hardwood, chaparral), vegetation type from the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) classification scheme, and canopy cover and size class estimates for forest stands. A Kauth Thomas algorithm (a transformation of spectral data to brightness, greenness, and wetness) applied to multitemporal Landsat imagery provided information for magnitude and direction of land cover change (Rogan et al. 2003).

The mapping protocol has evolved over time and been updated by the USFS when needed, and now forms the basis of EVEG (“existing vegetation”). EVEG is a Landsat-derived product that captures vegetation characteristics using automated, systematic procedures that map large areas of California and is supplemented with onsite field visits. The current map attributes consist of vegetation types using the CALVEG classification system and forest structural characteristics such as tree and shrub canopy cover and tree stem diameters. Current map product characteristics include a 1-ha (2.5-ac) MMU for most vegetation conditions (there is no MMU for lakes and conifer plantations); life form (conifer, mix, hardwood, shrub, grass, barren, agriculture, urban, ice/snow, water), within-life-form classes that are “crosswalked” to state and regional vegetation mapping standards, information on canopy closure of conifer and hardwood forests, mapped as a function of canopy closure in 10 percent classes, and size of overstory tree as interpreted from aerial photography and satellite imagery.

Vegetation maps derived from Landsat data have been used widely to study California spotted owl habitat (Bond et al. 2004, Hunter et al. 1995, Moen and Gutiérrez 1997). Landsat imagery, as well as the statewide vegetation map product derived from Landsat (i.e., EVEG), has been used since the 1990s for mapping wildlife habitat (Gottschalk et al. 2005) and is being used increasingly in sophisticated species distribution models that map habitat suitability for important wildlife species in California. The broad coverage and spectral detail of the Landsat sensors are useful for large-coverage mapping of species and canopy cover, but this imagery is not able to detect the residual tree component of forests dominated by medium-sized trees that is a critical component driving use by owls in these younger forests (García-Feced et al. 2011, Moen and Gutiérrez 1997). Residual trees are large trees within younger forests that may possibly serve as nest trees and influence forest stand temperature. These detailed aspects of forest structure are now better able to be mapped using a range of “active” remote sensing methods, such as LiDAR.

High Spatial Resolution Imagery

There have been a number of launches of satellites carrying high spatial resolution (approximately 5 m [16.5 ft] or less) multispectral sensors that have been used to map forests. The first of these was IKONOS, which was launched in 1999 with a 3- to 5-day return interval and imaged in panchromatic (1-m [3.3-ft]) and multispectral (4-m [13.2-ft]) modes. The QuickBird satellite (panchromatic band = 60 cm [24 in], multispectral bands = 2.5 m [8.3 ft]) was launched in 2001, and 2003 saw the launch of the OrbView satellite, which acquires multispectral imagery in either multispectral (4-m [13.2-ft]) or panchromatic (1-m [3.3-ft]) mode. In 2008, RapidEye was launched with five satellites as part of a public-private partnership with numerous European partners. This satellite constellation provides almost daily coverage of the Earth at 6.5-m (21.5-ft) resolution and was the first commercial satellite program to include the red-edge band, which is sensitive to changes in chlorophyll content, and therefore useful for vegetation mapping. WorldView-2 was launched in 2009 with an eight-band multispectral sensor (including a red-edge band) operating at 0.5 m (1.7 ft) in panchromatic and 1.8 m (5.9 ft) in the multispectral bands. These sensors provide detailed imagery with a timely repeat schedule and have been used to map forest habitat globally, although only IKONOS has been used in the context of California spotted owl mapping (Moghaddas et al. 2010).

Current and Emerging Technology

LiDAR

LiDAR provides highly detailed, extensive, and accurate vegetation structure data, which has long been identified as a key element of organisms' habitats (Lefsky et al. 2002, Popescu and Wynne 2004, Vierling et al. 2008). LiDAR data are collected from a laser-emitter scanner linked to an accurate positioning system. The round-trip time between pulse origination and return from target is measured, allowing the instrument to calculate the distance to a target object. LiDAR data can be broadly categorized into three classes depending on the type of sensor and deployment: (1) ground-based LiDAR, which samples the scattering returned by the entire laser pulse over a wide range of zenith angles and azimuth angles as it passes through the canopy from a stationary ground-based scanner (Henning and Radtke 2006, Strahler et al. 2008, Zhao et al. 2011); (2) small-footprint discrete return data in which the spatial coordinates of typically four discrete returns per laser pulse are recorded (Lefsky et al. 2002); and (3) large-footprint waveform data in which the pulse-return intensity over time is digitized (Lefsky 2010, Merrick et al. 2013, Vierling et al. 2008). Aircraft-based systems use onboard global positioning system (GPS) and inertial measurement units to establish position, whereas ground-based LiDAR uses GPS alone. The resolution and quality of the data depend on both the scanner and the pulse density (Merrick et al. 2013). The resulting data are either a detailed three-dimensional point cloud (e.g., ground and airborne LiDAR) or a collection of intensity returns (waveform); each of these can be manipulated in numerous ways to derive point-based and raster-based LiDAR metrics that capture aspects of the forest structure such as individual trees (Jakubowski et al. 2013b, Li et al. 2012) or other derived metrics. Most of the current literature describing LiDAR and wildlife habitat focuses on aircraft-based discrete return small-footprint LiDAR.

LiDAR metrics—

Numerous LiDAR metrics derived from the LiDAR point cloud have proved to be useful in wildlife habitat studies. Merrick et al. (2013) outlines primary metrics (those that can be derived directly from the LiDAR point cloud) and secondary metrics (those that are modeled based on LiDAR and field data) that have been used in wildlife studies. Primary metrics include canopy metrics (e.g., canopy surface model, canopy cover/closure, canopy/vegetation height model, canopy/vegetation profiles, canopy base height, canopy volume); vertical profile metrics (e.g., coefficient of variation of hits, foliage height diversity, standard deviation of vegetation height, mean absolute deviation height, vertical distribution of hits); topographic products (e.g., Digital Terrain Model, Digital Elevation Model and LiDAR return intensity). Secondary metrics include aboveground biomass, basal area, canopy complexity/diversity, tree diameter at breast height (d.b.h.), leaf area index (l.a.i.), timber/vegetation volume, and vertical distribution ratio. These metrics have been used to predict vegetation structure (e.g., biomass) and to scale-up field measurements to broader scales (Gonzalez et al. 2010; Hyde et al. 2005; Kane et al. 2011, 2015, 2013; Vierling et al. 2008, Wulder et al. 2008) to predict species performance based on structural associations (Lesak et al. 2011), to aid in vegetation classification and mapping (Swatantran et al. 2011), and in species distribution models to predict species presence or diversity.

Very high resolution imagery and microsatellites—
The 21st century can be characterized, in remote sensing terms, by the increased interest by private industry in the Earth observation domain (Melesse et al. 2007). There are several private companies providing high spatial resolution imagery at cost (e.g., IKONOS, QuickBird, Rapideye, and GeoEye). Additionally, there are numerous companies pioneering the deployment of so-called microsatellites, which are small and operate in low Earth orbit (Kramer and Cracknell 2008). Many of these have spatial resolutions of less than 1 m and operate in the multispectral and panchromatic mode. With multiple satellites operating in a constellation, image acquisition rates are expected to increase to more than one per day for some areas of the Earth. Finally, Google Earth™ (http://earth.google.com) has transformed the ways in which scientists and researchers can access and use high spatial resolution imagery, including assessing wildlife habitat (e.g., Hughes et al. 2011).

Characterizing Habitat Across Scales

Eighteen peer-reviewed journal articles from 1992 through 2013 revealed use of mapping technology to investigate California spotted owl habitat across scales (table 6-2). The organization of this review follows the habitat scales discussed in chapter 3 (i.e., nest, nest stand, core area, foraging habitat, and home range), but it was unclear from reading some papers what was the scale of investigation, so I categorized them loosely. There are tradeoffs among desired resolution, scale of imagery, and needed data given the application (e.g., moderate- to course-scale imagery such as Landsat is not appropriate for fine-scale mapping of habitat). Most papers used mapping technology to characterize forest structure around owl sites. The characterization of forest structure often involves the use of a fixed-radius buffer centered on nest sites or primary roost areas. The radius length dictates the

Table 6-2—Literature describing the mapping of California spotted owl habitat across scales

Reference	Map product/type	Nest	Stand	Core area	Foraging habitat	Home range	Study area
Bias and Gutiérrez 1992	Landsat-5 TM (Thematic mapper)			✓			Eldorado and Tahoe NF
Call et al. 1992	Field surveys; timber strata maps			✓	✓		Tahoe NF
Moen and Gutiérrez 1997	Landsat-5 TM			✓	✓	✓	Central Sierra Nevada
Lahaye et al. 2001	Landsat			✓	✓		San Bernardino Mountains
Temple and Gutiérrez 2002	Landsat: USFS EVEG			✓			Eldorado and Tahoe NF
Bond et al. 2002	CalFire Fire perimeter-maps			✓			Arizona, California, New Mexico
Bond et al. 2004	Landsat: USFS EVEG	✓	✓				Eldorado NF
Blakesley et al. 2005	Color aerial photography		✓	✓			Lassen NF
Hines et al. 2005	Landsat: USFS EVEG					✓	Southern California
Hyde et al. 2005	LiDAR: Waveform		✓				Sierra NF
Seamans and Gutiérrez 2007	Digital orthophoto quadrangles				✓	✓	Central Sierra Nevada
Irwin et al. 2007	Timber strata maps				✓		Northern California
Bond et al. 2009	Landsat: USFS EVEG; Relative differenced normalized burn ratio (dRNBR)			✓	✓	✓	Sequoia NF
Phillips et al. 2010	Digital orthophoto quadrangles and color aerial photographs		✓	✓			Eldorado and Tahoe NF
Moghaddas et al. 2010	IKONOS		✓	✓	✓		Plumas-Lassen NF
García-Feced et al. 2011	Discrete return LiDAR	✓	✓				Eldorado NF
Roberts et al. 2011	RdNBR		✓	✓			Yosemite NP
Williams et al. 2011	NAIP					✓	Eldorado and Tahoe NF
Lee et al. 2013	Color and CIR aerial photography; NAIP		✓				San Bernardino Mountains

USFS EVEG = U.S. Forest Service existing vegetation; NAIP = National Agriculture Imagery Program; LiDAR = light detecton and range, national forest; np = national park, CIR = color infrared.

scale of focus; and literature reports examples of radii <100 m (330 ft) (e.g., Call et al. 1992, Hyde et al. 2005) to >1 km (3,300 ft) (e.g., Dugger et al. 2011, Seamans and Gutiérrez 2007) covering circular areas from 1 ha (nest tree and stand scale) to greater than 1000 ha (2,500 ac; home range scale). The circular area described is then characterized using mapped data: either created new from field surveys, black and white or color air photos, or other remotely sensed imagery such as Landsat, or through the use of existing mapped products such as timber survey maps, Landsat-derived vegetation maps, or fire-severity maps. These results are often compared with an area of similar size that does not contain nest trees (e.g., a randomly selected stand). Other methods include the characterization of forests within some other noncircular area (e.g., minimum convex polygons describing nest and roost sites as in Moen and Gutiérrez (1997)] and Irwin et al. (2007). Existing mapped products have also been used to aid in sampling design, as in Bond et al. (2004) who used the USFS EVEG habitat map to identify the four strata in which to locate their random plots.

Mapping Nests and Nest Trees

Spotted owls nest in forests with dense canopy cover and large (>76 cm [30.5 in] d.b.h.) trees. They will use forests with medium-sized trees if they have dense canopy cover and residual trees (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). The ability to map individual trees and critical structural elements from remote sensing has been enhanced recently through the use of LiDAR (García-Feced et al. 2011, Hyde et al. 2005). Although canopy cover estimates from optical remote sensing are reliable, the mapping of individual and residual trees is difficult with coarse-scale optical imagery such as Landsat, particularly in dense canopy. García-Feced et al. (2011) evaluated the ability of LiDAR data to map these critical habitat elements in the Tahoe National Forest. They surveyed for spotted owls within this area during 2007 through 2009 and located four nest trees. They then used the LiDAR data to estimate the number, density, and pattern of residual trees (90 cm [36 in] d.b.h.) and to estimate canopy cover within 200 m of each of the nest trees (a circular area of 12.6 ha [31.5 ac]). They found that nest trees were surrounded by large numbers of residual trees and high canopy cover, and the LiDAR-based estimates agreed closely with residual tree counts and canopy cover estimates based on field data collected within 100 m (3 ha [7.5 ac]) of these nest trees.

Mapping Nest Stand Characteristics

California spotted owls nest and roost in complex, multlayered, late-successional forests with high canopy closure and cover, and numerous large trees (chapter 3). Using the classical buffer approach, Blakesley et al. (2005) mapped the forest stands surrounding 67 spotted owl sites using color aerial photographs, digital orthophoto quadrangles (from 1993 and 1998), and timber sale information within circular plots (with radii up to 2.4 km) in northeastern California. They examined the relationships between habitat composition in the area surrounding nest trees and variation in nest success over time (1990 through 2000) and site occupancy, apparent survival probability, and reproductive output over time (1993 through 1998). They found that large trees with high canopy cover were important for site occupancy at the stand scale (e.g., 203 ha) within the nest area, and the amount of nonforested areas and forest cover types not used for nesting or foraging negatively influenced occupancy. Additionally, the presence of large remnant trees within the nest stand facilitated nest success. They conducted their analysis at two spatial scales: nest area (203 ha [507 ac]) and core area (814 ha [325 ac]).

The first study to evaluate the use of LiDAR for mapping California spotted owl habitat was Hyde et al. (2005). They used large footprint, waveform LiDAR data acquired for the Sierra National Forest in October 1999 (leaf-on) to map forest structure: canopy height, canopy cover, and aboveground biomass. They used a LiDAR called Laser Vegetation Imaging Sensor, which is a full waveform-digitizing system that records the vertical distribution of target surfaces with 30-cm (12-in) vertical resolution. This was a large footprint system with a 12.5-m (31.5-ft) radius footprint on the ground. They compared LiDAR footprint returns to field data gathered in circular plots with an inner plot of 0.07-ha (1.18-ac; 15-m or 50-ft radius) and an outer plot of 1-ha (2.5-ac; 56.4-m or 186.1-ft radius). Results were encouraging: field and LiDAR canopy structure measures showed good agreement across a range of elevation and slope. They suggested that the correlation between the field plots and LiDAR data was amenable to scaling, and thus LiDAR was useful to characterize montane forest canopy structure over the wide range of environmental conditions that occur over the Sierra National Forest and might be useful to use for habitat mapping over large areas. The location of nest trees in relation to forest edges was examined by Phillips et al. (2010), who used a vegetation map of the Eldorado and Tahoe National Forests that had been created using aerial photography and digital orthophoto quadrangles from 1998 and 2000. Their geographic information system (GIS) database included a vegetation map with eight cover types, elevation data, nest tree locations, and one random location within each nest stand. Distances to forest edge from each nest and random location were compared, and they found no evidence in their study area that California spotted owls used nest sites closer to forest edges than one would expect by chance, and this was consistent over a wide range of elevations. They also suggested that the owls in the study area nested farther from high-contrast edges than expected by chance.

Mapping Core Use Area Characteristics

The primary areas used by spotted owls for nesting and foraging (core use areas) contain the contiguous forest an owl or owl pair uses consistently, including the nest and roosting area (Blakesley et al. 2005, Williams et al. 2011). It is pointed out in chapter 3 that because these forests contain nest sites, the characteristics between territory and nest stand often overlap. When mapping large areas such as owl core use areas (e.g., territories) on the order of 150 to 400 ha (500 to 1,000 ac), moderate-resolution imagery such as Landsat (resolution 30 m [99 ft]) has had a dominant yet contested role.

Hunter et al. (1995) used Landsat imagery and landscape metrics to understand spotted owl core use areas. While they focused on the northern spotted owl (*Strix occidentals caurina*), I have discussed the paper here because of the precedent it set. They used a single date Landsat-5 TM image and classified the core use area of the northern spotted owl in Humboldt County, California, into broad vegetation life-form classes. They then compared the landscape characteristics (land cover, fragmentation, and heterogeneity) within circular areas of 800-m (2,640-ft) radius (200 ha [520 ac]) around each spotted owl nest, roost, and random sites between 1988 and 1992. Nest and roost sites were characterized by lower amounts of nonvegetation and herbaceous land cover, and by greater amounts of mature and old-growth coniferous forest, which was less fragmented than random sites. They noted that the spectral similarities in the Landsat images between structurally similar seral stages made some age classification difficult. For example, differences between mature and old-growth forests were difficult to map using these data. Moen and Gutiérrez (1997) also used classified Landsat-5 TM imagery to examine the landscape characteristics within a 457-ha [1,142-ac] area surrounding 25 owl centers. They mapped minimum convex polygons that included both roosts and nests. The Landsat-5 image was classified by dominant species, size class, and canopy closure. This paper highlighted early on one of the main challenges for wildlife researchers using Landsat imagery and products—the typically poor ability of the Landsat pixel to capture the large tree (> 60 cm [24 in] d.b.h.) component of forests that appears to be critical to the spotted owl in particular.

Numerous researchers have focused on the impact of fire on spotted owl core area habitat. In a geographically broad study, Bond et al. (2002) examined the response of all three spotted owl subspecies to wildfire in Arizona, California, and New Mexico. They examined the response of owls after large (>540-ha [1,350-ac]) wildfires occurred within their territories. Large-fire locations were derived from the Fire Resources and Assessment Program fire perimeter database, which is a statewide geodatabase with wildfire history, prescribed burns, and other fuel modification projects current through 2013, and from the USFS. These digital fire data sets were critical for the study, and they called for more large-scale experiments to understand the effects of prescribed burning on spotted owls.

Seamans and Gutiérrez (2007) modeled the probability of territory colonization, territory extinction, and breeding dispersal in relation to the amount of mature conifer forest in the central Sierra Nevada. They used an existing map of forest cover developed from aerial photographs, digital-orthophoto-quarter quadrangles, and extensive ground sampling of the forest to classify tree size class and canopy closure (Chatfield 2005) and to estimate the amount of each forest class within a 400-ha (1,000-ac) circle (radius = 1128 m [0.7-mi] or half the mean nearest neighbor distance of occupied territories in their study area averaged over the years 1990 to 2002). They found that the amount of mature conifer forest (i.e., dominated by trees ≥30.4 cm (12 in) d.b.h. with canopy cover ≥70 percent) was correlated with spotted owl occupancy. Territories with more mature conifer forest had a higher probability of being colonized and a lower probability of becoming unoccupied. They also reported that alteration of mature conifer forest appeared to decrease the probability of colonization.

Roberts et al. (2011) examined the effects of fire severity on spotted owl site occupancy in late-successional montane forest in Yosemite National Park using a relatively new burn-severity metric called the relative differenced normalized burn ratio (RdNBR) (Miller and Thode 2007). Using images of an area before and after a fire remotely sensed by Landsat bands 4 and 7, they calculated the RdNBR to create a relative measure of vegetation change, which is then classified into four levels of fire severity:

- Unburned or unchanged
- Low severity
- Moderate severity
- High severity

A polygon map of fire severity for fires in Yosemite was used to compare owl site occupancy, and the authors reported that density estimates of California spotted owl pairs were similar in burned and unburned forests. They suggested that low- to moderate-severity fires might maintain habitat characteristics essential for spotted owls, and further that managed fires that emulate the historical fire regime of these forests may help maintain spotted owl habitat and protect this species from the effects of future catastrophic fires.

Lee et al. (2013) also examined the impact of fire and disturbance on spotted owl occupancy. They mapped the 203-ha (500-ac) forested area (radius approximately 800 m [0.5 mi]) surrounding a single owl nest tree location within each owl territory before and after fires in the San Bernardino and San Jacinto Mountains of southern California to investigate the influence of fire and salvage logging on spotted owls. Spotted owl sites affected by fire were those where the perimeter of the 203-ha (500-ac) core area overlapped the perimeter of one of the fires that occurred in the area from 2003 to 2007. The prefire map was created using 1-m resolution CIR aerial photographs and stereo pairs of color aerial photographs. Imagery from NAIP taken for the San Bernardino National Forest in October 2009 was used to remap vegetation in core areas that burned between October 2003 and October 2007. They also used Google Earth imagery to estimate the amount of the 203-ha (500-ac) area affected by extensive postfire tree removal. They found that sites where high-severity fire affected >50 ha (125 ac) of forested habitat could still support spotted owls and recommended that all burned sites should be monitored for occupancy before management actions such as salvage logging were undertaken.

Other researchers have modeled fire behavior to predict future impacts of fires on spotted owl habitat. Moghaddas et al. (2010) used two common fire modeling software programs FlamMap and FARSITE that were parameterized with vegetation maps derived from IKONOS imagery, ground-based plot data, and integrated data from ARCFUELS and the Forest Vegetation Simulator. They modeled conditional burn probability under 97th percentile weather conditions across Meadow Valley in the Plumas National Forest to investigate the impact of forest fuel treatments. The study area contained California spotted owl habitat areas, protected activity centers, and home range core areas. Fourteen percent of the study area was spotted owl core area. The modeled results indicated that the average conditional burn probability was reduced between pre- and posttreatment landscapes, and the stands designated for management of spotted owls as well as other resources were assumed to benefit from the landscape fuel treatments.

Mapping Characteristics of Foraging Habitat

Spotted owls forage in forests characterized by a mosaic of vegetation types and seral stages interspersed within mature forest as well as in contiguous stands of mature and old-growth forest (chapter 3). Landsat imagery was used by Lahaye et al. (2001) to classify vegetation into four categories: owl nesting and roosting habitat, owl foraging habitat, nonforested vegetation, and other non-owl habitats. They used this classification to estimate the proportion of the study area supporting owl nesting and foraging habitat in a study investigating timing and patterns of owl dispersal in the San Bernardino Mountains in southern California. This is a highly fragmented region with only 2 percent of the landscape covered by vegetation types that support spotted owls. They showed that the majority of owl dispersers settled in territories that were occupied by either pairs or single owls the previous year, some settled in vacant territories next to occupied sites, and a few settled at sites of unknown occupancy. No owls settled at unoccupied sites that were not adjacent to occupied sites.

Detailed forest habitat maps have been commonly made by private landowners and can be used in spotted owl research. For example, Irwin et al. (2007) used owl telemetry and existing vegetation maps provided by a private forestry company to evaluate owl foraging habitat. Sierra Pacific Industries inventoried their forests from August 1997 to March 1999 on an 80- by 200-m (264- by 660-ft) grid. They used this map to compare habitat values at owl and random locations within 95 percent minimum convex polygon home ranges. Results indicated that stands more likely to be chosen for foraging included those with intermediate values of the combined basal areas of three conifer species Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and red fir (*A. magnifica*) and greater basal area of large-diameter hardwoods. The relative probability of selection for foraging habitat decreased with increasing basal area of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). Topographic position, habitat heterogeneity, tree species composition, and forest density also influenced foraging site selection.

In 2002, the McNally Fire burned 610 km^2 of land in the southern Sierra Nevada, including forests containing four California spotted owl territories. Four years later, Bond et al. (2009) examined effects of fire on these seven radiomarked owls from these territories by quantifying, as a function of fire severity, owl use of forests for nesting, roosting, and foraging. They used the Landsat-based EVEG vegetation map to establish habitat within foraging ranges of spotted owl and Landsat-based RdNBR to quantify fire severity. They reported that within 1 km of the center of their foraging areas, spotted owls selected all severities of burned forest and avoided unburned forest. Beyond 1.5 km of a center of foraging area, there were no discernable differences in use patterns among burn severities, and owls foraged at low rates in burned and unburned areas. Owls foraged in high-severity burned forest with greater basal area of snags and higher shrub and herbaceous cover more than in all other burn categories.

Mapping Home Ranges

Owl home ranges encompass the area used by an owl to meet its requirements for survival and reproduction (chapter 3) and are large (e.g., 600 to 2200 ha [1,500 to 5,500 ac]). Mapping owl home ranges often requires moderate-scale resolution imagery. The first use of Landsat for California spotted owl habitat research was described in Bias and Gutiérrez (1992), who used Landsat imagery to investigate spotted owl home range characteristics across ownership. They used Landsat-5 TM images from 1986 and 1987 to measure the interspersion, or rate of change, of different habitat types along 50 randomly located transect lines throughout owl territories. Their study area crossed the boundaries of the Eldorado and Tahoe National Forests, and had a mixed ownership: 60 percent was public land and 40 percent was private land. Their analysis was largely pre-digital: they superimposed the Landsat-5 images onto base maps using a stereo zoom transfer scope and interpreted vegetation changes from the Landsat images based on recognition and identification of image characteristics (i.e., tone, texture, color). They defined habitat interspersion as the number of habitat changes along a segment divided by the scale-equivalent length of that segment. This metric (habitat change per kilometer) was then compared across public land, private land, and nest sites. Ownership pattern influenced roosting and nesting behavior: the majority of observed roosts and all owl nests were on public lands.

Tempel and Gutiérrez (2002) investigated whether the environment within an owl territory might affect stress hormone levels. They collected fecal samples from spotted owls in Eldorado and Tahoe National Forests to determine if certain environmental factors were correlated with elevated fecal corticosterone levels. The environmental variables they examined were largely derived from the USFS EVEG Landsat product, and included the amount of core and edge habitat, number of habitat patches, and the total length of roads within an owl territory. While a linkage between fecal corticosterone and environment was not found, they suggested protocols for sampling corticosterone in birds. Bond et al. 2009 used both the USFS vegetation EVEG map product and the RdNBR product to understand how spotted owls were using habitat after a fire. They found that spotted owls at two areas on the Sequoia National Forest foraged in a range of burn severities, illustrating that a mosaic of burn severities in California spotted owl territories apparently allows owl use 4 years after a fire.

The accuracy of the Landsat-derived vegetation maps were explicitly tested by Hines et al. (2005) who performed a sensitivity analysis of the EVEG product developed for the USFS in southern California to estimate how mapping errors in vegetation type, forest canopy cover, and tree crown size might affect the delineation of suitable habitat for the California spotted owl. In this cautionary note on the use of existing coarse-scale land cover products, the authors reported an increase in the estimated area of suitable habitat types for the spotted owl solely resulting from map uncertainty.

High spatial resolution imagery has also been used to map forest structure and owl habitat in greater detail than possible by Landsat. Williams et al. (2011) used the USFS, NAIP imagery from 2005 to estimate tree size, canopy cover, and hardwood or conifer forest in the Eldorado and Tahoe National Forests study area. They digitized the boundaries of vegetation patches and then classified the patches into eight vegetation classes based on tree size and canopy cover consistent with the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988). The vegetation of every owl home range in the Eldorado and Tahoe National Forests study area as well as 2,161 random locations throughout the study area was mapped and compared. They found that landscape heterogeneity (number of patches) was an important additional positive factor in owl home-range size, as well as owl foraging site selection.

Accuracy Assessment

Understanding the accuracy of a remotely sensed product is critical for determining its usefulness. I reviewed all papers assessed in this chapter for a description of accuracy, and the way in which accuracy might play a role in the use of the product. Under half (eight) of them explicitly discussed accuracy of products used. Currently, best practices for assessing and reporting accuracy of classified remotely sensed maps include the development of an “error matrix” in which reference values are checked against classified values across the types of land cover values (Congalton and Green 1999, Foody 2002). Reference data ideally should come from field data gathered contemporaneously with imagery. Because this is often difficult, many researchers use as reference data imagery at higher resolutions than the source imagery. Metrics derived from an error matrix include overall accuracy (percentage), and errors of omission (or Producer’s accuracy) and errors of commission (or User’s accuracy) for each land cover class mapped. These are important measures to evaluate prior to use of land cover maps as the most important classes for owl biology might be the classes that are difficult to accurately map. An additional metric—the kappa statistic—is often reported and gives the likelihood that a classification is better than random. When a remote sensing product is presented as a physical measure, such as canopy cover, its accuracy is reported using a correlation coefficient (r^2) or root-mean-square error (RMSE), which is based on regression between field-derived reference data and remotely sensed values.

Papers of several researchers I reviewed used the error matrix approach to evaluate mapped products (Chatfield 2005, Hunter et al. 1995, Phillips et al. 2010, Ripple et al. 1997, Seamans and Gutiérrez 2005, Williams et al 2011) reporting overall accuracies of mapped product from aerial photography interpretation generally above 80 percent and overall accuracies of Landsat classification at 76 percent (Hunter et al. 1995). Moen and Gutiérrez (1997) reported an accuracy of 76 percent for the Landsat habitat map, but noted that the product lacked the "residual tree" component that appears critical for owls for their use of medium-sized tree forests. Bond et al. (2009) used the error matrix approach to evaluate a burn-severity map, and found it was 93 percent correct (with 80 field validation sites).

The implication of the accuracy of the Landsat-derived vegetation maps was explicitly examined by Hines et al. (2005), who performed a sensitivity analysis of the EVEG product developed for the USFS in southern California to estimate how mapping errors in vegetation type, forest canopy cover, and tree crown size might affect the delineation of suitable habitat for the California spotted owl. They reported the overall accuracy for USFS Landsat-derived vegetation map was 73 percent, but individual class accuracy ranged from 25 to 100 percent. They used these error values in a simulation experiment to evaluate the role of mapped error in over or underpredicting owl habitat. In this cautionary note on the use of existing coarse-scale land cover products, the authors reported an increase in the estimated area of suitable habitat types for the spotted owl solely resulting from map uncertainty.

Accuracy assessment of LiDAR mapped products is more complicated than for optical imagery. Hyde et al. (2005) evaluated LiDAR-derived canopy height measures using regression between field and LiDAR canopy height measures and reported high r^2 and low RMSE. The positional accuracy of LiDAR-derived locations of individual trees requires taking a sample of tree locations in the field using high-quality GPS, and reporting the RMSE in x and y directions between reference and LiDAR. This is often not done owing to the difficulties in gathering sufficient samples in the field. García-Feced et al. (2011) compared in general terms the number and pattern of residual trees and canopy cover in the area surrounding four nest trees between LiDAR and field-derived values and show concordance of LiDAR with field sampling.

Chapter Summary

Mapping technology has been critical to understanding the ways owls use their forest habitat and to help manage forests for their sustainability. Many studies have relied on moderate-resolution Landsat imagery to map large areas of forest, but this is not without challenges. Of primary importance is the assessment of accuracy in mapped products. Despite the need to understand product quality, the accuracy of mapped products is not routinely evaluated. Fewer than half of the articles I reviewed included a description of any accuracy assessment. Recommended accuracy assessment approaches are not universally adopted in the remote sensing community (Foody 2002). Remotely sensed or GIS-derived products are often used as predictor variables in regression models without consideration of uncertainty. This is problematic as traditional regression-based statistical models assume that the covariates are measured without error when this is never the case. Additionally, although the overall accuracies of mapped products reviewed here were generally high (greater than 75 percent), individual class accuracies vary considerably, and can be quite low. Also of importance is the difficulty of optical remote sensing to capture much of the structural elements so critical to owls (e.g., high concentrations of large trees, multilayered canopy).

We can expect that new developments in high-resolution, multitemporal imagery, and particularly in active remote sensing methods such as LiDAR, will play increasing roles in wildlife research and management as their costs decrease. These tools provide more detail about the horizontal and vertical structure of forests, and when linked to accurate and often dynamic measures of animal location, a richer understanding of the use of the forest by these species can be developed. Yet despite great improvements in mapping provided by LiDAR and other high-resolution sensors, there are considerable outstanding needs for mapping of wildlife habitat. First, there is a need to better map important wildlife habitat elements within forests such as snags and large broken-top trees, which may be important to many wildlife species, including the spotted owl (Gutiérrez et al. 1992). Currently, remote sensors map these structural elements indirectly based on the vertical heterogeneity of the forest canopy (e.g., Martinuzzi et al. 2009), but they remain difficult to estimate accurately, particularly in dense forests (Blanchard et al. 2011). Second, research is ongoing to develop better metrics of vertical canopy structure for assessing habitat. Analysis of the discrete return point cloud can produce hundreds of structural and physics-based metrics (e.g., coefficient of variation of hits, or vertical distribution of hits), but many of these cannot be field verified, and they lack any management meaning. Simpler metrics that can be linked to management goals and ascertained in the field are needed. Synergies between ground-based LiDAR and airborne

LiDAR data might help to improve the characterization of vertical structure (e.g., Henning and Radtke 2006, Iavarone 2005). Third, species classification needs to be improved, particularly in mixed forests. The integration of LiDAR with other optical imagery (at fine and coarse resolutions) are proving very useful in mapping forests with increased species discrimination, as well as providing information on stress and biomass (Asner and Mascaro 2014, Gonzalez et al. 2010, Ke et al. 2010, Swatantran et al. 2011). Finally, optical and LiDAR fusion might also help to scale important forest structural measurements such as heterogeneity over spatial scales that are commensurate with owl home ranges (e.g., Chopping et al. 2012). These developments will likely augment the ways in which we map wildlife habitat in the near future.

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Chapter 7: Threats to the Viability of California Spotted Owls

John J. Keane[1]

Introduction

The California spotted owl (Strix occidentalis occidentalis) is a species of conservation concern owing to threats to its habitat and populations. Verner et al. (1992) first assessed the status of the California spotted owl "The California Spotted Owl: A technical Assessment of it's current status" (CASPO) and identified four factors as either threats or potential threats to the viability of California spotted owl populations: (1) timber harvest and forest management, (2) wildfire, (3) development of gaps in owl distribution across the Sierra Nevada, and (4) human population growth and development. Since the publication of CASPO, other factors have emerged as threats to California spotted owl population viability: (1) the invasion of the barred owl (*Strix varia*) into the Sierra Nevada, (2) climate change that could affect owls and their habitat, (3) the invasion of West Nile virus in the owl's range, (4) the potential impact to owls from secondary ingestion of rodenticides used to kill rodents that eat marijuana, *Cannabis* sp., and (5) reduction in genetic diversity. In this chapter, I review threats identified in CASPO and emerging threats to California spotted owls in the Sierra Nevada that have arisen since CASPO. I have relied on key findings from peer-reviewed literature of forest ecology and management and California spotted owl ecology.

Evaluation of Threats Identified in CASPO

Forest Management

Logging and fire suppression were identified in CASPO as primary threats to California spotted owls and their habitat in the Sierra Nevada (McKelvey and Johnston 1992, McKelvey and Weatherspoon 1992, Weatherspoon et al. 1992, chapter 5). Key uncertainties were (1) whether critical habitat elements (old, large-diameter trees and associated large downed logs) would be maintained and perpetuated under current and proposed even-aged silvicultural prescriptions; and (2) whether dense, high canopy cover stands important to owls could be maintained given increasing risk of high-severity fire owing to historical fire suppression (chapter 5). In general, both public and private lands were managed similarly prior to CASPO (McKelvey and Johnston 1992). McKelvey and Weatherspoon (1992) recommended development,

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adaptive monitoring, and experimental testing of forest management approaches that would move forest structure and composition toward a heterogeneous condition that likely persisted under the area's natural fire regime and to evaluate the effects of these approaches on California spotted owls and their habitat.

Following adoption of CASPO guidelines, forest management on national forests diverged from private land management. Overall, 83.4 percent of the timber volume harvested from 1994 through 2013 came from private lands (chapter 5). During this time, group selection, shelterwood removal, and clearcutting were dominant on private land. In contrast, commercial thinning, salvage logging following wildfires, and hazard tree removal were dominant on national forest lands. About 73 to 80 percent of important California spotted owl habitat types occur on national forest lands in the Sierra Nevada (chapter 5). Differences in forest management among national forests, national parks, and private lands, along with variation in wildfire, have produced variable and complex landscapes across much of the Sierra Nevada. The scope and scale of cumulative effects is illustrated using case study demonstration areas. Figures 7-1 to 7-4 illustrate the complex landscape patterns generated by fire and forest management treatments within and surrounding four long-term demographic studies (Lassen, Eldorado, and Sierra National Forests and Sequoia and Kings Canyon National Parks) and within an area of mixed private-public ownership in the central Sierra Nevada.

Effects of forest management on California spotted owls—

Despite extensive research on spotted owls, the effect of forest management on owls is not well understood (USFWS 2011). Empirical field studies have been observational and correlative. Further, the complex mix of treatment types and wildfire across space and time impedes research efforts to isolate effects of specific treatment types because few owls receive the same type of treatment (figs. 7-1 to 7-4). Although experimental studies designed to understand the effects of logging have long been advocated (e.g., Gutiérrez 1985, McKelvey and Weatherspoon 1992, Noon and Franklin 2002, Verner et al. 1992), such studies have not been conducted, in part because they are technically, logistically, politically, and financially challenging. Such studies require organizational leadership, capacity, and institutional will to integrate multiple management objectives in the development and sustained testing of alternative land management strategies over large enough spatial and temporal scales to generate meaningful results (Gutiérrez et al. 2015). Although observational and correlative studies are of significant value, especially when replicated, they cannot produce strong inference (Romesburg 1981).

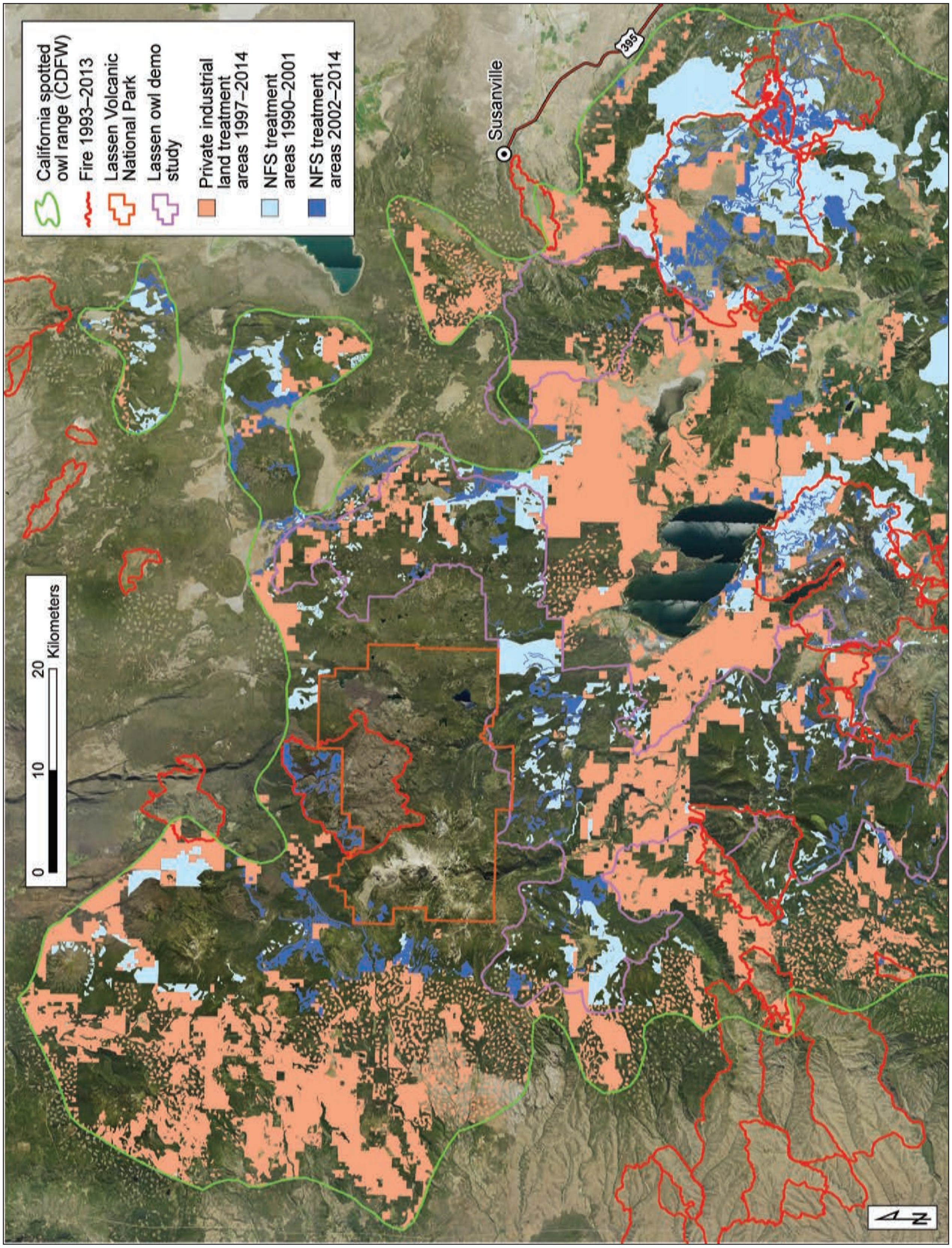

Figure 7-1—Distribution of forest management treatments on national forest and private industrial forest lands on the Plumas and Lassen National Forests in the region surrounding the long-term Lassen Demographic Study area during 1990–2014. CDFW = California Department of Fish and Wildlife, NFS = National Forest System. See text for further details.

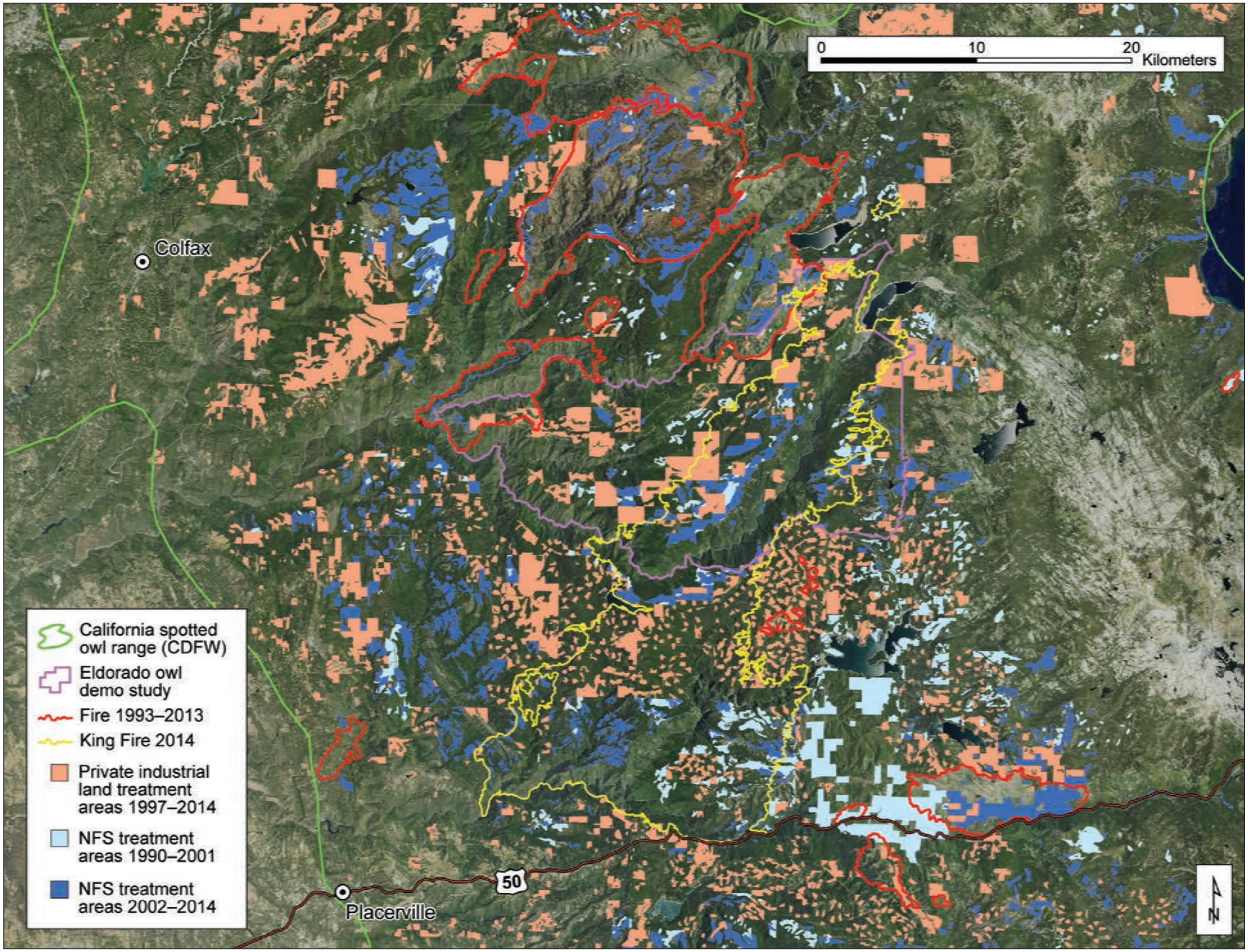

Figure 7-2—Distribution of forest management treatments on national forest and private industrial forest lands on the Eldorado National Forest in the region surrounding the long-term Eldorado Demographic Study area during 1990–2014. CDFW = California Department of Fish and Wildlife, NFS = National Forest System. See text for further details.

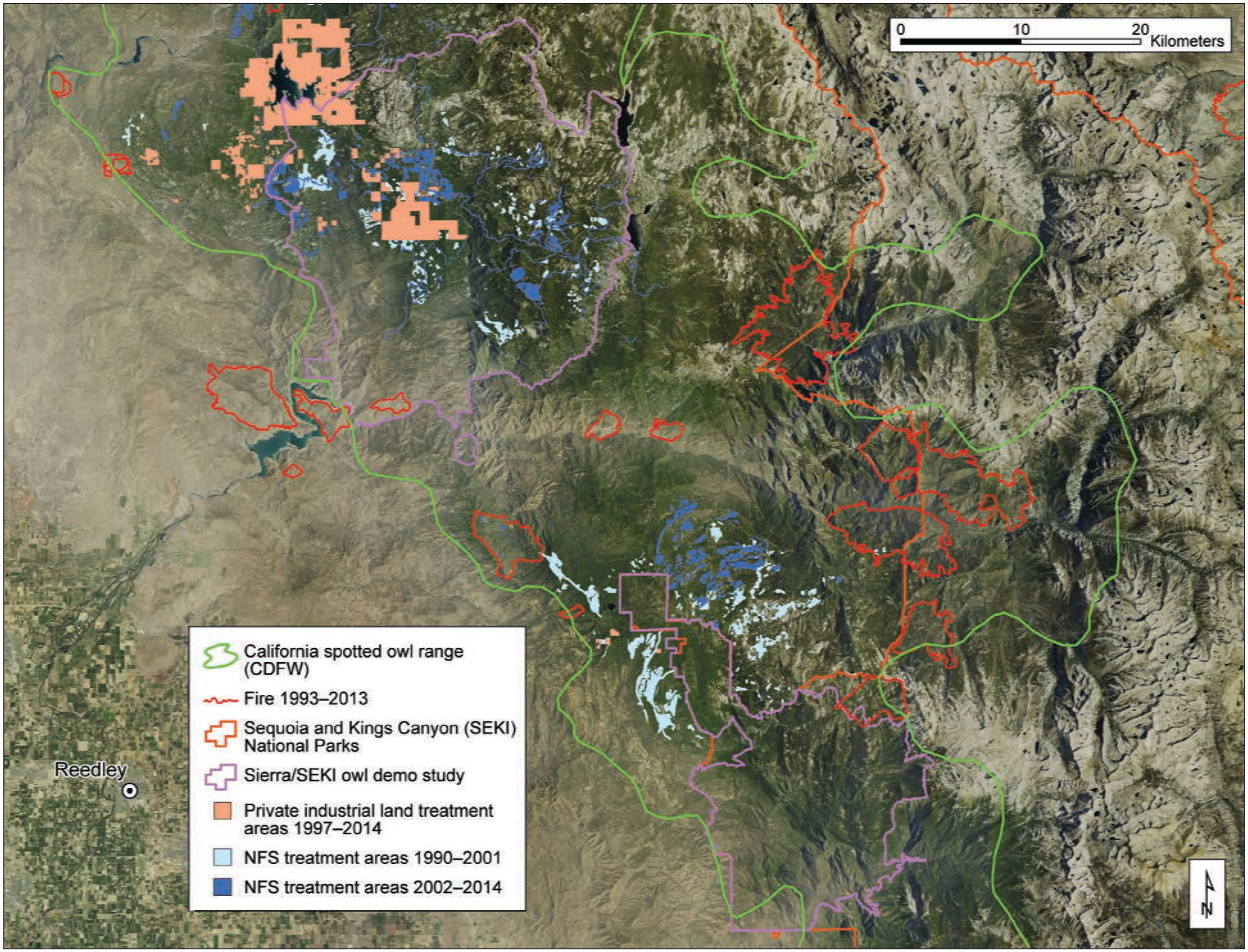

Figure 7-3—Distribution of forest management treatments on national norest and private industrial forest lands on the Sierra and Sequoia National Forests and Sequoia and Kings Canyon National Parks in the region surrounding the long-term Sierra and Sequoia-Kings Canyon Demographic Study during 1990–2014. CDFW = California Department of Fish and Wildlife, NFS = National Forest System.

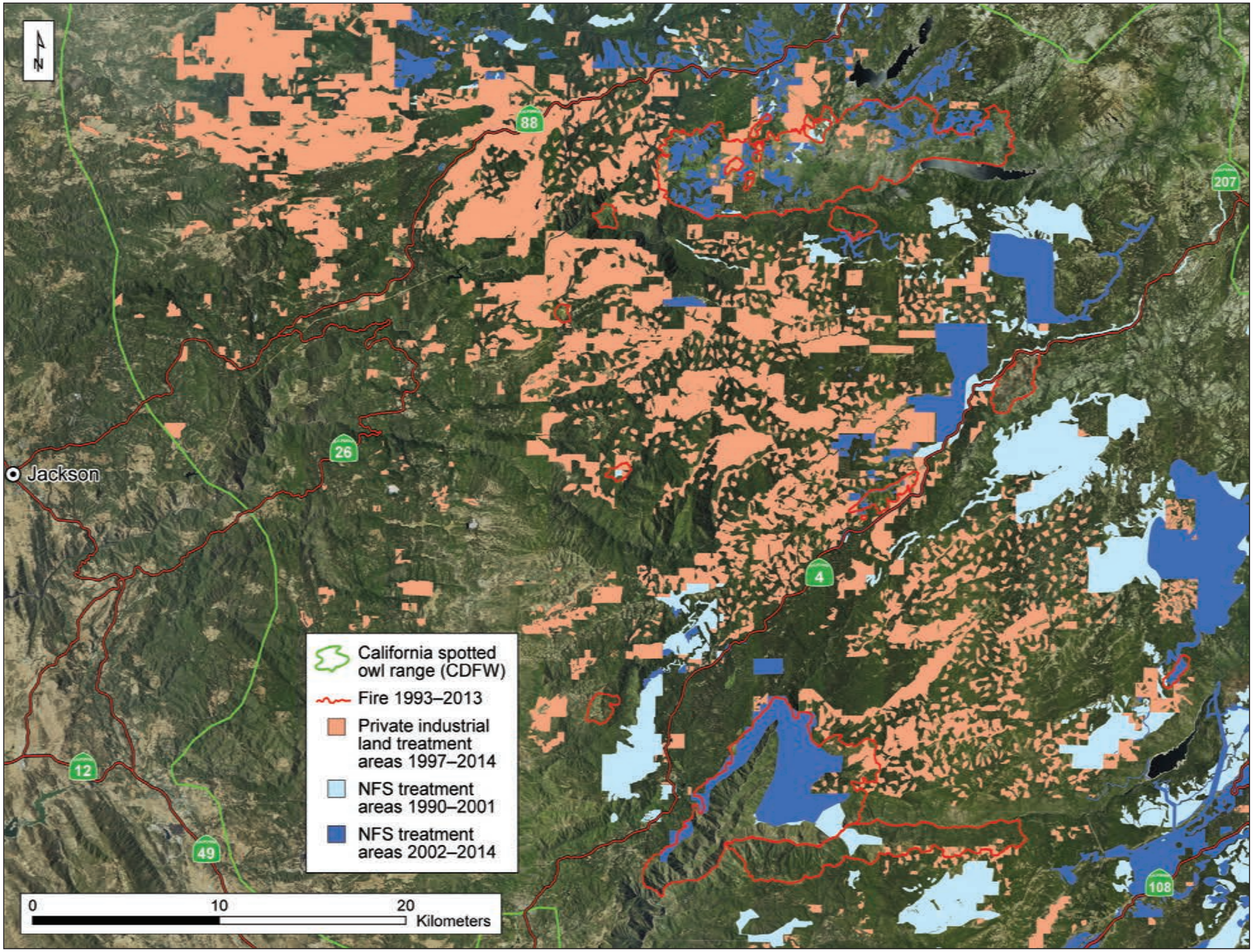

Figure 7-4—Distribution of forest management treatments on national forest and private industrial forest lands in a region of mixed public and private ownership on the Stanislaus and Eldorado National Forests during 1990–2014. CDFW = California Department of Fish and Wildlife, NFS = National Forest System.

Only three studies have explicitly addressed the effects of habitat change on California spotted owls at territory (Seamans and Gutiérrez 2007a, Tempel et al. 2014) and landscape spatial scales (Stephens et al. 2014). Seamans and Gutiérrez (2007a) concluded that California spotted owl territories with greater amounts of mature conifer forest defined as >70 percent canopy cover dominated by medium and large trees [30.4 to 60.9 cm (11.9 to 23.6 in) diameter at breast height (d.b.h.), and >60.9 cm >11.9 in d.b.h., respectively), had higher probabilities of being colonized and lower probability of being unoccupied relative to territories with lower amounts of mature conifer forest. Territories in which ≥20 ha (≥49.4 ac) of mature forest was altered experienced a 2.5 percent decline in territory occupancy probability. Breeding dispersal probability (the probability of territorial owls dispersing from an established site) did not change when ≥20 ha (≥49.4 ac) of habitat was altered in territories with >150 ha (>370.7 ac) of mature forest within a 400-ha (988.4-ac) circle centered on the site at the start of the study. However, an increase in breeding dispersal probability was observed at territories that started with <150 ha (<370.7 ac) of mature forest and experienced ≥2 ha (>49.4 ac) of habitat alteration. Thirty-eight of 66 territories in this study experienced habitat alteration, including fire at two territories and timber harvest at the other 36 territories. Timber harvest included clearcutting, thinning, and other prescriptions, but inferences were not made relative to a specific silviculture prescription.

Unlike earlier studies, Tempel et al. (2014) treated habitat change as dynamic over time and related annual patterns of change to owl survival, reproduction, population growth rate, and occupancy. Tempel et al. (2014) concluded that the amount of mature conifer forest >70 percent canopy cover; medium tree density (30.4 to 60.9 cm [11.9 to 23.6 in] d.b.h.) and large tree density (>60.9 cm [>23.6 in] d.b.h.) was the most important predictor associated with variation in demographic rates. This variable explained a large proportion of the variation in population growth rate and equilibrium occupancy, and was positively correlated with survival, equilibrium occupancy, and population growth, and negatively correlated with territory extinction probability. Further, medium-intensity treatments (such as thinning) were negatively correlated with reproduction and appeared to be related to reduced survival and territory occupancy when logging occurred in mature conifer forest that moved a class to a lower canopy cover state (e.g., canopy cover state changed from >70 percent cover to >40 to 70 percent). Of note, the probability of a territory going extinct was lower when the amount of mature conifer forest and high-intensity treatments (e.g., group selection, clearcut) increased and owl survival and population growth were positively related to the amount of habitat edge. Tempel et al. (2014) hypothesized that the juxtaposition of mature conifer forest and edge habitat with shrub/saplings may be important for increasing owl prey populations.

Only a single study has investigated the effects of landscape forest management on the owl (Stephens et al. 2014). They monitored owl territories annually after forest treatments within the 23 823-ha (58,867-ac) Meadow Valley Project Area (MVPA). Approximately 4161 ha (10,282 ac) of treatments were conducted during 2002–2008 (1784 ha [4,408 ac] of Defensible Fuels Profile Zone (DFPZ) treatments, 272 ha (672 ac) of group selections, 1440 ha (3,558 ac) of thinning, and 665 ha [1,643 ac] of prescribed fire). Seven to nine spotted owl sites were occupied in the MVPA before and during implementation of treatments during 2002–2007. However, the number of occupied sites declined to six from 2008 through 2010. In the third and fourth years of posttreatment, the number of occupied owl sites had declined to four (a 43 percent reduction in occupied owl sites in the MVPA). Thus, the landscape management strategy had negative short-term effects on spotted owls in the first 4 years after project completion; because there was a decline in occupancy of territories, owls responded to treatments by using larger areas. Further, there appeared to be a 2- to 3-year lag in spotted owl response time to the treatments. Although owls have been declining across the demographic study area over the past 25 years (Conner et al. 2013), the greatest magnitude of decline has been observed in the MVPA treatment landscape, suggesting a negative effect of the landscape treatment strategy (Stephens et al. 2014). Although, this study represents a quasi-experiment (observing behavior of owls after a treatment), the study is the first to monitor California spotted owl responses to a landscape-scale fuels treatment and logging strategy. It appears this landscape-scale management negatively affects spotted owls, which highlights the lack of robust adaptive management monitoring to assess the effects of fuels reduction and timber harvest on spotted owls.

Key findings from recent research on California spotted owl habitat associations—

There have been many studies of spotted owls since CASPO (chapters 2, 3, 4). These studies either confirm what was previously known, add detail (increased precision to estimates or nuances to early findings), or provide new insight (e.g., there is now strong evidence that California spotted owl populations are declining on areas of mixed U.S. Forest Service (USFS)–private land in the Sierra Nevada). The general patterns are that spotted owls are K-selected species having high survival and low annual reproductive output, that they select mature and old forest having high canopy cover (>60 to 70 percent) disproportionate to its availability, and that their occupancy is related to both the amount of this high canopy forest in their territories and the amount of forest that is lost to treatments. Moreover, the configuration of landscape types, amount, and distribution is apparently related to owl fitness (Dugger et al. 2005, Franklin et al. 2000, Tempel et al. 2014).

Current management—

Verner et al. (1992) identified habitat loss from forest management practices (logging and fire suppression), as a primary threat to California spotted owls. The CASPO strategy (1992) caused USFS forest management to diverge from private lands. The different forest management approaches by private and public land managers, along with wildfire and other disturbances, has resulted in spatially complex vegetation landscapes (see figs. 7-1 to 7-4 as examples of that complexity; see chapter 5 for details on available information on national forest and private lands treatment summaries).

Private industrial forests in the Sierra Nevada are managed using predominantly even-age silvicultural prescriptions (seed tree, shelterwood, and clearcut (chapter 5), although some private owners use uneven-age management. Because the owl is not federal or state listed, it does not receive special regulation on private land. Typically, a no-harvest buffer of 6 to 12 ha (15 to 30 ac) is established around active California spotted owl nest/activity centers (USFWS 2006). Previously known owl territories that are not currently occupied during project planning may receive no protection. McKelvey and Weatherspoon (1992) identified even-age management as a threat to owl habitat because critical habitat elements (old, large-diameter trees and associated large downed logs) and older forest stands would either decline or be lost eventually under this general system. There is no research on the specific effect of even-age management on owls and their habitat in the Sierra Nevada, but the northern spotted owl (*S. o. caurina*) was listed partially because of this type of silviculture. Recently, Sierra Pacific Industries (SPI) initiated research to assess the effects of even-age management on California spotted owls in the Sierra Nevada. Results from 2012 through 2014 indicate that owls are present across five study areas consisting of mixed SPI–Forest Service–other private owner lands, although further work is needed to assess habitat quality (chapter 4, Roberts et al.[2]). Alternatively, uneven-age forest management (e.g., hazard tree removal, selection harvest, thinning) remains a threat because of uncertainty regarding its effects on

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[2] **Roberts, K.; Hall, W.E.; Shufelberger, A.J.; Reno, M.A.; Schroeder, M.M. 2015.** The occurrence and occupancy status of the California spotted owl on Sierra Pacific Industries' lands in the Sierra Nevada of California. 11 p. Unpublished document. On file with: Sierra Pacific Industries, 3950 Carson Rd., Camino, CA 96049.

owls and their habitat (e.g., loss of residual trees, reduction of canopy cover, simplification of forest structure).

After implementation of the CASPO guidelines (Verner et al. 1992) in the Sierra Nevada, national forests experienced a decline in the area logged annually with the majority of logging being commercial thinning and thinning from below to reduce fire risk (chapter 5). McKelvey and Weatherspoon (1992) and Weatherspoon and Skinner (1996) proposed that tree thinnings should incorporate heterogeneity into prescriptions; commercial thinning as implemented has tended to produce homogeneous conditions within treatment units. As typically implemented, thinning has emphasized reduction in surface and ladder fuels, maintaining trees ≥76 cm (≥30 in) d.b.h., and posttreatment canopy cover ≥40 percent. Usually the remaining overstory trees are regularly spaced with little forest floor and understory diversity and low horizontal and vertical heterogeneity in stand structure (Knapp et al. 2012). Recent evidence suggests that these types of thinning prescriptions may have negative effects on California spotted owls (Stephens et al. 2014, Tempel et al. 2014). In recent years, emphasis has refocused on silvicultural prescriptions that attempt to restore finer scale vertical and horizontal heterogeneity that would mimic predicted historical vegetation patterns (Knapp et al. 2012).

Fire suppression also has significantly affected forest structure with changes in vegetation patterns at the landscape scale, as well as increases in stand density and shade-tolerant species, reductions in forest understory vegetation diversity, and reductions of vertical and horizontal heterogeneity at the stand scale (e.g., Dolanc et al. 2014, Knapp et al. 2013; chapter 5). At the landscape-scale, fire suppression has contributed to increased homogeneity in vegetation with increases in the distribution, amount and continuity of younger to mid-aged stands across the landscape, which under a more active natural fire regime would have likely been characterized by a finer scale, heterogeneous vegetation landscape. Fire suppression also has contributed to increased fuel loads and ladder fuels, which has increased risk of stand-replacing fire effects (see chapter 5 for further details).

Forest management remains a threat to California spotted owl habitat and populations. Significant uncertainty persists about the effects of both public and private land management on California spotted owls and their habitat, and whether current vegetation trajectories on forest lands in the Sierra Nevada will support viable populations of owls because long-term monitoring of several owl populations across the Sierra Nevada document that owls are declining except on one study area on a national park (see chapter 4). The only consistent difference among these owl populations is forest management. Logging in national parks has been limited to very specific purposes such as roadside hazard tree removal or fuels hazard reduction around infrastructure, whereas logging has been more prevalent on private and national forests. Additionally, national parks make greater use of prescribed fire and managed wildfire. Other differences between national forest and national park study areas are discussed in Franklin et al. (2004) and Blakesley et al. (2010). The greatest population declines are occurring on the Lassen and Eldorado National Forests study areas (Conner et al. 2013, Tempel and Gutiérrez 2013). Although causative linkages have not been established, the higher rates of decline on these two study areas are coincident with the greater amount and extent of national forest and private lands treatments (see chapter 5 for details on types of treatments used on national forest and private lands since CASPO) within the study areas and surrounding landscapes relative to the Sierra National Forest study site (figs. 7-1 to 7-3). Recent research has indicated that dispersal dynamics and recruitment dynamics across larger landscapes and regions outside of study areas may have significant effects on owl population dynamics within fixed study areas (Schumaker et al. 2014, Tempel et al. 2014, Yakusic et al. 2014; chapter 4). Although there still remains uncertainty regarding the effects of USFS and private land management on California spotted owls and their habitat, the declining owl populations on the three national forest study areas coupled with two studies that show declines related to forest management indicate that forest management remains a threat to California spotted owls and their habitat throughout the Sierra Nevada.

Research on owl habitat associations at the territory-scale clearly demonstrate the importance of dense-canopy stands composed of medium-large trees for owl reproduction, survival, occupancy, and population trends. On the other hand, research documents that when foraging, owls will expand their habitat use to patches of younger forest having shrubs and along habitat edges between mature forest and other vegetation types (Franklin et al. 2000; Irwin et al. 2007, 2013; Williams et al. 2011). Studies relating owl demographic parameters to habitat patterns indicate the importance of territory-scale habitat configurations consisting of core amounts of complex-structured mature forest with intermediate amounts of habitat edges between forest and other vegetation types that produce heterogeneity and foraging habitat. However, neither the optimal mix of patches nor the optimal spatial configuration of vegetation is known. This pattern has also been reported for owls that occupy areas that experience mixed-severity fires including low amounts of stand-replacing fires (e.g., Bond et al. 2009). Thus, California spotted owls may respond favorably to forest management designed to produce fine-scale heterogeneity that benefits prey, such as woodrats, *Neotoma* sp. and *Peromyscus* sp. However, there is significant uncertainty about the amounts of edge and fine-scale heterogeneity that might be beneficial to owls. Little information is available to evaluate how edges created by different mechanisms (e.g., fire versus mechanical treatment) affect the value of habitat over both short and long timeframes. Nevertheless, although incomplete, available information is adequate to formulate hypotheses regarding amounts and patterns of habitat at territory and within-territory scales that could have been tested through adaptive management. This is a suggestion articulated both in CASPO and the Sierra Framework documents, but was not done.

Management in the Sierra Nevada is challenging because of vegetation and topographic variability owing to elevation and latitudinal gradients. This variation is further influenced by multiple ownerships, each of which is managing the land differently. Consequently, landscapes are diverse and subject to a mix of cumulative effects. Despite this reality, most studies center on either the territory-scale and within-territory-scale habitat associations. Less research has been conducted on landscape scales (Zabel et al. 2003). The spotted owl is a territorial species whose spatial organization appears to be structured according to an ideal despotic distribution (Franklin et al. 2000, Zimmerman et al. 2003). Understanding of the relationship between variation in landscape condition and population density and occupancy of owl territories is an important existing information gap to understand the status of owls in the Sierra Nevada, and to predict how density may be affected by changes in habitat proposed under alternative forest management scenarios.

Wildfire

At the time of the CASPO, little information existed about the response of spotted owls to wildfire (Verner et al. 1992). Wildfire was recognized as a potential threat to owl habitat because of increasing fuels loads resulting from fire suppression policies and the vulnerability of owl habitat to high-severity wildfire (McKelvey and Weatherspoon 1992, Weatherspoon et al. 1992).

Wildfire distribution and severity patterns in the Sierra Nevada: 1993–2013—Since CASPO, research has documented an increase in the amount of high-severity wildfire in the Sierra Nevada (Miller and Stafford 2012, Miller et al. 2009). Increases have occurred in both the amounts of high-severity fire and also the percentage of each fire burning at high severity for low- and mid-elevation conifer forest types. Loss of owl habitat to high-severity wildfire is an increasing threat to California spotted owls and their habitat, particularly in the context of climate change, high tree densities, high levels of tree mortality, and high forest fuels loads (Westerling et al. 2006; chapter 5).

Information on wildfire extent and severity patterns is available through the USFS Pacific Southwest Region Fire History database (Miller et al. 2009). About 445 154 ha (1.1 million ac) of conifer, hardwood, and mixed-conifer-hardwood vegetation types within the range of the California spotted owl in the Sierra Nevada experienced wildfire between 1993 and 2013 (table 7-1; figs. 7-5 to 7-8). About 35 612 ha (88,000 ac) of owl protected activity centers (PACs), representing about 15 percent of the total PACs acres, burned during 1993–2013. The PACs are a 121-ha (300-ac) management unit established to protect core nest/roost areas of owl territories (chapters 2 and 3). Recent research has documented the value of PACs as a management strategy (Berigan et al. 2012, Ganey et al. 2014). However, the effect of high-severity wildfire on PACs is of concern. Comparison of overall burn severity patterns in vegetation types that comprise PACs (conifer, hardwood, and mixed-conifer hardwood) across the Sierra Nevada to burn severity patterns in PACs indicates that the percentage of high-severity fire in PACs (28 percent) is similar to the percentage of high-severity fire across all burned acres (hectares) (26 percent). The percentage of moderate-severity fire is slightly higher in PACs (27 percent) versus overall (20 percent), while amounts of low-severity fire (PACs 36 percent, overall 40 percent), and unburned acres within fire perimeters (PACs 11 percent, overall 12 percent) are similar (table 7-1) (Keane, unpubl. data). These results indicate that PACs burned with similar proportions of high-severity fire compared to overall landscape fire severity patterns during 1993–2013. Similar to patterns throughout the Sierra Nevada (Miller et al. 2012), the number of PAC acres (hectares) experiencing fire, and high-severity fire has increased in recent years (fig. 7-9).

Table 7-1—Distribution of wildfire acres by burn severity class in protected activity centers (PACs) and across the range of the California spotted owl in the Sierra Nevada, 1993–2013[a]

	Burn severity class for acres within wildfire perimeters					
	Total acres	Burned acres	High	Moderate	Low	Unburned
			Percent			
Rangewide	7,466,532	1,092,814	26	27	36	11
PACs	557,165	88,021	28	20	40	12

[a] Percentages by burn severity class only include acres for conifer, hardwood, and mixed-conifer-hardwood vegetation type life forms that experienced wildfire. See text for further details.

Sources: Vegetation type life forms from California Fire and Resource Assessment Program 2006 30-m raster; fire severity from U.S. Forest Service (USFS) Pacific Southwest Region (R5) vegetation burn severity data; owl PACS from USFS R5 and Sierra Nevada National Forest management units; owl range from California Department of Fish and Wildlife.

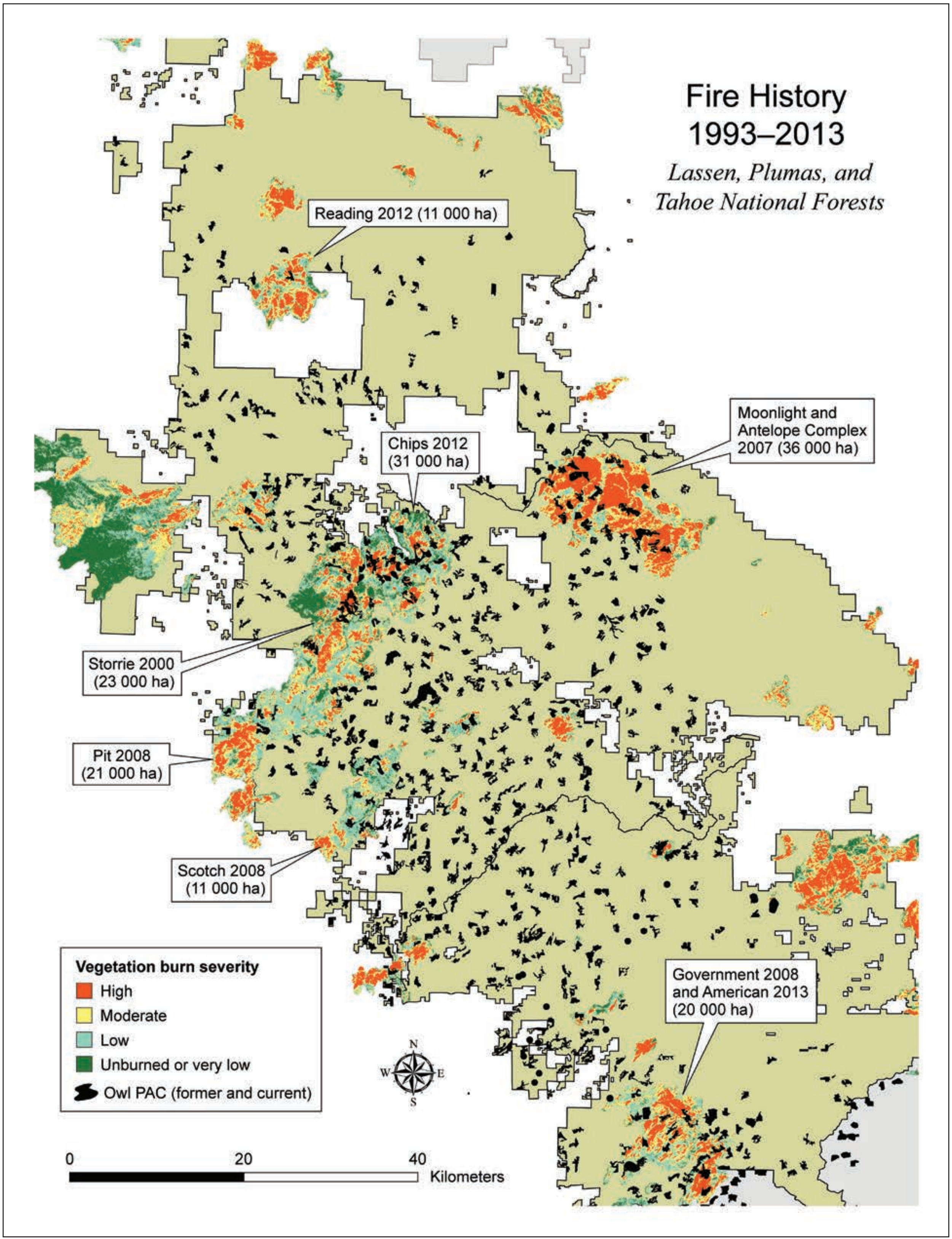

Figure 7-5—Distribution of wildfire hectares (ha) by burn severity class and California spotted owl protected activity centers (PACs) on the Plumas, Tahoe and Lassen National Forests in the northern Sierra Nevada and southern Cascades, 1993–2013.

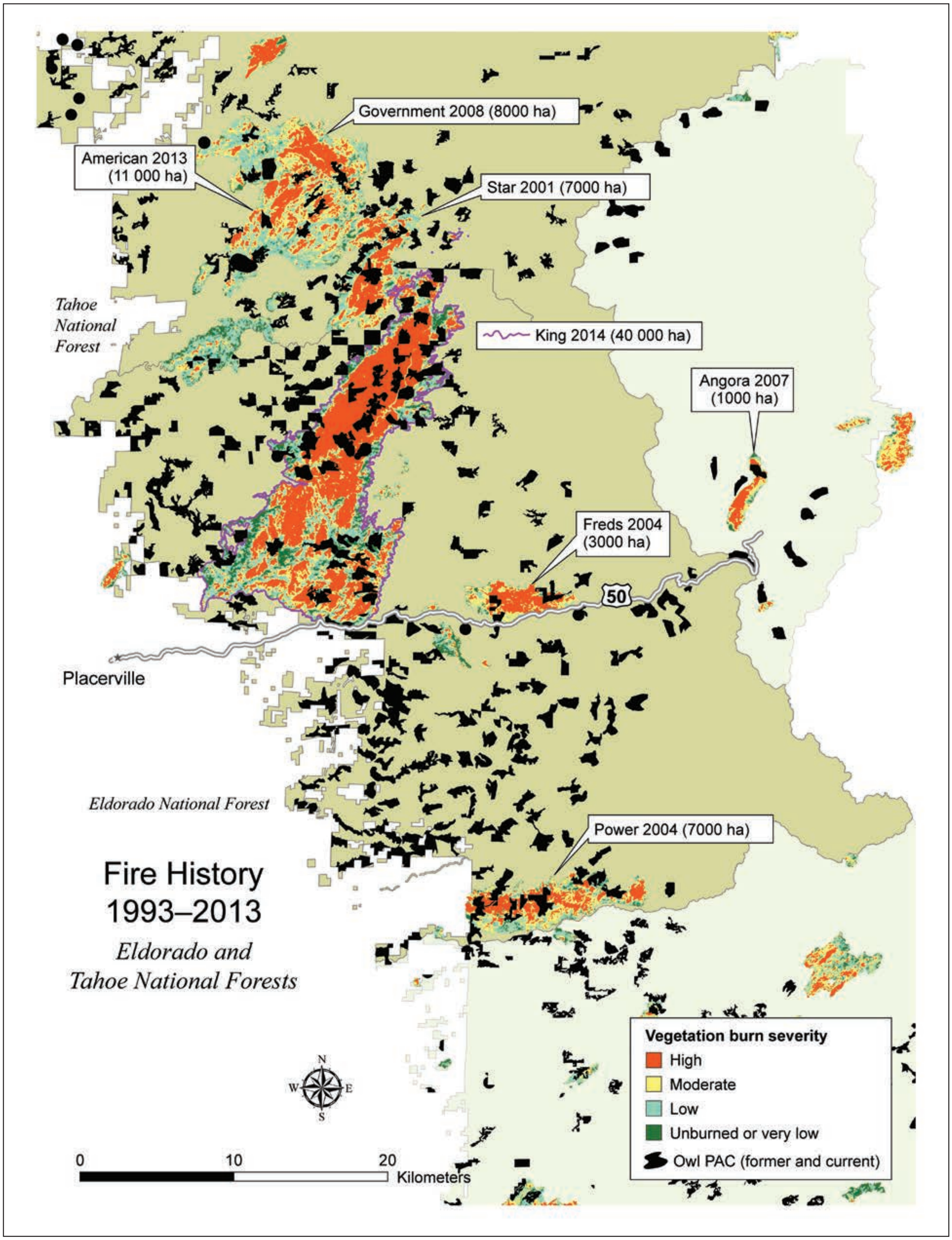

Figure 7-6—Distribution of wildfire acres (ac) by burn severity class and California spotted owl protected activity centers (PACs) on the Tahoe and Eldorado National Forests in the Sierra Nevada, 1993–2013. Includes the 2014 King Fire for comparison.

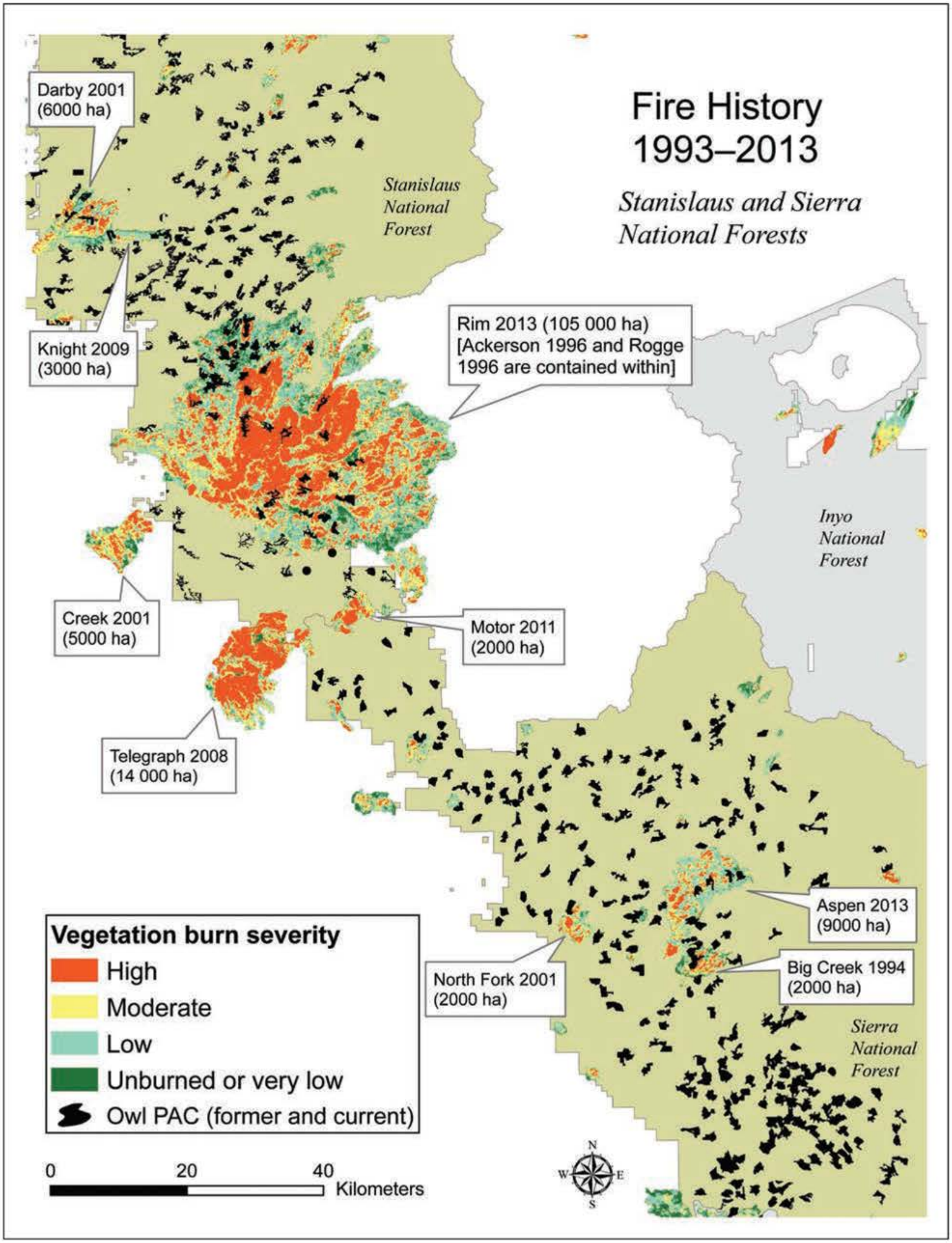

Figure 7-7—Distribution of wildfire hectares (ha) by burn severity class and California spotted owl protected activity centers (PACs) on the Stanislaus and Sierra National Forests in the Sierra Nevada, 1993–2013.

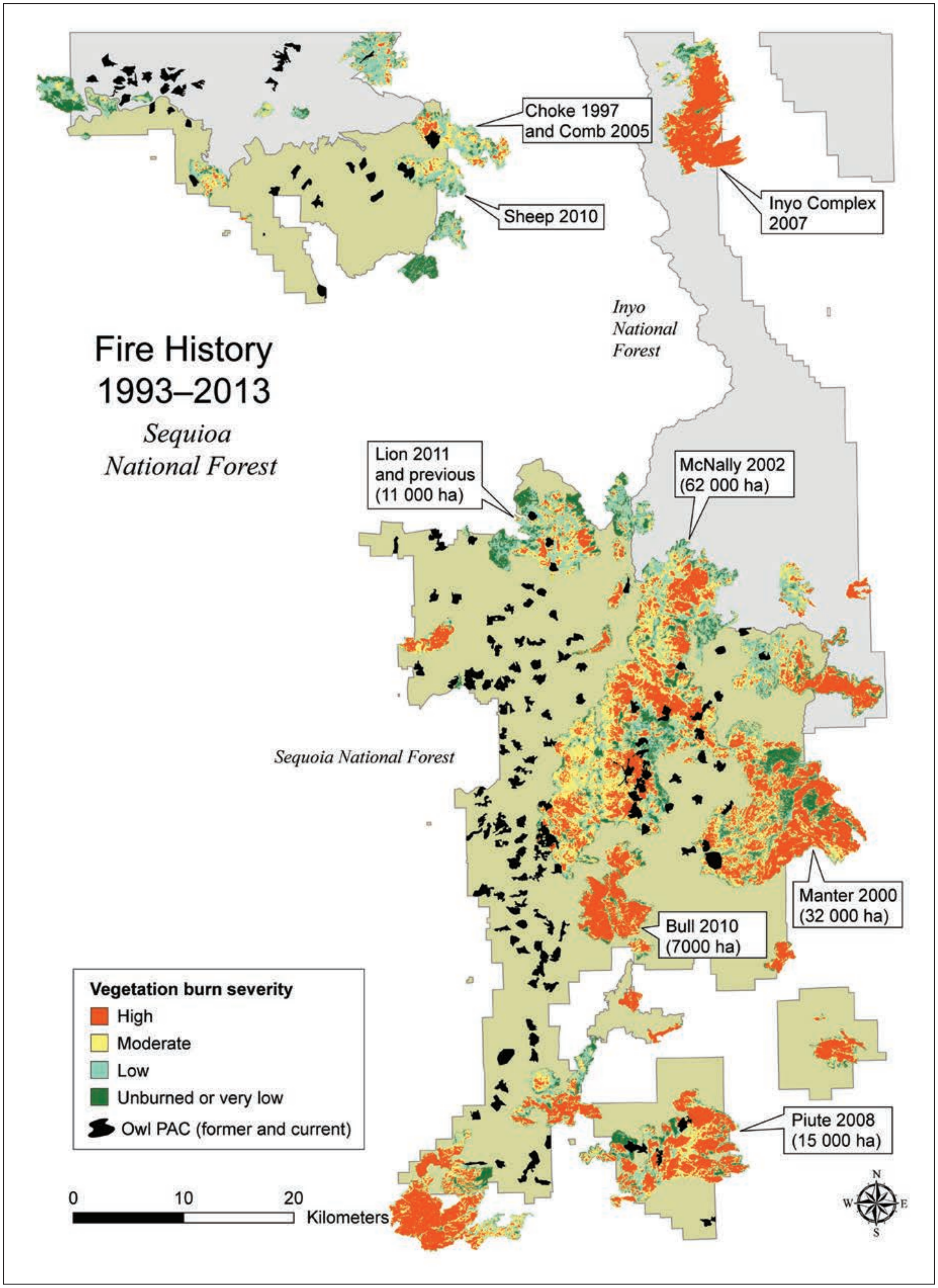

Figure 7-8—Distribution of wildfire hectares (ha) by burn severity class and California spotted owl protected activity centers (PACs) on the Sequoia National Forest in the Sierra Nevada, 1993–2013.

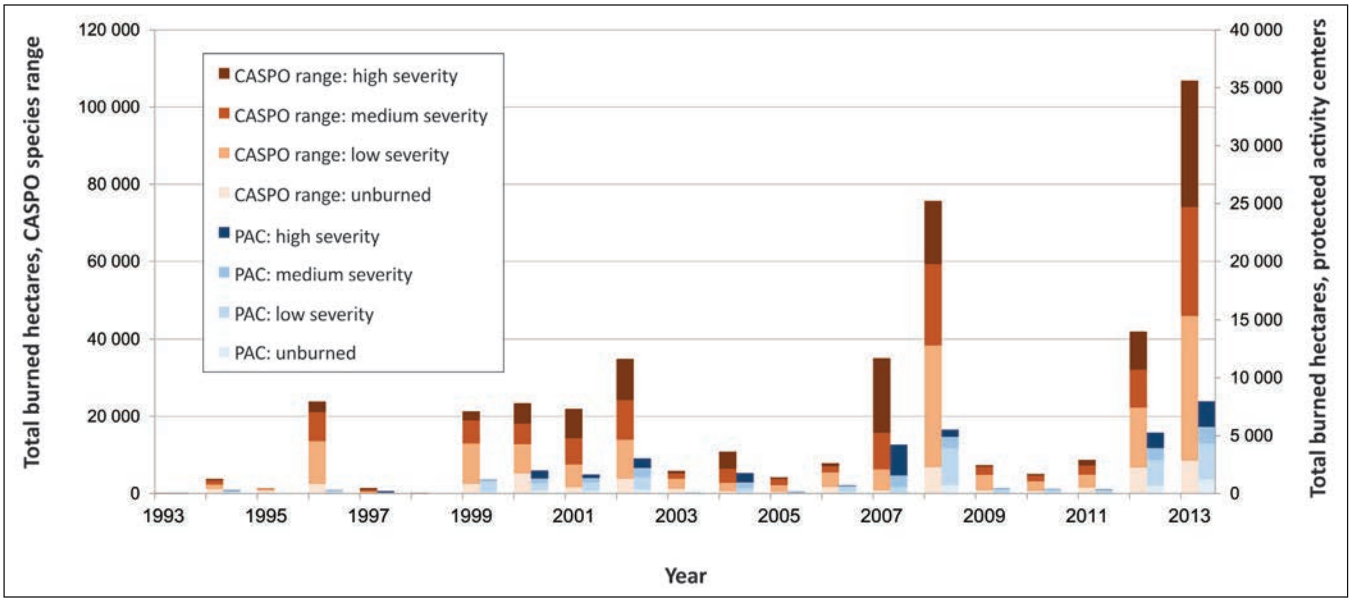

Figure 7-9—Distribution of wildfire hectares (ha) by burn severity class in protected activity center (PAC) and across the range of the California spotted owl by year, 1993–2013. Percentages by burn severity class for conifer, hardwood, and mixed-conifer-hardwood vegetation type life forms only include hactares (ha) within fire perimeters. See text for further details.

California spotted owl–wildfire associations—

Recent research indicates that California spotted owls persist at territories that experience low-moderate severity and mixed-severity (i.e., low-moderate fires with inclusions of high-severity) wildfire (see chapter 3) (Lee et al. 2012, Lee et al. 2013, Lee and Bond 2015, Roberts et al. 2011). Occupancy of sites by owls after fire appears to be a function of the amount of suitable habitat remaining postfire, the amount of suitable habitat burned at high severity, and whether postfire salvage logging is conducted. Available evidence indicates that postfire salvage logging may negatively affect postfire habitat suitability and confounds our understanding of owl response to fire (Lee et al. 2013). However, little is known about how salvage of commercially valuable trees affects owls. Further, no information is available to assess the response of owls to a range of postfire restoration management approaches that might emphasize primary objectives of ecological restoration rather than a sole focus on maximizing commercial value. Experiments are required to compare owl response at territories with and without salvage or postfire restoration management to disentangle the effects of treatments from the effects of high-severity fire, particularly at owls sites where >50 to 100 percent of suitable habitat burns at high severity (Lee et al. 2012, Lee 2013). Clark et al. (2013) concluded that northern spotted owl site occupancy declined in the short term (3 to 5 years) following fire, with postfire occupancy jointly influenced by prefire habitat conditions owing to management, fire severity patterns, and postfire salvage logging. Information on California spotted owl foraging in postfire landscapes is limited to one study conducted at four owl territories that experienced limited amounts of high-severity fire (mean = 9 percent, range 4 to 12 percent of owl home ranges) (Bond et al. 2009, 2013). Further research is needed on owl foraging habitat use across a broader gradient of territories to assess California spotted owl foraging habitat use patterns in postfire landscapes that experience greater total amounts, and increased patch sizes, of high-severity fire. While owls use the edges of high-severity fire patches, it is uncertain if they will use the interior of large patches of high-severity fire, such as the large patches observed in the 2013 Rim and 2014 King Fires.

Current status on the threat of wildfire—

While recent studies indicate that California spotted owls continue to occupy sites that experience low-moderate severity and mixed-severity wildfire, the threshold of the proportion of high-severity fire that owls can tolerate within their territory is unknown. No information exists on long-term survival, reproduction, and fitness of owls within burned territories. Further, no information is available to assess owl foraging behavior and habitat use patterns at territories that experience 50 to 100 percent high-severity fire. There is no information available to evaluate how landscape-scale population density is affected by large fires. These information gaps are important given increases in the amounts and patch sizes of large-scale, stand-replacing fires in the Sierra Nevada (Miller et al. 2009, 2012; chapter 5).

California spotted owls may exhibit both short- and long-term responses to fire. Owls may persist over the short term even when habitat quality is reduced because of site fidelity. No information is available about short- versus long-term occupancy dynamics and demographic relationships to fire and habitat quality. While recent research suggests owls persist in territories after low-moderate and some mixed-severity fire, current and projected future increases in the amount and patch sizes of high-severity fire is an increasing threat to owl viability.

Integration of Forest Management and Wildfire

A key recommendation from CASPO was the need to develop, test, and monitor forest management strategies that reduce fuels accumulation and increase stand and landscape-scale heterogeneity to provide habitat for California spotted owls (McKelvey and Weatherspoon 1992). Limited progress has been made toward evaluating these activities of forest management (see Stephens et al. 2014, Tempel et al. 2014 for examples). Simulation studies have suggested that fuels reduction and forest restoration treatments may be compatible with reducing fire risk and providing owl habitat (Ager et al. 2012, Gaines et al. 2010, Lee and Irwin 2005, Roloff et al. 2012). However, no empirical studies have been conducted to test and validate modelling predictions. Recent work by Tempel et al. (2015) suggests that fuels treatments may provide long-term benefits to California spotted owls if sites experience fire under extreme conditions, but in the absence of fire, fuels treatments can have long-term negative effects on owls. Recent increasing trends in high-severity fire amounts and patch sizes (Miller 2009, Miller and Stafford 2012) coupled with projected future increases in high-severity fire under future climate scenarios (Liu et al. 2013, Westerling et al. 2006) emphasize the risk posed by high-severity fire to owl viability. Comprehensive, spatially explicit population models are not available to estimate how many owls and in what distributional pattern are needed to provide a high probability of sustaining a viable population and how owl population size and territory quality are predicted to change under alternative fuels reduction and forest restoration scenarios. Of particular note, large trees are well-documented to be key habitat elements for owl nesting and roosting; however, large trees are declining across the Sierra Nevada, driven by multiple factors acting separately or synergistically including logging, hazard tree removal, drought, insect mortality, fire suppression (increased stress owing to competition with other trees), wildfire, and climate change (Dolanc et al. 2014, Knapp et al. 2013, Lutz et al. 2009). The fundamental need to develop and test integrated strategies to reduce fire risk, restore forests, and provide habitat for a viable owl population identified by CASPO remains unresolved.

Areas of Concern: Gaps in the Distribution of California Spotted Owls in the Sierra Nevada

Beck and Gould (1992) reported that there appeared to be no gaps in the distribution of owls in the Sierra Nevada. However, they identified eight land areas of concern (AOCs) within the Sierra Nevada where potential gaps in the distribution could develop because of the following conditions: (1) naturally fragmented distribution of habitat and owls, (2) populations become isolated, (3) habitat becomes highly fragmented, and (4) areas where crude density of owls becomes low (table 7-2, fig. 7-10). No research is available to assess change in owl numbers or distribution across each of the AOCs. However, AOCs 2 (Northern Plumas County) and 4 (Northern Eldorado County) could be assessed for the long-term demographic monitoring study areas on the Lassen and Eldorado National Forests where owl populations have been declining (Conner et al. 2013, Tempel and Gutierrez 2013, Tempel et al. 2014) (chapter 4). Extensive forest management treatments have been implemented within AOCs 1 (Lassen County) and 3 (Northeastern Tahoe National Forest), while AOCs 5 (Northwestern Stanislaus National Forest) and 8 (Northeastern Kern County) have experienced extensive wildfire from 1990 through 2013. AOC 7 (Northwestern Sierra National Forest) also has experienced lower levels of disturbance (app. 7-1).

Table 7-2—Descriptions and reasons for areas of concern identified in the assessment of the California spotted owl report

Area number	Name	Reason for concern
1	Lassen County (FS, NPS, IP)	Habitat in this area is discontinuous, naturally fragmented, and poor in quality owing to drier conditions and lava-based soils.
2	Northern Plumas County (FS, IP, pvt.)	A gap in known distribution, mainly on private lands, extends east-west in a band almost fully across the width of the owl's range.
3	Northeastern Tahoe NF (FS, IP, pvt.)	An area of checkerboard lands; much dominated by granite outcrops and red fir forests; both features guarantee low owl densities.
4	Northern Eldorado NF (FS, IP, pvt.)	Checkerboarded lands and large, private inholdings; owl densities unknown on some private lands and very low on others.
5	Northwestern Stanislaus NF (FS, IP, pvt.)	Has large private inholdings; owl densities unknown on most private lands.
6	Southern Stanislaus NF (FS)	Burned in recent years; the little remaining habitat is highly fragmented.
7	Northwestern Sierra NF (FS)	Habitat naturally fragmented, owing partly to low elevations and dry conditions; fragmentation accentuated by logging.
8	Northeastern Kern County (FS)	Only small, semi-isolated groups of owls in the few areas at elevations where habitat persists at the south end of the Sierra Nevada.

Ownership codes: FS = USDA Forest Service; NF = national forest, NPS = National Park Service; IP = industrial private lands; pvt. = multiple, small, private ownerships.

Source: Verner et al. 1992; fig. 14, p. 47 and discussion p. 45.

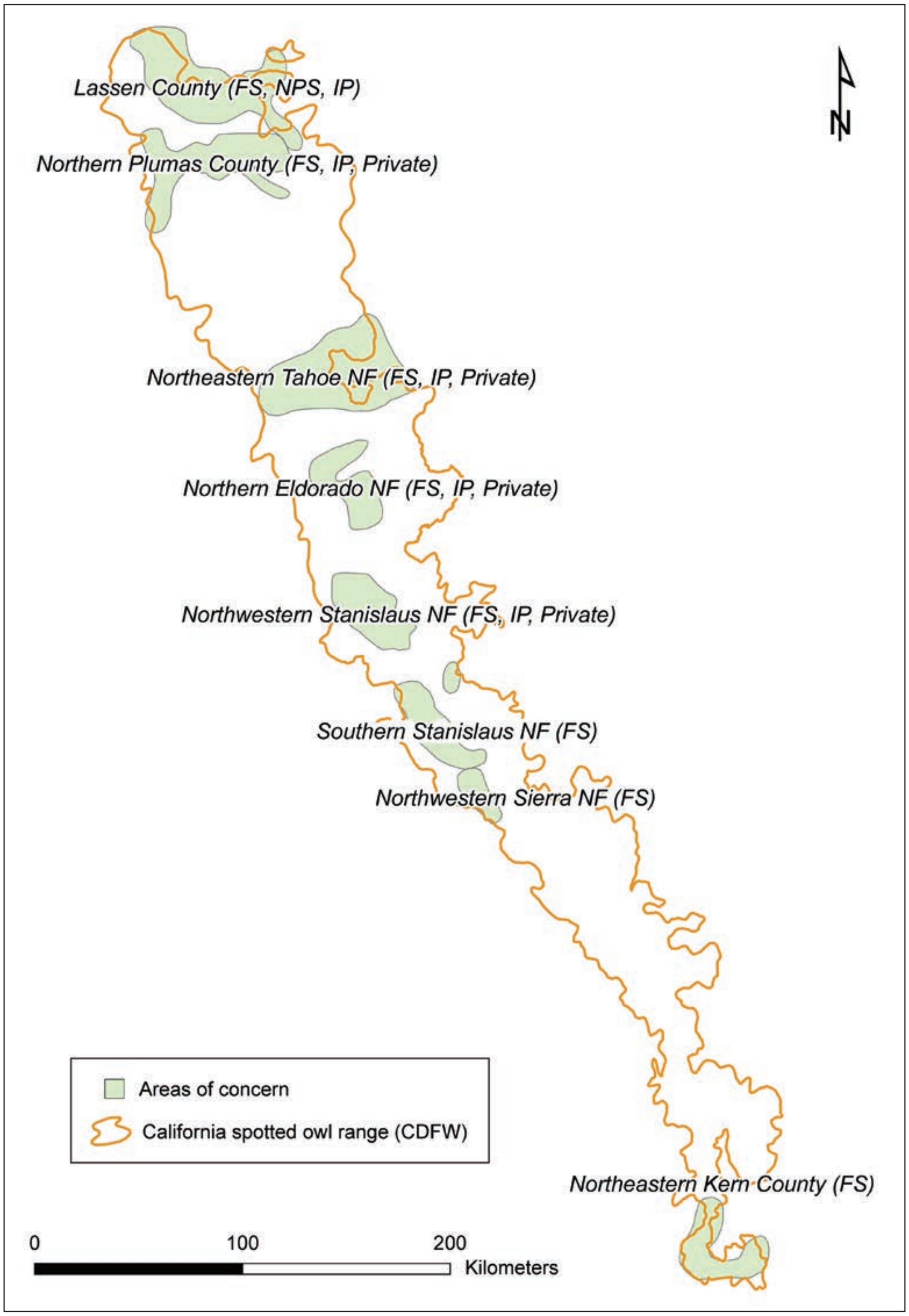

Figure 7-10—Areas of concern identified in the California spotted owl assessment area (CASPO) report (1992) where land ownership, topographic features, habitat fragmentation or amounts that may lead to future gaps in the distribution of California spotted owl populations or habitat in the Sierra Nevada. FS = Forest Service, NPS = National Park Service, IP = private industrial lands, CDFW = California Department of Fish and Wildlife.

Available evidence indicates that the threat of gaps in distribution has likely increased since CASPO. Documented owl population declines in AOCs 2 and 4, along with uncertainty about the status of owls within AOCs 1, 3, 5, and 8 where extensive forest management treatments have occurred, contribute to the increased threat. Development of gaps in owl distribution in the Sierra Nevada could have negative demographic effects because dispersal among geographic areas likely would be reduced. Spotted owls in the Sierra Nevada have low genetic diversity (chapter 4), and future fragmentation and isolation of owl populations within the Sierra could lead to further reductions in genetic diversity.

Human Development

McKelvey and Weatherspoon (1992) identified human population growth as a threat to owls and their habitat within the low to mid elevations of the Sierra Nevada. No information is available to evaluate effects of human population and residential development growth on owls and their habitat. Low- and mid-elevation zones of the west slope of the Sierra Nevada continue to experience growing human populations, expansion of communities, and increased dispersed, low-density housing (FRAP 2010). These human-induced changes result in habitat loss, habitat degradation, disturbance, and increased fuels treatments and forest thinning in wildland-urban-interface (WUI) zones to protect communities. About 50 percent of known owl sites occur within WUIs. Despite extensive forest management conducted within WUIs, no monitoring studies have been conducted to evaluate effects. These sites provide an opportunity to examine, retrospectively, the effects of fuels treatments and forest thinning on owls and their habitat.

Evaluation of Emerging Threats

Barred Owls

Barred owl range expansion has posed a significant threat to the viability of the northern spotted owl (Gutiérrez et al. 2007, Weins et al. 2014). Along with past and current habitat management, barred owls are considered a primary threat to northern spotted owl persistence (USFWS 2011). Barred owls have invaded western North America over the past century (Livezey 2009). Barred owls were first documented in British Columbia in 1943, and have dispersed southward through Washington, Oregon, and California (USFWS 2011). They are now sympatric across the entire range of the northern spotted owl (Gutiérrez et al. 2007). Barred owls are currently expanding their range into the Sierra Nevada and are an increasing threat to California spotted owls (Dark et al. 1998, Keane 2014).

Ecology and interactions with spotted owls—
Gutiérrez et al. (2007) predicted that two similar-sized, congeneric owls in newly established areas of sympatry would likely compete and that stable coexistence was unlikely. Recent work indicates this is occurring through competition for food and habitat as well as interference competition with barred owls being the dominant species (Dugger et al. 2011; Wiens et al. 2014; Yackulic et al. 2012, 2014). For example, northern spotted owl detection rates and site occupancy probabilities are lower in the presence of barred owls (Bailey et al. 2009; Crozier et al. 2006; Dugger et al. 2011; Kroll et al. 2010; Olson et al. 2005; Yackulic et al. 2012, 2014), with increased extinction probabilities and decreased colonization probabilities when barred owls are present (Dugger et al. 2011, Olson et al. 2005, Yackulic et al. 2014).

Dugger et al. (2011) reported that site occupancy dynamics of northern spotted owls were correlated through an additive interaction of habitat and barred owls. Extinction probabilities increased as the amount of old-forest habitat decreased around core areas, and these probabilities increased by a factor of two to three times when barred owls were detected. Colonization probabilities ranged from 0.33 to 0.73 and decreased with increasing fragmentation of older forest around core areas, and were much lower (0.03 to 0.20) when barred owls were detected. Occupancy probabilities increased when the proportion of old forest increased, and decreased with increasing fragmentation, and occupancy probabilities decreased dramatically when barred owls were present regardless of habitat condition (Dugger et al. 2011). Dugger et al. (2011) also noted that barred owls were increasing on their study area and had not reached an equilibrium population size and that the relationship between habitat and barred owls may change as barred owls continue to increase.

Yackulic et al. (2012) modeled hypothesized relationships between barred owls on spotted owls. Theoretically, these relationships were influenced by local and regional population sizes of each species that affects the numbers of recruits available for colonization (Yackulic et al. 2012), and dynamic patterns of competition that shift over time in response to the populations sizes of both species and amounts of important habitat types (Yackulic et al. 2014). Yackulic et al. (2012) also predicted that both the regional occupancy status of barred owls (i.e., regional population size available to produce recruits) and habitat were important factors affecting barred owl site occupancy dynamics. In contrast to previous speculation that habitat constraints would limit expansion of barred owls, Yackulic et al. (2012) concluded that habitat segregation would not likely limit either habitat use by barred owls or its numerical increase.

Yackulic et al. (2014) extended their previous work by examining the joint occupancy dynamics of barred and spotted owls over a 22-year period, as well as how intraspecific and interspecific occupancy dynamics were related to local competition, habitat, and local and regional population sizes. Dynamic changes in the availability of recruits to colonize sites for each species and their overlap in preferred habitat appeared to be key factors in determining the role of competition. Yackulic et al. (2014) found that including competition between the two species at the site scale resulted in increased extinction probabilities for spotted owls and reduced equilibrium occupancies, or population sizes, but was unlikely to lead to full competitive exclusion under the hypothesized scenarios they examined.

Competition between barred and spotted owls is likely because of broad overlap in their habitat use and diets (Hamer et al. 2001, 2007; Wiens et al. 2014) as well as the aggressive behavior of barred owls. Both species show similar preference for old-forest habitat with large trees and high canopy closures (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014), but barred owls use a broader suite of vegetation types (Hamer et al. 2007, Wiens et al. 2014). Spotted owls tend to use areas with steeper slopes relative to barred owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). Using radio-marked birds, Wiens et al. (2014) estimated that mean overlap in proportional use of habitat types was 81 percent (range = 30 to 99 percent) and that both species used old-conifer forest (>120 years old) in greater proportion to its availability. In addition, both species used riparian-hardwood types along streams for foraging. Spotted owls concentrated foraging and roosting in forest patches with large trees (>19 in [>50 cm] d.b.h.) on steep slopes in ravines, whereas barred owls showed strongest associations with patches of large hardwood and conifer trees on relatively flatter slopes.

Wiens et al. (2014) further investigated spatial patterns of resource use between barred and spotted owls and found that home ranges overlapped between adjacent home ranges but that there was minimal overlap of core-use areas, suggesting that interference competition has resulted in interspecific territoriality. Spotted owl home ranges increased in size as the probability of barred owl presence increased, suggesting that spotted owls expanded their home ranges presumably to avoid barred owls. Further, relative probability of habitat use by spotted owls declined as a function of increased proximity to barred owl core areas. Wiens et al (2014) concluded that the patterns of spatial segregation and habitat use of these sympatric owls provided strong evidence of interference competition. Aggressive interactions between barred owls and spotted owls provided further support for interference competition and indicated that barred owls are the behaviorally dominant species (Van Lanen et al. 2011)

There is significant diet overlap between species, yet barred owls prey on more species (Hamer et al. 2001, Livezey and Bednarz 2007, Wiens et al. 2014). Both species prey primarily on small mammals, including flying squirrels, tree voles, woodrats, pocket gophers, mice, and lagomorphs, but barred owls also prey on a wider variety of terrestrial and aquatic prey, and diurnally active prey such as tree squirrels, birds, and reptiles (Hamer et al. 2001, Wiens et al. 2014). Diet overlap also appears to vary regionally and seasonally possibly because of spatial and temporal variation in prey availability and abundance (Graham 2012, Hamer et al. 2001, Wiens et al. 2014). Wiens et al. (2014) concluded that similarity in habitat use patterns and dietary overlap provided evidence for exploitative competition between the species, and that the magnitude of this competition may vary over space and time in response to variation in prey availability.

Barred owl home ranges are two to four times smaller than those of sympatric spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). Differences in home range sizes are likely a function of differences in diet; presumably the broader diet allows barred owls to meet their energetic demands with less foraging area. Thus, barred owls have the potential to reach population densities two to four times greater than spotted owls. Wiens et al. (2014) provided the first evidence of demographic performance of the species. Over the course of their study, barred owls had higher survival estimates than spotted owls (0.92 vs. 0.81), and barred owl pairs produced an average of 4.4 times more young than spotted owl pairs over the 3-year study period. Spotted owl pairs nesting within 0.9 mi (1.5 km) of a nest used by barred owls failed to successfully produce, and the number of young produced increased linearly with increasing distance from a barred owl core area (Wiens et al. 2014).

Barred owl removal experiments—

Barred owl removal experiments have been started to test the effects of barred owls on northern spotted owls and to assess whether removal may be a feasible management strategy (Diller 2013; Diller et al. 2012; USFWS 2008, 2011). Preliminary results suggested that barred owl presence causes declines in spotted owl occupancy and reductions in spotted owl calling behavior (Crozier et al. 2006, Diller et al. 2012). Diller et al. (2012) removed barred owls from nine historical northern spotted owl sites located on private timberland in northern California. All sites were reoccupied by spotted owls within 1 year. One site was occupied by a female not detected for 7 years, while overall, four sites were occupied by the original resident spotted owls and five sites were occupied by new, unknown spotted owls. Barred owls again displaced spotted owls at three sites in 1 to 4 years after initial removal. Diller et al. (2012) hypothesized that preliminary results suggested that barred owl removal may have broader positive neighborhood effects on spotted owls by increasing density of owls, which serves as a cue to settlement by dispersing owls (see Seamans and Gutierrez 2006).

Barred owl status and distribution within the range of the California spotted owl—

Through 2013, 51 barred and 27 “sparred” (hybrids between the two species) owls, and 1 unknown (fig. 7-11) (Keane, unpublished data) have been detected in the Sierra Nevada. None have been found in either southern or central coastal California. All sightings are incidental because no formal surveys for barred owls have been conducted.

The first record of barred owl detected in the Sierra Nevada was in Lassen County in 1989 (Keane, unpublished data). Only four owls (three barred owls, one sparred owl) were found between 1989 and 2001 and were limited to Sierra, Plumas, and Lassen Counties in the northern Sierra Nevada and southern Cascade Range (Dark et al. 1998, Keane unpublished data). There was an extensive survey effort by the USFS to inventory spotted owls from 1987 through 1992, which established a baseline for barred owls. Detections of barred and sparred owl increased between 2002 and 2013, largely because of increased spotted owl survey effort on spotted owl demographic study areas in the northern Sierra and southern Cascade Range. The first detections in the central and southern Sierra Nevada were in 2004 (Seamans et al. 2004, Steger et al. 2006). Six barred owls were detected in the southern Sierra Nevada during 2011–2012. The number of barred and sparred owls on the four long-term demographic study areas has remained low, although they may be increasing gradually in the northern Sierra Nevada, with eight barred and two sparred owls present on the Lassen National Forest demography study area in 2013. This is the pattern observed in the range of the northern spotted owl—a slow increase followed by a rapid one.

The invasion of the barred owl into the Sierra Nevada poses a significant threat to California spotted owls. Based on the limited observations discussed above, it is possible that they will ultimately colonize the entire Sierra Nevada. Without control efforts, barred owls can potentially become a primary threat to the California spotted owl in the Sierra Nevada.

Climate Change

Climate change is projected to have significant effects on Sierra Nevada forests (GEOS Institute 2013[3] Lenihan et al. 2008; chapter 5). Long-term climate change may have both direct and indirect effects on the owl. Increases in temperature and

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[3] **GEOS Institute. 2013.** Future climate, wildfire, hydrology, and vegetation projections for the Sierra Nevada, California: a climate change synthesis in support of the vulnerability assessment/adaptation strategy process. Unpublished report. On file with: Geos Institute 84 Fourth Street, Ashland, OR 97520.

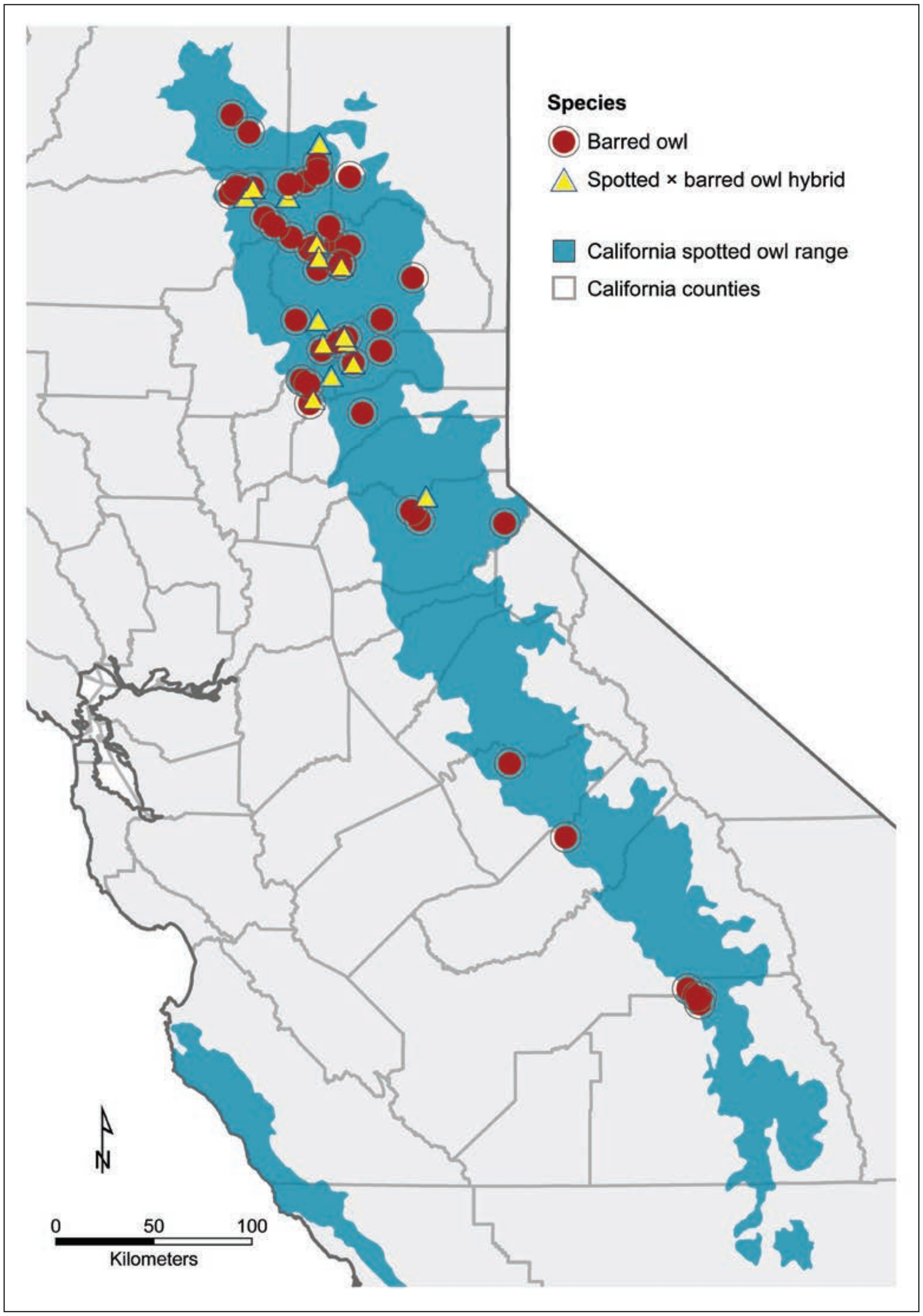

Figure 7-11—Barred owl and sparred owl records within the range of the California spotted owl in the Sierra Nevada, 1989–2013.

changes in precipitation patterns may have direct effects on spotted owl physiology, survival, reproduction, recruitment, and population growth. Climate change may also precipitate indirect effects such as (1) geographical shifts in habitat distribution, abundance, and quality; (2) increase of high-severity wildfire; (3) increase in mature/large tree mortality caused by insects and disease; (4) changes in prey distribution, abundance, and population dynamics; (5) changes in interspecific interactions with competitors and predators; and (6) changes in disease dynamics associated with changing temperature and precipitation patterns.

Weathers et al. (2001) determined the thermal profile, upper and lower critical temperatures, and basal and field metabolic rates of California spotted owls. The thermal neutral zone ranged from 18.2 to 35.2 °C. Above the upper critical temperature, owls experienced heat stress at rates greater than predicted for birds of similar size. Many studies have documented the negative effects of wet, cold weather during the winter and early-breeding season on spotted owl reproduction (Dugger et al. 2005, Franklin et al. 2000, Olson et al. 2004), survival (Franklin et al. 2000, Glenn et al. 2011, Olson et al. 2004), recruitment (Franklin et al. 2000), and population growth (Glenn et al. 2010). Wet, cold winter weather may increase energetic demands on owls by raising thermoregulation energy costs or reducing availability of prey and hunting success during inclement weather, which may negatively affect survival and reproduction. Wet, cold weather during the early breeding season may affect spotted owls by reducing egg viability owing to chilling, cause direct mortality of nestlings, or lower prey abundance or availability (Rockweit et al. 2012). Inclement winter weather may also affect recruitment through overwinter mortality of dispersing juvenile spotted owls (Franklin et al. 2000; Glenn et al. 2010, 2011).

Increases in late summer precipitation have been linked to increased survival, recruitment, and reproduction (Glenn et al. 2010, 2011; Olson et al. 2004; Seamans et al. 2002). Late-season precipitation may either reduce negative effects of summer drought, support greater plant production and primary productivity such as seeds and fungi that are important food for small mammal prey, or support increases in prey species abundance and availability. Drought and hot temperatures during the previous summer have been linked to lower survival and recruitment of spotted owls (Franklin et al. 2000, Glenn et al. 2011).

Across their range, spotted owls exhibit population-specific demographic responses to local weather and regional climates (Franklin et al. 2000; Glenn et al. 2010, 2011; Peery et al. 2012). These results indicate that population-specific variation may lead to population-specific responses to future climate scenarios, which may range from neutral to significantly negative effects and increased vulnerability (Glenn 2011, Glenn et al. 2010, Peery et al. 2012).

Glenn et al. (2010, 2011) investigated relationships among survival, recruitment, and population growth rate of six northern spotted owl populations in Oregon and Washington relative to local weather and regional climate. Local weather and regional climate variables explained 3 to 85 percent of the annual variation in growth rate in these populations, with the relative importance of weather and climate factors varying among the six populations. Peery et al. (2012) similarly found evidence for population-specific and regional variation in the relationship between spotted owl survival and reproduction with climate and projected response to future climate scenarios. Mexican spotted owl populations in New Mexico and Arizona were negatively associated with hot, dry conditions, and populations were projected to decline rapidly under future climate scenarios. In contrast, a population of California spotted owls in the mountains of southern California was negatively associated with cold, wet springs, with the population projected to exhibit low response to projected future climate conditions. In general, projected population growth rates were more affected by changes in temperature than precipitation, and by stronger climate effects on reproduction than survival (Peery et al. 2012).

Seamans and Gutiérrez (2007b) reported that temperature and precipitation during incubation most affected reproductive output, and conditions in winter associated with the Southern Oscillation Index (SOI) most affected adult survival on the Eldorado National Forest. Weather variables explained a greater proportion of the variation in reproductive output than they did survival. Further, these two weather variables were also included in the best models predicting annual population growth rate (Seamans and Gutiérrez 2007b). Subsequently, MacKenzie et al. (2012) found that SOI or other weather variables explained little variation in annual reproduction for this same population of owls over a longer time series. Unlike results for California spotted owls in southern California reported in Peery et al. (2011), subsequent analyses testing for effects of weather variables on demographic parameters showed no clear temporal associations for owls on the Eldorado National Forest in the Sierra Nevada. Other than the assessment conducted for the population of California spotted owls in the mountains of southern California (Peery et al. 2012), no studies have conducted similar analyses relating spotted owl demographic parameters (survival, reproduction, recruitment, and population growth) to climate variables and subsequently projected population growth under future climate scenarios for any California spotted owl populations in the Sierra Nevada.

In addition to direct effects on spotted owl vital rates, climate-induced changes in temperature, precipitation, and water moisture may lead to shifts in the distribution of California spotted owls. Siegel et al. (2014) assessed the potential vulnerability of California spotted owls in the Sierra Nevada to future climate scenarios using

NatureServe's Climate Change Vulnerability Index (CCVI) and predicted California spotted owls to be presumed stable over the next 50 years under the climate scenarios they investigated. Carroll (2010) recommended that ecological niche models based on temperature and precipitation envelopes have value for projecting potential effects of climate change on spotted owl distribution, although these types of coarse models have limitations because they do not incorporate additional important factors. A more rigorous assessment of climate change on spotted owls requires development of dynamic models that relate owl vital rates or occupancy to vegetation dynamics and effects of competitor and key prey species, in addition to climate variables.

Responses of California spotted owls to climate change are likely to be governed by complex interactions of factors that directly affect owls and their habitat, as well as indirect factors that can affect habitat (e.g., insect pests, disease, increased fire risk, vegetation type conversions, and distributional shifts) and ecological relationships (e.g., disease, competitors, predators, prey). While ecological niche models suggest that projected changes in temperature and precipitation may have minimal effects on California spotted owl distribution in the Sierra Nevada, results from demographic assessments and projections suggest that future climate change may have population-specific effects that likely will vary over geographical, elevational, and ecological gradients. Further, climate change projections of future vegetation distribution in the Sierra Nevada suggest that much of the low- and mid-elevation forests that currently comprise owl habitat are vulnerable to conversion of forests to woodlands, shrublands, and grasslands, especially with increased fire probabilities (chapter 5).

Climate change has emerged as a threat to California spotted owls in the Sierra Nevada given uncertainty regarding direct and indirect effects on owls and the potential for significant effects on the distribution and amounts of owl habitat. This threat may be partially mitigated over ecological time scales if mixed-conifer forests advance upslope, thereby providing habitat for owls where none now exists (e.g., Peery et al. 2012). However, it should be recognized that individual plant species exhibit species-specific responses to changes in temperature and precipitation, with vegetation communities reorganizing as a result of individual species responses (Briles et al. 2011; Davis 1981, 1986). Climate change may result in novel future vegetation communities that differ in species composition and richness relative to contemporary communities. Further, large trees that function as nest trees for owls and help moderate within-stand temperatures require many decades to centuries to attain large diameters and complex structures. Thus, it may require long time periods to develop the large tree vertical structure used by owls in areas where such structure does not now exist.

Disease, Parasites, and Contaminants

Little information exists on disease prevalence in spotted owl populations, and no information exists about the effects of disease on individual fitness or population viability. West Nile virus (WNV), a primarily mosquito-borne flavivirus that was first detected in eastern North America in 1999 and then throughout California by 2004, has been a concern (Reisen et al. 2004). West Nile virus has been demonstrated to be highly lethal to owls (Gancz et al. 2004, Marra et al. 2004). The primary route of infection is through the bite of an infected mosquito, with secondary routes of infection possible through consumption of infected prey and possibly feces (Kipp et al. 2006, Komar et al. 2003).

There has been no evidence to indicate that WNV has affected California spotted owl populations. Hull et al. (2010) screened samples for WNV antibodies from 209 California spotted owls collected from the southern (Sierra National Forest, Sequoia and Kings Canyon National Parks) or northern (Plumas and Lassen National Forests) Sierra Nevada during 2004–2008. Positive test results for antibodies would indicate exposure and survival (Hull et al. 2010). Results were negative for all 209 California spotted owls. Hull et al. (2010) hypothesized that populations either may have had little to no exposure to WNV, or infected birds had high mortality and were not available to be sampled, or no birds attained detectable immune response by antibody titers. However, because spotted owls have high annual survival rates, it is possible that WNV has not yet made a large impact on these birds (Blakesley et al. 2010, Conner et al. 2013). Because there is no general surveillance program through the Sierra Nevada, it has been unclear if owls have been locally affected by WNV or if climate change will change the disease dynamics.

Several species of ectoparasites (Hunter et al. 1994, Young et al. 1993), endoparasites (Gutiérrez 1989; Hoberg et al. 1989, 1993), and blood parasites (Gutiérrez 1989, Ishak et al. 2008) have been identified in spotted owls. Gutiérrez (1989) reported 100 percent blood parasite infection rates across all three spotted owl subspecies, suggesting long-term adaptation to high parasitism rates. Ishak et al. (2008) reported a prevalence of 79 percent for blood parasites of California spotted owls in the northern Sierra Nevada, with 79 percent of individuals positive for at least one infection, while 44 percent of individuals tested positive for multiple infections (Ishak et al. 2008). Ishak et al. (2008) reported that infection rates were higher in California spotted owls (79 percent) than in northern spotted owls (52 percent) and west coast barred owls (15 percent). Ishak et al. (2008) documented the first case of a *Plasmodium* sp. infection in a northern spotted owl and noted that barred owls may pose the risk of introducing novel infections into spotted owl populations. High rates of infection in California spotted owls compared to barred owls may position them at a competitive disadvantage compared to barred owls (Ishak et al. 2008), or the opposite could be true. The potential effects of parasites on spotted owl behavior, survival, or reproductive success has not been studied. However, disease and parasites can interact with other stressors to affect the condition of individuals, resulting in lower survival or other impacts.

Environmental contaminants have not been identified as potential ecological stressors on California spotted owls. However, recent reports of high exposure rates of fisher (*Pekania pennanti*) to rodenticides, likely associated with illegal marijuana cultivation, across the southern Sierra Nevada (Gabriel et al. 2012) may have implications for spotted owls and other forest carnivores, as they feed extensively on rodents. Ongoing research has reported 62 percent exposure of barred owls (44/71 owls) to rodenticides on the Hupa Reservation in northern California.[4]

Available evidence suggests that disease and parasites do not pose a significant threat at the current time, although WNV remains a possible future threat. Rodenticides pose a significant emerging threat to California spotted owls, though no information is available at the time to evaluate the magnitude and demographic consequences of this threat. High exposure rates recently recorded in barred owls in an area where they are sympatric with spotted owls indicates that spotted owls likely have experienced high exposure rates given broad dietary overlap between the species.

Human Recreation and Disturbance

Disturbance resulting from human recreation and management activities can potentially affect California spotted owls. Impacts from recreation can range from the presence of hikers near owl nests and roosts to loud noises made by chainsaws or motorized vehicles. Additionally, disturbances can be acute (short term) or chronic (long term) depending on the type of impact. Measures of behavioral response or fecal corticosterone hormone levels (hormones that reflect stress) have been used to assess spotted owl response to disturbance.

Mexican spotted owls exhibited low behavioral responses of any type to hikers who were ≥55 m (≥180 ft) distance, and juveniles and adults were unlikely to flush from hikers at distances >12 or >24 m (>39 or 78 ft), respectively (Swarthout and Steidl 2001). Additionally, owls did not change their behavior when hikers were near nests, although cumulative effects of high levels of recreational hiking near

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[4] **Higley, M. 2016.** Personal communication. Wildlife biologist, Hoopa Valley Tribal Forestry, 40 Orchard St., Hoopa, CA 95546.

nests may be detrimental (Swarthout and Steidl 2003). No differences in reproductive success were observed between Mexican spotted owl nests exposed to helicopter and chainsaw noise; however, owls exhibited behavioral responses to both stimuli but with greater behavioral response to chainsaw noise than helicopter noise (Delaney et al. 1999). Results from this study supported management guidelines of a 400-m (0.25-mi) disturbance buffer around active Mexican spotted owl nests. Wasser et al. (1997) reported higher corticosterone levels in male northern spotted owls within 0.41 km (0.25 mi) of roads in Washington, suggesting that higher stress levels were correlated with proximity to roads. In contrast, Tempel and Gutiérrez (2003, 2004) found little evidence for disturbance effects from chainsaws and roads, as measured by fecal corticosterone hormone levels for California spotted owls in the central Sierra Nevada. Recently, Hayward et al. (2011) reported a more complex association between road noise and northern spotted owl response on the Mendocino National Forest in California. They found no association between baseline hormone levels and distance to roads. Rather, owls had higher corticosterone levels when exposed to continuous traffic exposure, and they found that owl response may vary with age of owls and physiological body condition. Of note, they reported lower reproductive success for owls near roads with continuous loud noise versus owls near quiet roads.

The effect of disturbance will likely remain high across the Sierra Nevada, but probably localized in space and time. Current limited operating period (LOPs) management standards and guidelines used on national forest lands that limit noise within 400 m of nest/roost areas during the nesting period appear effective for mitigating acute, direct noise and activity disturbance on owls at the project level.

Genetics

Current information supports the subspecies classification of California spotted owls. Further, genetic differences between California spotted owl populations in the Sierra Nevada and southern California owls suggests that these populations could be considered as distinct management units. Within the Sierra Nevada, genetic variation is low, raising concern that adaptation to future environmental change may be constrained (chapter 4). Further reduction in genetic diversity of owls in the Sierra Nevada is likely to be an increasing threat if current population declines continue and gaps in owl distribution develop. However, the types of genetic assays completed so far are not reflective of adaptive genetic traits, so additional genetic work needs to be done.

Chapter Summary

California spotted owls are faced with significant threats. Overall, the population of this subspecies appears to be declining, although population trajectories differ between national forest and national park lands (see chapter 4). The CASPO identified timber harvest and even-aged forest management, fire suppression and increased wildfire, potential development of gaps in distribution, and human development as threats to these owls (Verner et al. 1992). These threats have remained or increased since publication of the CASPO report. Since CASPO, range expansion of barred owls, climate change, contaminants, and low genetic diversity have arisen as additional significant threats.

Forest management remains a primary factor for California spotted owl habitat and populations on national forest and private industrial forest lands. Timber harvest on national forest lands has declined over the past few decades and most timber volume taken from the Sierra Nevada is harvested from private land. McKelvey and Weatherspoon (1992) identified both even-aged forest management and fire suppression as threats to California spotted owls and their habitat. They recommended development and experimental evaluation of forest management strategies to reduce fuel accumulation and the presence of ladder fuels and their associated risk of high-severity fire; increase vegetation heterogeneity at stand and landscape scales; and produce habitat to maintain populations of California spotted owls. Little progress has been made toward testing the effects of forest management strategies and silvicultural prescriptions that reduce wildfire risk on California spotted owls and their habitat, even though many treatments have occurred since CASPO (but see Stephens et al. 2014 and Tempel et al. 2014 for exceptions). Forest management practices on both national forest and private lands have likely exacerbated the concerns expressed in CASPO (Seamans and Gutiérrez 2007a, Stephens et al. 2014, Tempel et al. 2014, Verner et al. 1992). Dominant management activities on national forests have been mechanical thinning and fire suppression, and there is growing recognition that standard prescriptions for thinning to reduce fuels promotes stand homogeneity, as does fire suppression. In addition, even-aged forest management on private lands has likely reduced the amount of older, large-diameter tree, closed-canopy forest habitat. Further, widespread declines in large trees, a key owl nesting and roosting habitat element, have been reported from across the Sierra Nevada. Emerging strategies that protect existing, and increase future recruitment of, large trees integrated with prescriptions that create tree clumps and canopy gaps hold promise for providing favorable habitat conditions for owls while reducing the risk of habitat loss to fire or climate change-driven drought and insect tree mortality.

Much has been learned about California spotted owl response to fire, although significant scientific uncertainty and concern remains regarding effects of large-scale, stand-replacing fire effects on owls and their habitat. Recent increases in the amounts and patch sizes of high-severity fire, such as observed on the 2013 Rim and 2014 King Fires, along with projected future increases in fire activity associated with climate change, indicate the increased risk associated with high-severity fire.

Declining owl populations, uncertainty about effects of Forest Service and private land forest management, and increasing risk of high-severity fire contribute to increased risk of gaps developing within the distribution of the owl in the Sierra Nevada. Owl populations are documented to have declined in two areas of concern identified in CASPO. Continued loss and degradation of habitat because of residential development on private lands, primarily at low and mid elevations, is an increasing threat given continuing human population growth across the west slope of the Sierra Nevada.

Range expansion of the barred owl into the Sierra Nevada poses a significant new threat to California spotted owls. Unlike the situation with northern spotted owls, it is unlikely to have contributed to documented declines of California spotted owls because their density is low and they are largely restricted to the northern Sierra Nevada. However, recent increases in their number and dispersal into the central and southern Sierra Nevada portend an expansion throughout the Sierra Nevada. If such an expansion follows the pattern within the northern spotted owl range, California spotted owls will likely face extirpation. Research has shown that barred owl removal is technically and economically feasible (Diller 2013).

Direct effects of climate change on California spotted owls are difficult to project and may differ along elevational and latitudinal gradients across the Sierra Nevada. Of particular concern are related impacts of climate change such as drought and its indirect impacts on owl habitat characteristics and important habitat elements such as large trees, as well as the potential for vegetation type conversions from conifer forest types to hardwood, shrub, and grass vegetation types within the low- and mid-elevation zones of the Sierra Nevada. Recent reports of wildlife contamination from rodenticides associated with illegal marijuana cultivation in the Sierra Nevada poses an increasing threat to California spotted owls and their prey. To date, no available evidence has demonstrated negative effects of West Nile virus on California owls, though this remains a potential threat given high mortality from this disease that has been observed in many captive owl species. Disturbance from human management and recreational activities does not appear to be a significant threat to California spotted owls as existing standards and guidelines (e.g., LOPs) appear to be sufficient for mitigating direct, short-duration effects of forest management activities (e.g., timber harvest, prescribed fire, etc.), while recreational effects appear to be localized with potential impacts to a few owl sites.

Evaluating the current status of threats to California spotted owls is hampered by lack of reliable information on the current status, and recent trends, of California spotted owl habitat across the Sierra Nevada. Given the preeminent importance of understanding the current status and past trends in owl populations and habitat, lack of such habitat information could be considered a threat to successful owl management and conservation, as well as for comprehensive forest management for wildlife. Further detailed discussion of owl habitat mapping issues is presented in chapter 6.

Based on the best scientific information available, there are significant threats to California spotted owls that have either increased in magnitude or arisen since CASPO (Verner et al. 1992). The most significant primary threats are (1) continued effects of forest management on both public and private land; (2) increasing trends in large-scale, stand-replacing fire; (3) invasion of barred owls; (4) potential climate change direct effects on owl populations or climate-driven vegetation type conversions and increased fire activity; and (5) increasing human population growth and development. Two additional issues that can potentially become significant threats are (1) illegal rodenticide use and (2) West Nile virus. These threats can potentially, functioning singly or in concert, contribute to development of gaps in the distribution of owls, which can have negative demographic consequences for owls. For example, climate change, fire, and forest management activities may interact to limit the amounts and distribution of habitat available to owls, which can be further affected by increases in the barred owl population. This overall threat assessment coupled with documented ongoing declines in owl populations clearly indicates the need for careful management, monitoring, and research to address key uncertainties for these threats.

Significant challenges exist for addressing the multiple threats to owls and for developing forest management strategies that integrate owl conservation needs within the broader context of forest ecosystem management and restoration in the face of increasing fire risk and climate change. Over 20 years have passed and only limited progress has been made toward resolving the questions, threats, and challenges posed in the CASPO report. Progress will involve development and testing forest management strategies, with success predicated upon increased organizational capacity and effective collaboration between management and research.

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Appendix 7-1—Distribution of Forest Management Treatments and Wildfire During 1990–2014 Within the Areas of Concern Identified in the 1992 CASPO Report

The following maps show the distribution of Forest Management Treatments and Wildfire During 1990–2014 Within the areas of concern Identified in the 1992 "The California Spotted Owl: A Technical Assessment of Its Current Status" CASPO report.

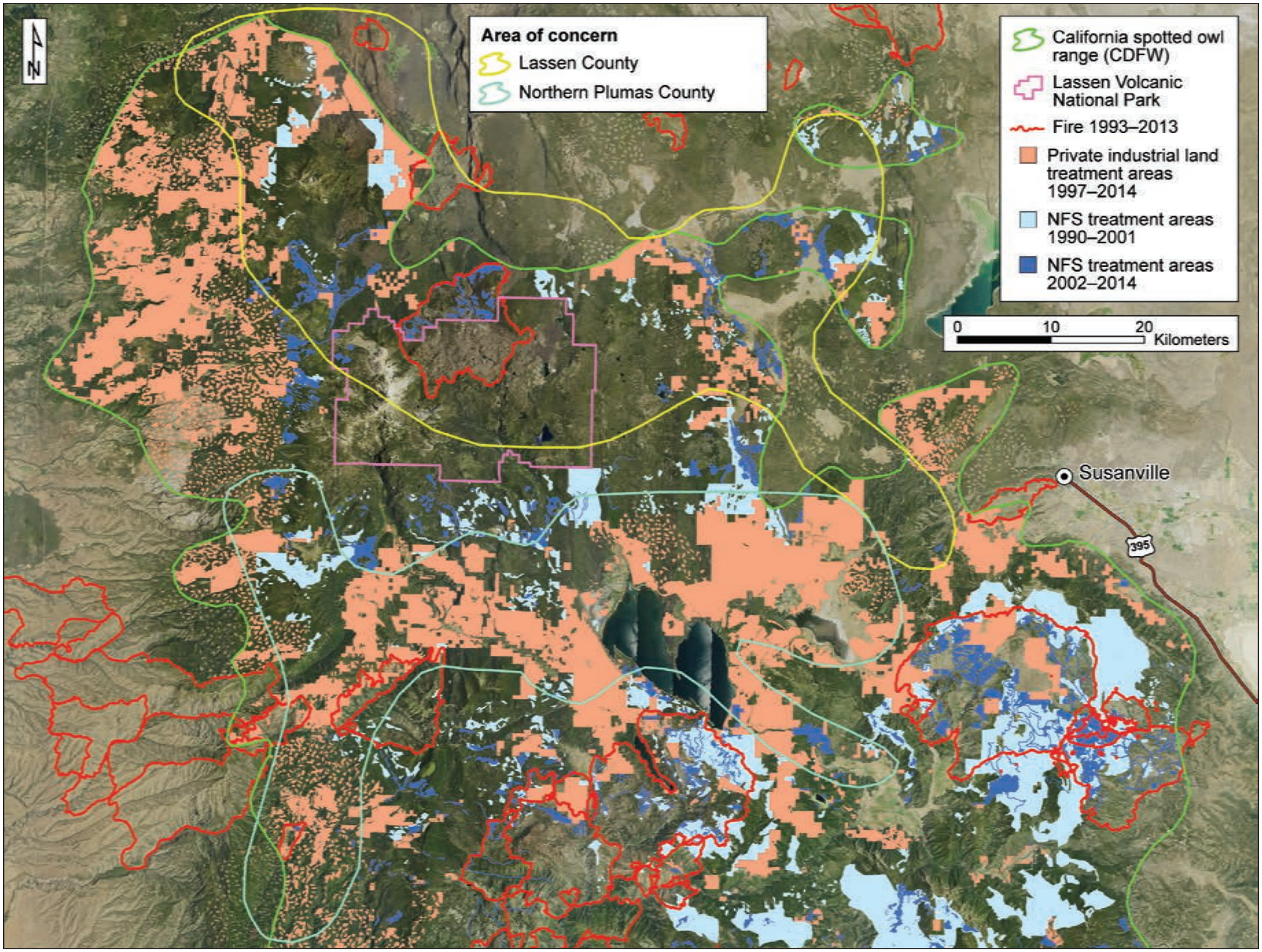

Figure A-1—Distribution of forest management treatments and wildfire on national forest and private industrial forest lands in the California spotted owl assessment (1992) areas of concern 1 (Lassen County) and 2 (Northern Plumas County) on the Plumas and Lassen National Forests, 1990–2014. Sources: National Forest System (NFS) treatments extracted from U.S. Forest Service (USFS) Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Region [R5] silviculturist), private industrial treatments courtesy of California Department of Forestry Forest Practice Geographic Information System (Suzanne Lang), fire perimeters from USFS R5 vegetation burn severity data, National Agricultural Imagery Program photography from U.S. Department of Agriculture Farm Service Agency Aerial Photography Field Office, owl range from California Department of Forestry, and Wildlife (CDFW), owl areas of concern from general technical report PSW-GTR-133 (1992).

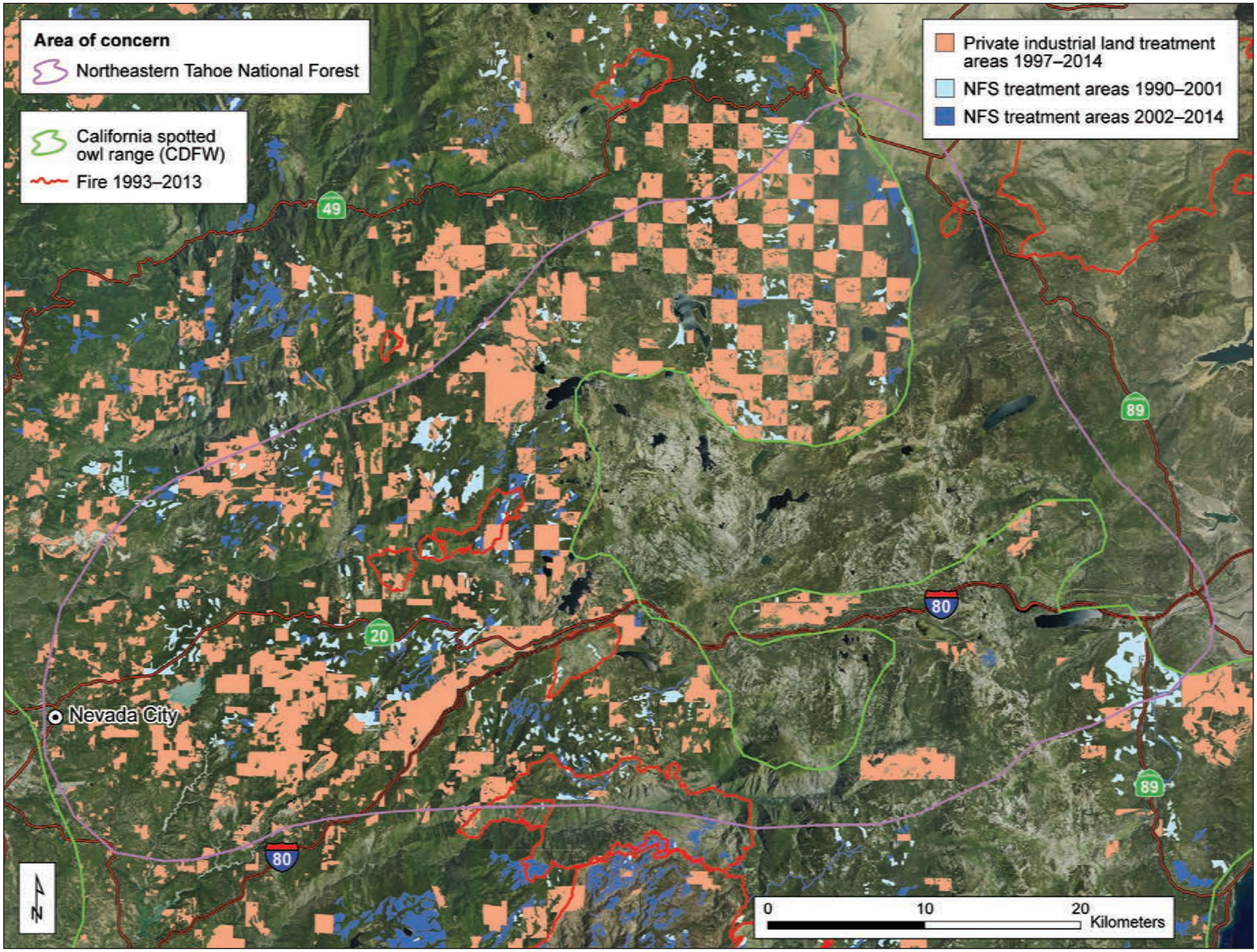

Figure A-2—Distribution of forest management treatments and wildfire on national forest and private industrial forest lands in the California spotted owl assessment (1992) area of concern 3 (Northeastern Tahoe National Forest) on the Tahoe National Forest, 1990–2014. Sources: National Forest System (NFS) treatments extracted from U.S. Forest Service (USFS) Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Region [R5] silviculturist), private industrial treatments courtesy of California Department of Forestry Forest Practice Geographic Information System (Suzanne Lang), fire perimeters from USFS R5 vegetation burn severity data, National Agricultural Imagery Program photography from U.S. Department of Agriculture Farm Service Agency Aerial Photography Field Office, owl range from California Department of Forestry and Wildlife (CDFW), owl areas of concern from general technical report PSW-GTR-133 (1992).

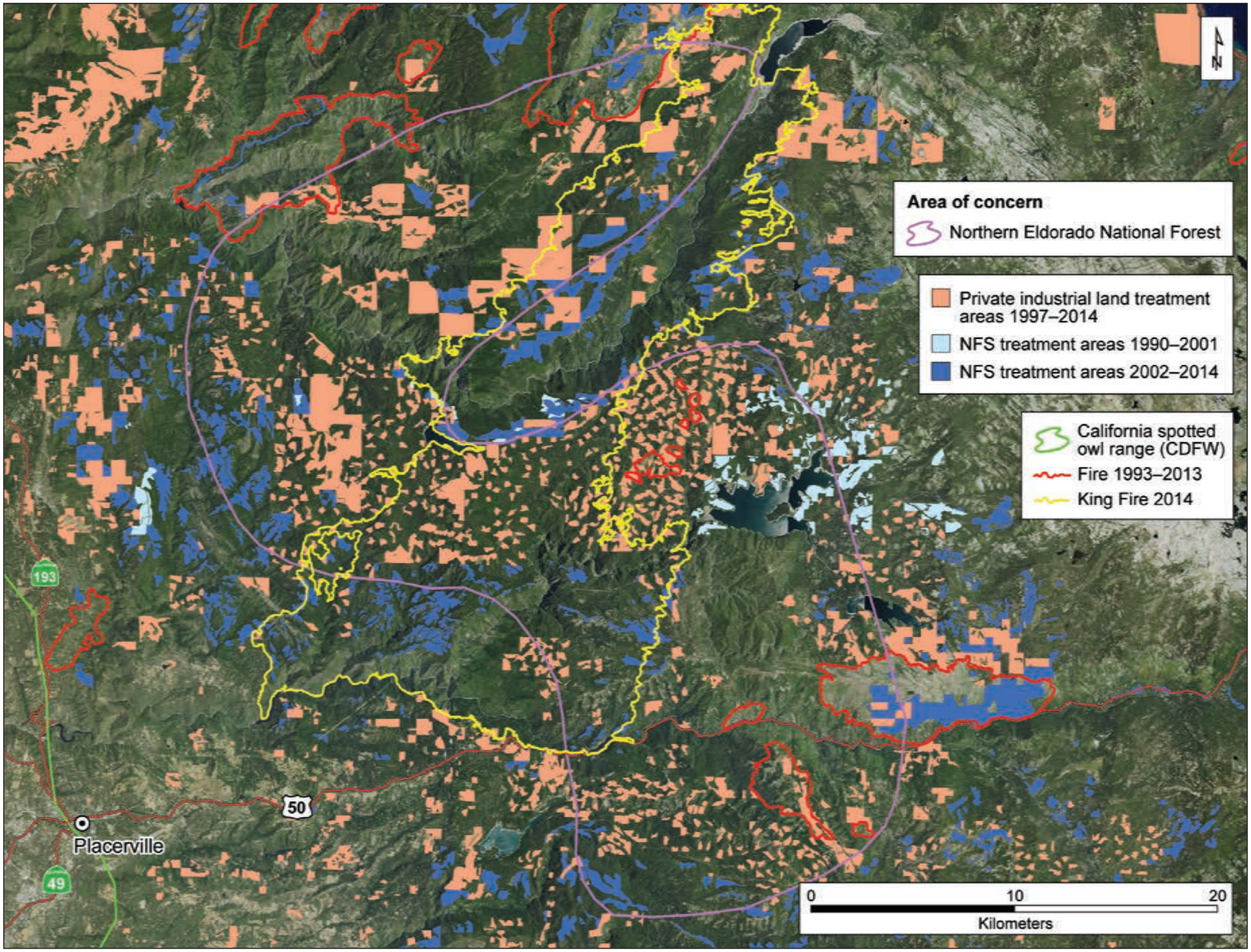

Figure A-3—Distribution of forest management treatments and wildfire on national forest and private industrial forest lands in the California spotted owl assessment (1992) area of concern 4 (Northern Eldorado National Forest) on the Eldorado National Forest, 1990–2014. Sources: National Forest System (NFS) treatments extracted from U.S. Forest Service (USFS) Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Region [R5] silviculturist), private industrial treatments courtesy of California Department of Forestry Forest Practice Geographic Information System (Suzanne Lang), fire perimeters from USFS R5 vegetation burn severity data, National Agricultural Imagery Program photography from U.S. Department of Agriculture Farm Service Agency Aerial Photography Field Office, owl range from California Department of Forestry and Wildlife (CDFW), owl areas of concern from general technical report PSW-GTR-133 (1992).

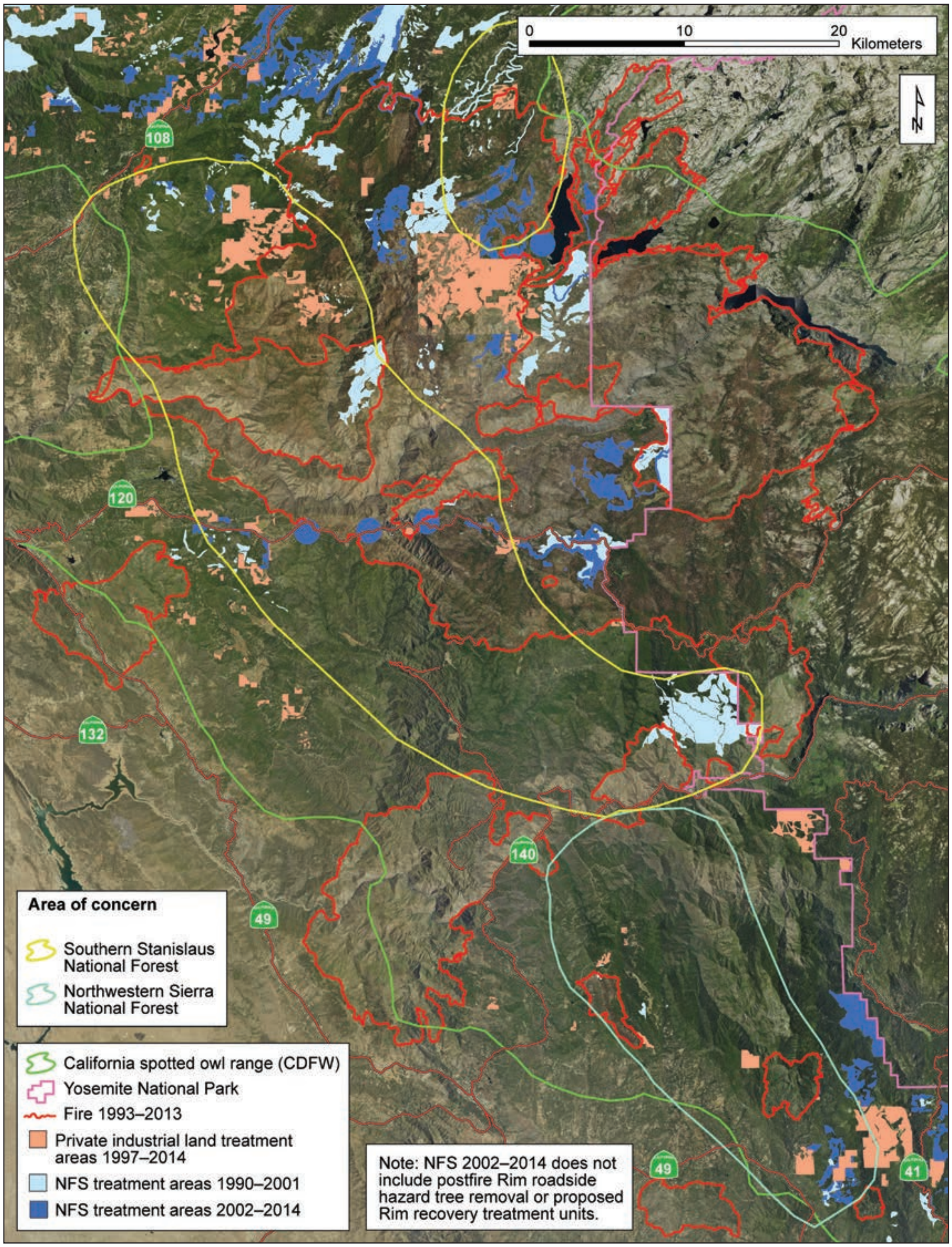

Figure A-4—Distribution of forest management treatments and wildfire on national forest and private industrial forest lands in the California spotted owl assessment (1992) areas of concern 6 (Southern Stanislaus National Forest) and 7 (Northwestern Sierra National Forest) on the Stanislaus and Sierra National Forests, 1990–2014. Sources: National Forest System (NFS) treatments extracted from U.S. Forest Service (USFS) Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Region [R5] silviculturist), private industrial treatments courtesy of California Department of Forestry Forest Practice Geographic Information System (Suzanne Lang), fire perimeters from USFS R5 vegetation burn severity data, National Agricultural Imagery Program photography from U.S. Department of Agriculture Farm Service Agency Aerial Photography Field Office, owl range from California Department of Forestry and Wildlife (CDFW), owl areas of concern from general technical report PSW-GTR-133 (1992).

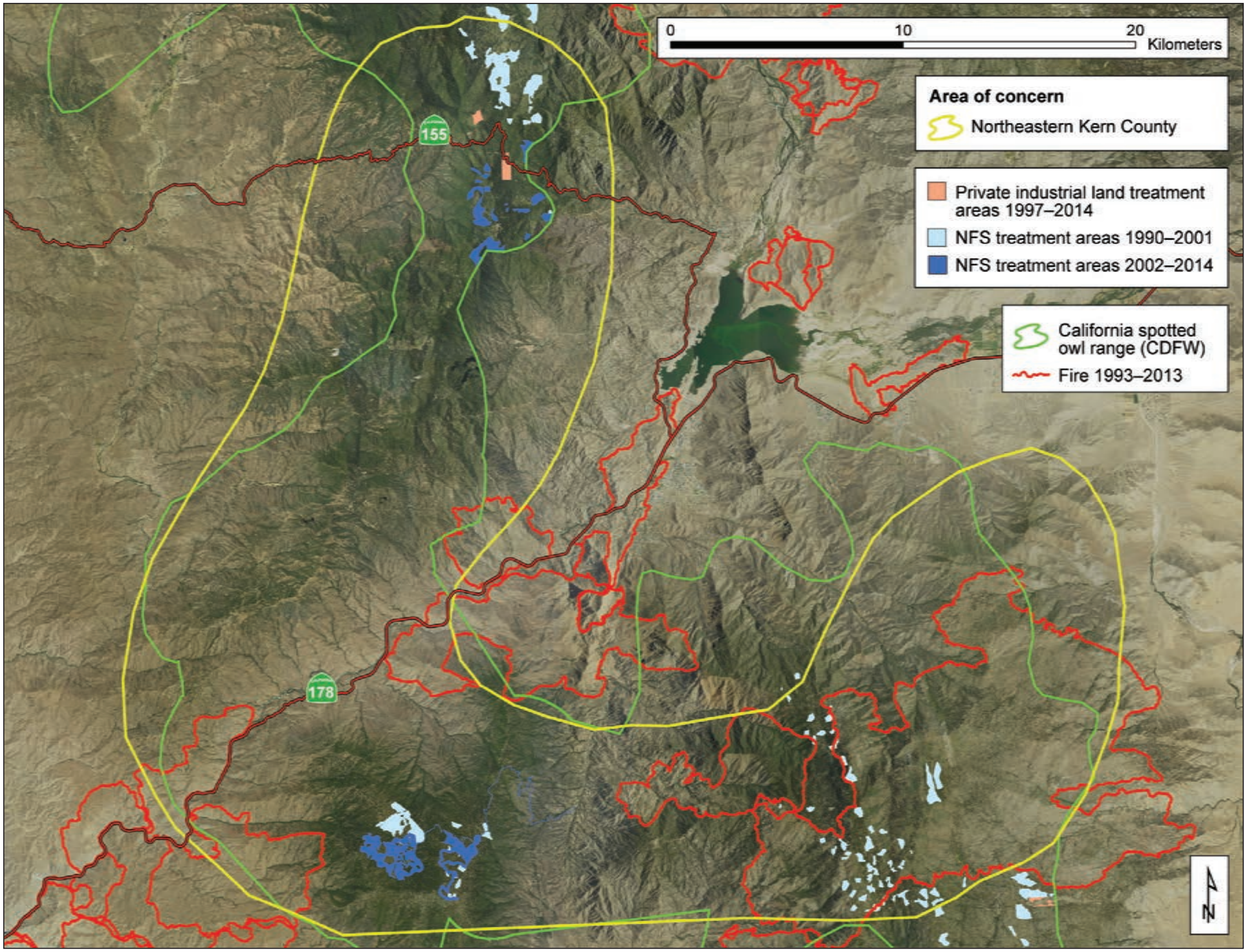

Figure A-5—Distribution of forest management treatments and wildfire on national forest and private industrial forest lands in the California Spotted Owl Assessment (1992) area of concern 8 (Northeastern Kern County) on the Sequoia National Forest, 1990–2014. Sources: National Forest System (NFS) treatments extracted from U.S. Forest Service (USFS) Forest Activities Tracking System courtesy of Joe Sherlock (Pacific Southwest Region [R5] silviculturist), private industrial treatments courtesy of California Department of Forestry Forest Practice Geographic Information System (Suzanne Lang), fire perimeters from USFS R5 vegetation burn severity data, National Agricultural Imagery Program photography from U.S. Department of Agriculture Farm Service Agency Aerial Photography Field Office, owl range from California Department of Forestry and Wildlife (CDFW), owl areas of concern from general technical report PSW-GTR-133 (1992).

Chapter 8: The Spotted Owl in Southern and Central Coastal California

R.J. Gutiérrez, Douglas J. Tempel, and M. Zachariah Peery[1]

Introduction

Spotted owl populations found in southern and central coastal California have received much less attention than those inhabiting the Sierra Nevada because of economic (effect of habitat conservation measures on timber harvest) and social issues (community stability and desire for naturally functioning ecosystems). Yet there has been continued concern over the status of owl populations in this region since the first technical assessment of the California spotted owl "The California Spotted Owl: A Technical Assessment of Its Current Status" (CASPO) in 1992 (Eliason and Loe 2011,[2] LaHaye and Gutiérrez 2005, Verner et al. 1992c). In this chapter, we first summarize the areas of concern for southern California and central coastal California (hereafter we refer to this region as "southern California") portrayed in CASPO (Verner et al. 1992b). We then summarize new information gained since CASPO and revisit the status of threats to the owls. Finally, we provide some observations on the status of owls in southern California and potential management implications derived from new information.

Since the CASPO report, most new information on spotted owls stems from work on the San Bernardino population, which is the largest owl population in southern California (see below). This information has been reported in scientific journals and symposia or as part of targeted monitoring in a few mountain ranges. Whereas lack of funding within the U.S. Forest Service (USFS) has limited the acquisition of new information, the USFS has developed a California spotted owl strategy for southern California (see footnote 2; Loe and Beier 2004[3]). The original strategy was motivated by the extensive fires in southern California during 2003. This region-specific strategy was developed as a response to CASPO (Verner et al. 1992b).

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[2] **Eliason, E.; Loe, S. 2011.** Management indicator species account for California spotted owl in the southern California province. 61 p. Unpublished report. On file with: USDA Forest Service, San Bernardino National Forest, 602 S Tippecanoe Ave., San Bernardino, CA 92408.

[3] **Loe, S.; Beier, J.L. 2004.** Conservation strategy for the California spotted owl (*Strix occidentalis occidentalis*) on the national forests of southern California. Unpublished report. On file with: USDA Forest Service, San Bernardino National Forest, 602 S Tippecanoe Ave., San Bernardino, CA 92408.

CASPO Assessment of Areas of Concern

In CASPO, four general areas of concern were identified for the California spotted owl (*Strix occidentalis occidentalis*) in southern and central coastal California (Verner et al. 1992b: 7):

1. The first was the potential loss of connectivity among mountain ranges in the region and between this region and the Sierra Nevada.
2. The second was the potential fragmentation of habitat within these insular areas that define the distribution of the owls in southern California (see below).
3. The third was the loss of habitat owing to water usage that leads to decline of riparian forest, high-severity fires that result in loss of habitat, and recreational use that results in either loss of habitat or disturbance to owls.
4. The fourth concern was the lack of land use policies on private lands, adjacent to public lands, which could be used to mitigate the potential effects of development.

The CASPO also noted that if the owl metapopulation did not function sufficiently to facilitate demographic rescue, then populations would have to function independently (depend on their own population dynamic processes), which meant that these populations would have to depend solely on the amount and quality of habitat available to them to remain viable.

Distribution and Metapopulation

The spotted owl in southern California is distributed from Monterey County south to Mount Palomar near the Mexican border (fig. 8-1), and is found as far south as the Sierra San Pedro Martir in Baja California Norte (Gutiérrez et al. 1995). Both the Sierra San Pedro Martir and Sierra Juarez are southern extensions of the Peninsular Ranges that contain most of the populations in southern California. The subspecies of owl found on these two Mexican ranges is unknown but by its geographic location is thought to be the California spotted owl. Owls also occur in the Tehachapi Mountains that potentially link this population, by closest proximity, to the Sierra Nevada (Verner et al. 1992b). Notable is the apparent absence of owls from the Santa Cruz Mountains, which apparently have suitable forest types for spotted owls. Based on geographic proximity, the Carmel Valley should not have presented a substantial barrier to dispersal for birds inhabiting the south side of the

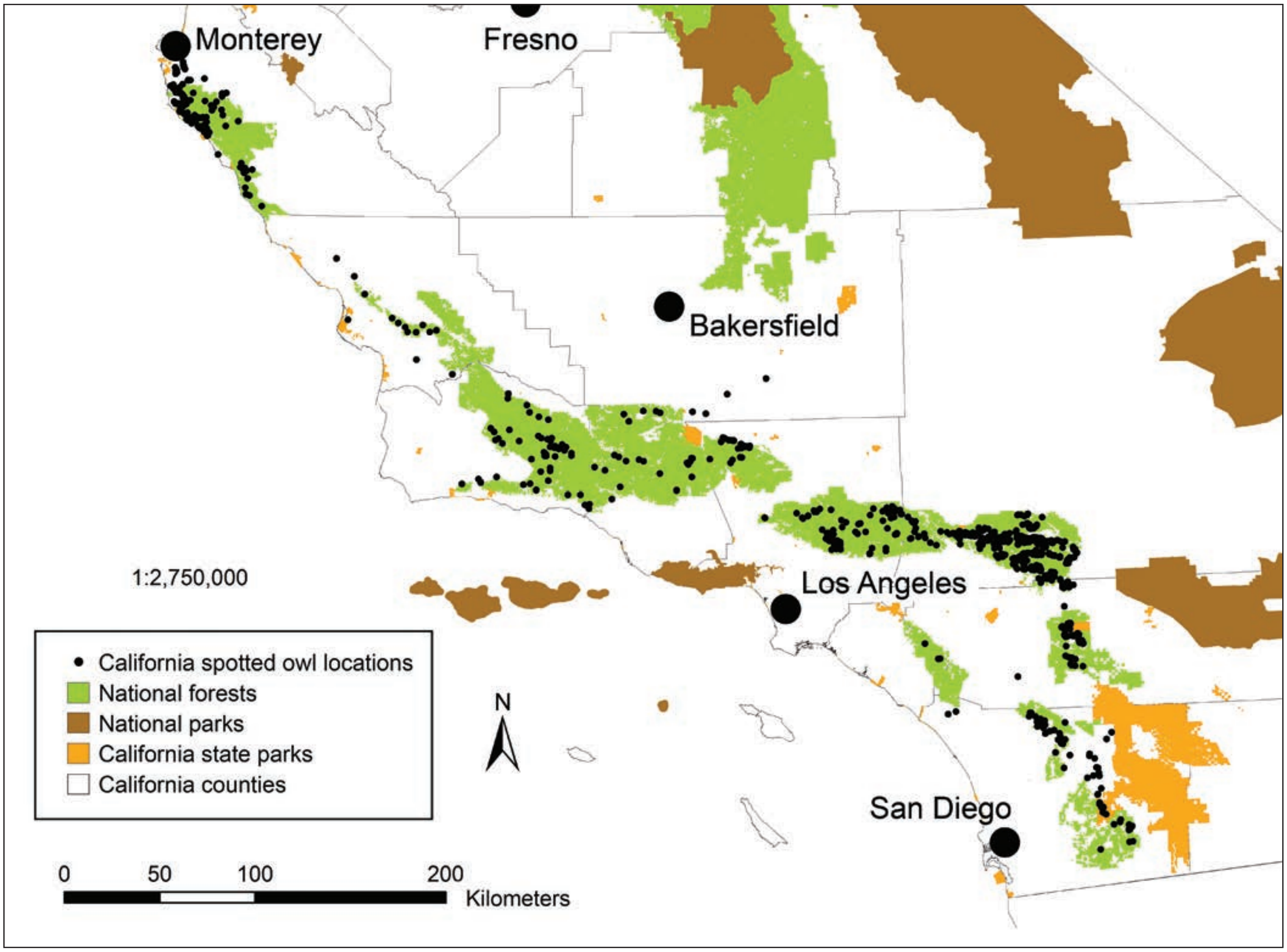

Figure 8-1—Approximate territory locations and distribution of the California spotted owl in southern California, 2014. The Sierra Nevada is also depicted on the map to show the proximity of the Sierra Nevada population with the southern California owl metapopulation.

Carmel Valley in the Santa Lucia Range. At the time of CASPO, there had been no systematic surveys for spotted owls in the Santa Cruz Mountains (Verner et al. 1992b). This was still the situation in 2016.

Within this large geographic distribution, the spotted owl in southern California is unique among west coast spotted owl populations because it occurs as a presumed metapopulation (LaHaye et al. 1994). Metapopulations are defined by distinct populations of individuals that function independently yet their dynamics are interrelated because of dispersal among populations (Hanski and Gilpin 1991). For the California spotted owl, the key issue is that the distance between populations is farther than owls typically disperse (Gutiérrez and Harrison 1996). The populations are generally distinct and isolated from each other because they exist within the high-elevation forests that are found above the unsuitable shrub and semiarid vegetation zones that serve as barriers to movement among populations. In metapopulations, all populations have an equal likelihood of extinction, which predicts that persistence of the regional spotted owl population is dependent on there being enough populations. However, this is not the case in southern California so, theoretically, some populations will have to serve as source populations to "rescue" populations that go extinct (Gutiérrez and Harrison 1996, LaHaye et al. 1994, Noon and McKelvey 1996, Noon et al. 1992). Hence, the spatial structure of populations and habitats within and among populations is critical to the functioning of this metapopulation (Gutiérrez and Harrison 1996, Noon and McKelvey 1996). Thus far, there is scant evidence that dispersal among populations is a central property of the metapopulation dynamics of owls in southern California because there have been no records of movement even between populations in relatively close proximity (i.e., adjacent mountain ranges) (LaHaye et al. 2001, 2004). The lack of documented owl movement among populations for this region is in stark contrast to that of Mexican spotted owls (*S. o. lucida*) in the American Southwest, where movement among mountain ranges (i.e., populations) is common and the population is generally considered to have a metapopulation structure (Gutiérrez et al. 1996, May et al. 1996). In addition, two habitat conditions affect spotted owls generally (habitat fragmentation and habitat heterogeneity); these conditions increase the complexity and also the risk of extinction for owls in the southern California metapopulation (LaHaye et al. 1994). In this regard, most of the detailed ecological studies of southern California have occurred in the San Bernardino Mountains, which harbors the largest population of owls in southern California, and consequently these results likely provide the most optimistic view of owls in southern California.

LaHaye et al. (1994) and Noon et al. (1992) modeled the dynamics of this metapopulation, while Beck and Gould (1992) provided verbal and visual descriptions of areas of potential concern for the southern California metapopulation. These studies clearly indicate that owl populations and habitat within populations are discontinuous. Noon et al.'s (1992: 189) simulation of the southern California metapopulation employed (and acknowledged) optimistic assumptions for owl survival rates in suitable habitat (i.e., they set survival rates high enough so that annual population growth rate [λ] = 1) and allowed for the possibility that λ increased by 2 percent per year. The reason for these assumptions was to examine how the habitat distributed over this large area might affect the metapopulation dynamics. At the time of their analysis (Noon et al 1992), there was only one owl demographic study in southern California, and its relatively short duration did not allow a meaningful estimation of the effect of environmental conditions on that population. They noted that it is critical to examine the effects of both demographic and stochastic (random variation owing to such things as drought and fires) variation on owl population dynamics. Some of the assumptions posed for metapopulation theory have been that dispersal capability of owls to move among independent populations (i.e., mountain ranges) must be sufficient, that the distances between mountain ranges affect system dynamics, that the risks to owls when moving between or among mountain ranges is not excessive, and that small populations with high turnover have to be augmented by immigration to persist. From these basic assumptions, they concluded that the San Bernardino population was critical to the persistence of the entire metapopulation because the many small populations benefited in the simulation by having a large source population (i.e., the San Bernardino/San Gabriel Mountains). Noon et al. (1992) also evaluated the effect of potential habitat configurations on owl demography and key properties of the metapopulation (e.g., how the spacing of habitat islands affected dispersal). Evidently, simulated populations were strongly affected by dispersal risks both within and among ranges, sizes of individual populations, and the distances among populations.

Noon et al. (1992) felt it was premature to assess extinction risk for the southern California owl metapopulation because there was insufficient data on several important variables (e.g., stochastic environmental variation, correlation in environmental conditions among populations), but LaHaye et al. (1994) had access to additional data and conducted such an analysis. They used a spatially structured metapopulation model that considered the number, size, and spatial location of each habitat patch and allowed for interaction among these patches (stochastic growth and dispersal among populations) and for correlation among environmental variation within the region (i.e., the degree to which environmental conditions were similar among areas supporting populations). Because they did not have information on all the populations, they relied on demographic information from the San Bernardino (i.e., the largest population in the metapopulation) and the San Jacinto Mountains (i.e., one of the smallest populations). They found that dispersal between these close populations was very low (no dispersal of color-marked owls was observed in 6 years of study), so they modeled a variety of dispersal rates and also modeled dispersal as a function of distance (i.e., dispersal rates declined with increasing distance between populations). Because they suspected that rainfall (a form of environmental variation) was correlated with spotted owl population dynamics (now demonstrated to be true; see LaHaye et al. [2004] and below), they modeled a range of environmental correlation even though rainfall was strongly correlated among the four mountain ranges examined. The correlations of rainfall amounts among the San Bernardino, Santa Ynez, and Santa Ana Mountains and Mount Palomar ranged from 0.81 to 0.89. Their simulations suggested the metapopulation would likely either go extinct within the next 30 to 40 years or, under alternative hypotheses of deterministic decline and environmental fluctuations, would undergo a substantial decline but not go extinct, respectively. The effects of high environmental correlations and the vital rates were strong in influencing simulation results. They discussed a variety of alternative explanations for their results, most of which were not optimistic about the state of the metapopulation.

The insular nature of these populations also presented a unique opportunity to study particular facets of the owl's ecology (e.g., dispersal) that were more difficult to study in larger contiguous populations as shown by LaHaye et al. (1994). At the time of CASPO, only one long-term and several short-term studies were available for the technical assessment team (Verner et al. 1992c). One of these studies in the San Bernardino Mountains continued until 2000, while the others (San Jacinto Mountains and Mount Palomar) ended either before or shortly after CASPO was completed. Intensive study has been replaced by irregular monitoring sponsored by individual natinal forests (see footnote 2). Because of the very low numbers of birds in some populations and the apparent low dispersal, some of these populations appear to be in precarious conservation status, which makes this paucity of information an even greater concern (see footnote 2).

General Ecology

The ecology of spotted owls has been well described (e.g., chapter 2; Gutiérrez et al. 1995, Verner et al. 1992a), and the general ecology of spotted owls in this region does not appear to differ substantially from that of California spotted owls elsewhere (note: there is almost no information on spotted owls in Baja California Norte [Gutiérrez et al. 1995]). However, the details of environment, particularly climate, vegetation, and insularity, may affect the dynamics of the owl in southern California differently than they do in the Sierra Nevada (Gutiérrez and Pritchard 1990; Gutiérrez et al. 2011; LaHaye et al. 1992, 2001, 2004). The differences between owls in this region and the Sierra Nevada also have to be viewed not only within the context of the spatial fragmentation of populations (disjunct mountain ranges leading to metapopulation structure [i.e., insularity]), but also with respect to the spatial fragmentation of individuals (discontinuities of habitat owing to topography, elevation, soils, aspect, wildfire, and human impacts) and the natural heterogeneous makeup of cover types within owl territories. Very little is known about home range sizes of spotted owls in southern California but limited information suggests that home range size is variable (Zimmerman et al. 2001). Habitat fragmentation occurs when habitat is discontinuous and that discontinuity affects population processes as a binary outcome (habitat or no habitat) (Franklin and Gutiérrez 2002). In contrast, habitat heterogeneity is the diversity of vegetation and successional stages within an area of interest (e.g., an owl territory), such that it reflects a multistate outcome (Franklin and Gutiérrez 2002).

Habitat

There are four major cover types used by spotted owls in southern California: riparian/hardwood forests and woodlands, live oak (*Quercus chrysolepis* Liebm.)/bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) forest, mixed-conifer forest, and redwood (*Sequoia sempervirens* Lamb. ex D. Don Endl.)/California laurel (*Umbellularia californica* Hook. & Arn.) Nutt.) forest (Gutiérrez et al. 1992). Unlike the Sierra Nevada, most owls occur in cover types other than mixed-conifer forest (Gutiérrez et al. 1992) because mixed-conifer forest is only found at the highest elevations in most of these isolated mountain ranges.

Smith et al. (2002) found owls distributed over a large altitudinal gradient (800 to 2600 m [2,625 to 8,530 ft]) in the San Bernardino Mountains, which was the limit of available habitats in this mountain range. Of the major cover types used by owls in this range, canyon live oak/bigcone Douglas-fir cover type had both the most territories and the highest density of territories (56 and 0.39/km^2 [0.15 mi^2], respectively; see also density comparisons with other areas in California below). The density of the 40 owl territories found in mixed-conifer/hardwood forest was 0.29 territories/km^2 (0.11 territories/mi^2), and the density of the 48 territories found in mixed-conifer forest was 0.16 territories/km^2 (0.06 territories/mi^2); Smith et al. (2002) partitioned the mixed-conifer type of Gutiérrez et al. (1992) into two categories based on the proportion of hardwoods found in the understory and subcanopy layer of the forest. LaHaye et al. (1997) speculated that the high density of owls in canyon live oak/bigcone Douglas-fir forests may be related to high densities of prey in the chaparral that typically surrounds this cover type because more young fledged in this forest type than other types in the San Bernardino Mountains. They reported that owl territories were clumped in space rather than being randomly distributed, which resulted in the mean nearest neighbor distance (1497 m [4,911 ft]) being significantly less than the distance between an equal number of random points (1787 m [5,862 ft]) (Smith et al. 1999).

Smith et al. (2002) also assessed vegetation patterns at three arbitrary scales and one biologically based scale (3, 20, 79, and 177 ha [7, 49, 195, and 437 ac]) within owl territories and compared these patterns to those found at same-sized plots at randomly chosen sites. These analysis areas were circular plots with radii of 100, 250, 500, and 750 m (328, 820, 1,640, and 2,460 ft), respectively. The 3-ha area represented the immediate area surrounding a nest or primary roost site, the 20-ha (49-ac) area was used to assess both natural and human-induced fragmentation, the 79-ha (195-ac) area represented a larger area around the nest but probably much less than a core area, and the 177-ha (437-ac) area represented half the nearest neighbor distance, which approximated the size of a territory (see chapters 2 and 3). Collectively, they classified 17 cover types that they collapsed to four cover types for ease of analysis and to focus on forested vegetation (Smith et al. 2002: 140). At all analysis scales, spotted owl sites contained more closed-canopy forest and less nonforest, open forest, and chaparral cover types than random areas. Moreover, these closed-canopy areas were in fewer but larger patches. Their analysis showed that as the amount of closed-canopy forest increased so did the probability that a site contained owls.

Although riparian/hardwood forests are used by owls in southern California, the owls in the San Bernardino Mountains that had riparian habitat in their home ranges had only minor portions of their home ranges in this cover type (Gutiérrez and Tempel, pers. obs.). These streamside forests and woodlands are also important owl habitats in other mountain ranges in southern California (Verner et al. 1992b).

Many studies of habitat structure have shown that spotted owls are habitat specialists (i.e., they use some cover types in greater proportion than their availability in the landscape), and this is also true for owls inhabiting the San Bernardino Mountains (Gutiérrez et al. 1995, LaHaye et al. 1997, Verner et al. 1992b). LaHaye et al. (1997) showed that owls in the San Bernardino Mountains used areas that had greater canopy cover and more complex vegetation structure than what was available to them (i.e., randomly selected areas; table 8-1) (LaHaye et al. 1997). Owls also selected nest sites that had greater canopy cover, larger trees, and greater basal areas of hardwoods and conifers than what was available to them.

Population Dynamics

There have been many analyses of owl population dynamics in southern California (Franklin et al. 2004; Gutiérrez and Pritchard 1990; Gutiérrez et al. 2011; LaHaye et al. 1992, 1994, 2001, 2004; Noon et al. 1992; Peery et al. 2012). Of these, five were comprehensive studies that provided estimates of finite rate of population change; all of these involved the same San Bernardino long-term demography study (Franklin et al. 2004; LaHaye et al. 1992, 1994, 2004; Noon et al. 1992). The others were focused more specifically on elements of population dynamics or climate change (Gutiérrez and Pritchard 1990, Gutiérrez et al. 2011, LaHaye et al. 2001, Peery et al. 2012).

Table 8-1—Structure characteristics of spotted owl habitat and random areas in the San Bernardino Mountains

Habitat variable	Nest points (N = 103)		Random points (N = 296)	
	Mean[a]	*Percentage CV*[b]	*Mean*	*Percentage CV*
Percentage canopy closure	79.3	22.3	52.4	49.9
Percentage slope	54.2	49.8	32.1	68.7
Broken-top tree basal area[c]	2.9	174.3	0.5	322.9
Snag basal area	4.8	116.7	1.8	217.8
Hardwood basal area (30.1 to 45 cm diameter at breast height [d.b.h.])	3.2	216.7	0.9	332.8
Hardwood basal area (>45 cm d.b.h)	4.9	144.7	0.8	380.4
Total conifer basal area	37.1	59.5	20.1	85.8
Conifer basal area (50.1 to 75 cm d.b.h.)	9.6	100.3	4.9	130.1
Conifer basal area (>75 cm d.b.h.)	19.1	77.4	6.7	124.2

[a] Includes zero values for all variables.

[b] Percentage coefficient of variation.

[c] Square meters per hectare.

Source: Reproduced with permission from the *Wilson Journal of Ornithology* [formerly the *Wilson Bulletin*].

Density

Crude densities (the density irrespective of cover types present on the landscape) of owls in southern California are lower than densities in other areas of California (table 8-2), which reflects the spatial fragmentation of suitable habitat across the landscape. However, ecological density (the density of owls within all suitable cover types on the landscape) is similar to one population of northern spotted owls in northwest California before its decline (Franklin et al. 1990). This suggests that the habitat in southern California has a similar capacity for supporting spotted owls as the more mesic forests in northwestern California, the latter of which have been highly fragmented by logging during the last half of the 20th century. We note that almost all populations of spotted owls are declining throughout its range so current densities will be lower (e.g., see table 8-2 for northwestern California example).

Reproduction

Franklin et al. (2004) estimated fecundity (number of female young produced per territorial female) for the San Bernardino Mountain population and found uncertainty among the models which represented hypothesized relationships. Their top model specified an even-odd pattern for reproduction, but this model was only slightly better than the “null” (intercept-only) model. Moreover, the parameter coef-

Table 8-2—Crude (density over an entire study area) and ecological (density within cover types that are preferentially selected relative to available cover types) densities of spotted owls in California

	Crude density		
Time period 1980–early 1990s	**Time period most recent**	**Location**	**Source**
		Owls/km^2	
0.015	No recent estimate	San Bernardino Mountains	LaHaye et al. 2004, Smith et al. 2002
0.059[a]	0.051[b]	Lassen National Forest	Keane 2016[c]
0.18[a]	0.16[b]	Eldorado National Forest	Keane2016[c]
0.151[a]	0.151[b]	Southern Sierra Nevada	Keane 2016[c]
0.184[a]	0.184[b]	Sequoia and Kings Canyon	Franklin et al. 2004,. Keane 2016[c]
1.21	No recent estimate	San Jacinto Mountains	Noon et al. 1992
0.64	No recent estimate	Mount Palomar	Gutiérrez and Pritchard 1990
0.235	0.123	Northwest California	Franklin et al. 1990, Franklin 2016[d]
		Ecological density	
0.58	No recent estimate	San Bernardino	Smith et al. 2002
0.544	No recent estimate	Northwestern California	Franklin et al. 1990

[a] Year of lowest density within span of years (1990–2000) studied by Franklin et al. 2004; density calculated from raw data because density was not estimated by Franklin et al 2004.

[b] Year of lowest density within span of years (1990–2005) studied by Blakesley et al. 2010; density calculated from raw data because density was not estimated by Blakesley et al.

[c] Keane, J. K. 2016. Personal communication. Research wildlife ecologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618.

[d] Franklin, A. F. 2016. Personal communication. Supervisory research biologist and project leader, Wildlife Pathogens and Food Security & Safety Project, USDA/APHIS/WS National Wildlife Research Center, 4101 Laporte Avenue, Fort Collins, CO 80521-2154.

ficient for the even-odd relationship was not significantly different than zero. The estimate of fecundity derived using the top model was 0.362 female young produced per female, which was similar to the Lassen (0.336), slightly lower than the Eldorado (0.409), and slightly higher than the Sierra and Sequoia and Kings Canyon (0.284 and 0.289, respectively) long-term demography studies (Franklin et al. 2004).

LaHaye et al. (2004) used several more years of data than did Franklin et al. (2004) and derived different analyses from those of Franklin et al. (2004) in two significant ways. First, they created models that hypothesized relationships between weather and owl reproduction and other vital rates (see below). Second, they estimated rates of population change using a different approach than Franklin et al. (2004; see also chapter 4). Many studies of spotted owls have used weather variables to examine patterns in owl vital rates (e.g., Franklin et al. 2000, Seamans et al. 2002, Seamans 2007). Weather has been shown to affect animals directly (e.g., by affecting energy needs) and indirectly (e.g., by affecting plants, which produce food for the prey upon which the owl depends). Thus, analyses that assess weather effects have provided insight into environmental processes and conditions that have the potential to affect owls.

In the San Bernardino Mountains, LaHaye et al. (2004) showed that fecundity varied annually from 0.00 to 0.47 for subadult owls to 0.18 to 0.51 for adult owls. The top model suggested that the data were best explained by the additive effects of age and weather covariates. Owls experienced reduced fecundity during wet springs but increased fecundity when the previous weather year was wetter. Thus, owls reproduced best during a dry spring that followed a wet winter. Interestingly, this weather relationship (model) explained 100 percent of the temporal process variation in the data where 62 percent of the variation in the data was process variation and 38 percent was sampling variation. Process variation is the variation in the data that is attributable to the underlying processes that affect fecundity, whereas sampling variation is the variation attributable to sampling error.

Owls use old forest for nesting sites (Gutiérrez 1985). However, as has been shown for other California spotted owl populations (Gutiérrez et al. 1992), owls in the San Bernardino Mountains will use other nest structures besides old trees (LaHaye et al. 1997). Spotted owls used nine tree species for nesting, and the majority of nest types were platform nests (59 percent). Cavity (24 percent) and broken top (17 percent) nests were used less frequently (LaHaye et al. 1997). However, they found no difference in nesting success among owls using different nest structures (LaHaye et al. 1997). Moreover, they found no difference between successful and unsuccessful nests with respect to habitat at the spatial scale of either the nest or nest stand (LaHaye et al. 1997). However, owls nesting in canyon live oak/bigcone Douglas-fir forests had higher reproduction than those nesting in other forest types, and the authors speculated that this may have been due to higher prey densities in chaparral surrounding this forest type.

Survival

We restrict our comments to the most recent population analyses for the San Bernardino Mountains because earlier studies used smaller datasets from this population (Franklin et al. 2004, LaHaye et al. 2004). Apparently, survival probabilities of adult spotted owls were estimated to be 0.815 (Franklin et al. 2004) or 0.796 (LaHaye et al. 2004), which were similar to estimates for most Sierra Nevada populations of owls. In addition, LaHaye et al. (2004) also estimated separate survival probabilities for first- and second-year subadults as 0.692 and

0.88, respectively. The slight difference between these estimates is related to the use of several additional years of data by LaHaye et al. (2004). LaHaye et al. (2004) also found that estimates of survival were most correlated with the age of owls and precipitation in the preceding winter, but there was uncertainty among weather variables in competing models. However, second-year subadult survival was higher than adult survival (0.88 and 0.80, respectively), which was different than other spotted owls populations. They also estimated juvenile survival to be 0.37. Analyses of the population have yielded the only unbiased estimates of juvenile spotted owls based on mark-recapture data (Zimmerman et al. 2003). LaHaye et al. (2004) also reported finding no temporal process variation in nonjuvenile survival, suggesting it was nearly constant over time.

Dispersal

The demographically closed nature of the San Bernardino study area has provided insight on dispersal for both juvenile and adult owls (Gutiérrez et al. 2011, LaHaye et al. 2001). Spotted owls exhibit obligate juvenile dispersal (i.e., they always disperse from the natal areas in their year of hatching) (Gutiérrez et al. 1995). In the San Bernardino population, of 478 juveniles banded between 1987 and 1998, 67 males and 62 females successfully dispersed (i.e., they were relocated as a territorial bird elsewhere on the study area) from their natal areas. Males dispersed slightly less distance than females, but the difference was not statistically significant (mean for males = 10.1 km [6.3 mi], SD = ± 7.6 km [4.7 mi]; mean for females = 11.7 km [7.3 mi], SD = ± 8.1 km [5.0 mi]). In general, female birds disperse farther than male birds, but there are many exceptions to this generality (Greenwood 1980). By age 4, almost all birds had settled on territories, but about 40 percent of them took 2 to 4 years to settle, which indicated they were floaters during that time. Floater owls, as described in chapter 2, will usually not exhibit territorial behavior (i.e., hoot in response to vocal lures or other owls hooting). The rather short dispersal distances reported by these authors were likely a reflection of a “reflective boundary” of unsuitable habitat at the edge of the study area (LaHaye et al. 2001). No spotted owls have been found successfully dispersing between or among the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent ranges, despite surveys and banding of owls within all three ranges (LaHaye et al. 2001, 2004). This suggests that interpopulation dispersal, the key to maintenance of a metapopulation structure, is rare, which seems to support the more pessimistic projections of LaHaye et al.’s (1994) metapopulation modeling.

LaHaye et al. (2001) evaluated the dispersal distances between and among juveniles fledged in pairs and triplets, respectively. They found no correlation in the distances that related birds dispersed. In addition, they also found evidence for conspecific attraction because most owls settled at or near sites that were occupied the prior year (LaHaye et al. 2001).

Peery and Gutiérrez (2013) used the same dataset as LaHaye et al. (2001) to assess whether juvenile survival was influenced by parental reproductive output under the hypothesis that the offspring of parents producing large broods would have relatively low survival probabilities, as expected under classic life-history theory (i.e., there is a cost to the owls because of the effort required to reproduce). They found that individuals that fledged in pairs had a greater probability of surviving their first year than individuals that fledged as singletons or in triplets. Moreover, improved survival for individuals that fledged in pairs carried over to subadult and adult stages. These authors also showed that indices of territory quality based purely on reproductive output were strongly correlated with indices based on offspring fitness that accounted for heterogeneity in survival rates. Thus, if reproductive output of owls within territories is known, the information could be used in conjunction with occupancy and survival information to rank territories for conservation planning.

Almost a third (29 percent) of all territorial females and nearly a fifth (19 percent) of males on the San Bernardino study area dispersed at least once during that 12-year study (Gutiérrez et al. 2011). Spotted owls may disperse following either the breaking of a pair bond or when a mate dies. Gutiérrez et al. (2011) found that birds that had higher reproductive output than the population average were less likely to disperse, which suggests that birds based their choices on the perceived quality of either particular territories or particular mates. The former hypothesis was supported by a post-hoc analysis that birds occupying territories of higher quality (i.e., territories whose occupants over time had higher than average reproductive output) were less likely to disperse. Of course, the territory and the individuals occupying a territory were confounded in their analyses, which was reflected in the relatively low variation explained by their models. Birds that dispersed following the death of their mate tended to improve their reproductive output, but it was not clear that birds that divorced improved their reproductive output. However, this latter result was likely related to paucity of data.

Occupancy

The most complete data on territory occupancy in southern California exists for the San Bernardino and San Jacinto Mountains within the San Bernardino National Forest (SBNF). In addition to surveys conducted under the demographic study from 1987 through 1998 on the SBNF, extensive monitoring of known owl territories was resumed from 2003 through 2011 within the two mountain ranges. This monitoring revealed (see footnote 2) a significant decline (about 50 percent) in territory occupancy from 1989 through 2010 on the SBNF. Although Eliason and Loe only reported naïve estimates of territory occupancy (i.e., conducted no statistical modeling to account for imperfect detection), their naïve occupancy estimates likely were unbiased because a large number of surveys (up to six) were typically conducted at each territory during a given year. Surveys were also conducted within other national forests in southern California from 2003 through 2011, but we can make no inferences about trends in occupancy within other mountain ranges because only a small number of locations were sporadically surveyed. As discussed in chapter 4, Lee et al. (2013) found no statistically significant effects of fire or salvage logging on spotted owl territory occupancy in the San Bernardino Mountains from 2003 to 2011. However, they recognized that fire and salvage logging may have had negative effects on occupancy that were biologically meaningful. For example, territories that experienced fire had a 0.062 less probability of being occupied by an owl pair the following year than unburned sites; postfire salvage logging reduced this probability by an additional 0.046. In particular, local extinction markedly increased when >50 ha (124 ac) burned at high severity within a 203-ha (502-ac) region around territory centers.

Population Trends

The most comprehensive studies of the San Bernardino owl population by Franklin et al. (2004) and LaHaye et al. (2004) differed in their approaches and intent. Franklin et al. (2004) conducted a meta-analysis of all extant California spotted owl demographic studies so they were intent on keeping methodologies and data structures similar. In the former case, they used Pradel’s temporal symmetry model to estimate population rate of change because the Sierra Nevada study areas were demographically open and thus had biased data with respect to juvenile survival. However, as also noted above, the San Bernardino population was closed so they used a Leslie projection matrix to estimate population rate of change because estimates of juvenile survival were not biased by undetected emigration (LaHaye et al. 2004, Zimmerman et al. 2007). The Pradel model answers the question: “Are the owls on the study area being replaced?” The Leslie projection matrix answers the question “Are the owls on the study area replacing themselves?” Thus, both estimators are valid; they simply confer different inferences.

Franklin et al. (2004) found a linear decline in population over the time considered ($\lambda = 0.98$), but the confidence interval overlapped 1.0 so there was uncertainty about an actual decline. In contrast, LaHaye et al. (2004) estimated λ = 0.91 and the confidence limit did not overlap 1.0, which indicated that the population in the San Bernardino Mountains declined approximately 9 percent/year over the period of study (1987–1998). LaHaye et al. (2004) also analyzed their data using the same time period as Franklin et al. (2004) and estimated that λ = 0.92, which was still a significant decline but much lower than Franklin et al.'s (2004) estimate. This difference relates to the closed San Bernardino population, which allowed LaHaye et al. (2004) to use a Leslie projection matrix to estimate lambda. Finally, Franklin et al. (2004) developed a metric called "realized population change" that depicted the change in population size over time relative to the initial population size. Consistent with their estimate of lambda, realized change for the San Bernardino population was not significantly different than 1. This metric was developed because it is difficult to detect trends in populations when they are small (Franklin et al. 2004, Tempel and Gutiérrez 2013). Thus, estimates of the decline of owls in the San Bernardino Mountains were supported by an estimator that was able to take advantage of the internal dynamic processes (stage-specific survival and reproduction) exhibited by this owl population.

Threats

Here we return to the factors noted by CASPO as threats to the long-term viability of the southern California owl metapopulation (Verner et al. 1992b: 7). In addition, we address the concerns raised by LaHaye and Gutiérrez (2005) and provide new potential concerns that have surfaced since CASPO (see footnote 2) (Peery et al. 2012).

Natural Connectivity Among Populations

Successful dispersal among populations is the only way that this metapopulation can continue to function naturally (LaHaye et al. 2004, Verner et al. 1992b). Connectivity among populations is influenced by barriers and by dispersal habitat. In 1992, the threat of barriers was urban and suburban development, while the threat to habitat was the elimination of riparian areas that might serve as corridors. The current situation is worse because development continues unabated within both the Los Angeles Basin and the surrounding deserts. Moreover, many wind turbines have been erected in several areas that could serve as potential dispersal corridors between mountain ranges and between the southern California region and the Sierra Nevada. Wind turbines pose a potential threat of unknown magnitude to owls. There are no intact riparian forests that could act as corridors to assist owls dispersing among mountain ranges. At the time of CASPO, reservoirs were not specifically considered a barrier to dispersal, but at least one owl drowned in its apparent attempt to cross one in the area between the San Bernardino and San Gabriel Mountains.[4] Thus, we add two types of infrastructure development as potential threats to dispersal—wind farms and large reservoirs. Finally, the link between the Sierra Nevada population and southern California through the Transverse Ranges has also not improved and likely has deteriorated owing to continued human development.

Integrity of Habitat Supporting Each Population

With dispersal reduced among populations, rescue effects will not be a factor in the functioning of the metapopulation. Rather, each population will persist or go extinct, in part, as a function of its own habitat conditions. Habitat loss could result from fires and salvage logging (see above). There are as yet, no restrictions on logging on private forest land within the range of the owl other than those imposed by the California Forest Practices Act. Habitat is also being lost or fragmented as a result of primary and secondary home building (LaHaye and Gutiérrez 2005). However, there is no longer any commercial timber harvest on national forests within the owl's range in southern California (see footnote 2). Yet we still do not know if key habitat elements are declining (e.g., large residual trees).

Water Diversion and Stream Channelization

LaHaye and Gutiérrez (2005) provided no evidence for current loss of riparian habitat owing to the water diversion threat noted by Verner et al. (1992b). Yet this threat remains as well as the threat of channelization to control waterflow (i.e., flood protection). Some owls, particularly those at low elevations, have parts of their territories within riparian habitats and these activities either degrade or eliminate these riparian areas. Riparian areas have high species diversity so they likely represent suitable owl foraging sites if they contain tree cover. The U.S. Forest Service has made some progress by requiring that water be hauled into some vacation homes and camps instead of being diverted from streams (see footnote 2). This should reduce some negative impact to riparian areas, but the effect of these new regulations has not been quantified (see footnote 2).

Wildfire

Wildfire has long been a concern for its potential impact on owls and their habitat, but its overall effect on owl populations is not clear (see chapters 3 and 4 as well as

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[4] **LaHaye, W.S. 1996.** Personal communication. Wildlife biologist, 10156 Pine Place, Morongo Valley, CA 92256.

above discussion). Given the loss of habitat owing to other factors (e.g., urbanization and drought, see below), fires are likely a contributing factor in this loss.

Human Recreation

Southern California has a very large and dense human population and the surrounding mountain ranges are used heavily for recreation. LaHaye and Gutiérrez (2005) and others (see footnote 2) voiced concern that recreational activities could negatively affect owls indirectly through disturbance and degradation or loss of habitat to accommodate this recreational activity.

Drought

LaHaye et al. (2004) showed that precipitation was correlated with reproductive patterns. Thus, the general drought pattern that has been affecting southern California for the past two decades will probably have some negative impact on owl demography, primarily by reducing reproductive output. The recent and future droughts will only exacerbate this concern.

Air Pollution

Air pollution is a well-known phenomenon in southern California. It can potentially affect vegetation dynamics, which in term could affect the habitat of owls and their prey (LaHaye and Gutiérrez 2005). Although air pollution is an issue that is being addressed at many levels through policies and law, it still is affecting some of these owl habitat islands. It also poses a direct threat to owls because birds do not possess a DNA repair mechanism for lung tissue (Rombout et al. 1991).

Mining

Several owl territories in the San Bernardino Mountains are possibly being affected by carbonate mining operations (see footnote 2). The two impacts stemming from these mining operations are side-casting of rock from roads and tailings and water diversion that affects riparian habitat.

Marijuana Cultivation

We are unaware of the extent of marijuana (*Cannabis* sp.) cultivation in southern California, but it is prevalent throughout the rest of rural and mountainous California. Recent evidence indicates widespread use of rodenticides to control rodents that eat these plants has led to secondary poisoning of Pacific fishers (*Pekania pennanti*) in the southern Sierra Nevada (Gabriel et al. 2012). These rodenticides are now being found in a high percentage of barred owls (*Strix varia*) in northwestern California.[5] If barred owls are being poisoned, then spotted owls are probably also being affected because these species often use the same habitats where they co-occur (Gutiérrez et al. 2007). Thus, we feel it prudent to list this activity as a potential threat to spotted owls in southern California.

Cumulative Effect of Small-Scale Management Actions

Many small-scale activities are conducted by land managers within the range of the owl in southern California, which by themselves may not significantly affect owls but could do so collectively. Some examples of these are hazard tree removals for roads, powerlines, building camps, building vacation homes, diverting water for special uses, and developing ski areas (see footnote 2).

Invasive Species and Disease

The barred owl potentially was first observed in southern California in January 2016 in Los Angeles County but has not yet been verified.[6] In addition, West Nile virus occurs in southern California, but there is no evidence it is affecting owls (chapter 7). However, invasive plants may be a threat to owl habitat (see footnote 2). Plant species such as cheatgrass (*Bromus tectorum* L.), Chinese tree of heaven (*Ailanthus altissima* (Mill.) Swingle), and tamarisk (*Tamarix ramosissima* Ledeb.) can potentially affect owl habitat either through competition and displacement or providing fuel for fires. Sudden oak death syndrome has also affected owl habitat in some parts of the Los Padres National Forest (see footnote 2).

Climate Change

Intuitively, California spotted owls in southern California would seem to be vulnerable to the warmer and drier conditions expected under climate change scenarios given the xeric nature of this region (relative to other areas occupied by this subspecies). Peery et al. (2012) assessed the potential impacts of climate change on California spotted owls in the San Bernardino Mountains by first correlating annual demographic rates (survival and reproduction) to weather conditions, and then using demographic-weather relationships to project the population forward in time under

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[5] **Higley, J.M. 2015.** Personal communication. Wildlife biologist, Hoopa Valley Tribe, 80 Willow Ln, Hoopa, CA 95546.

[6] **Garrett, K.L. 2016.** Personal communication. Ornithology collections manager, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

alternative climate change scenarios. According to their model, viability at the end of the 21st century was relatively insensitive to climate change under all scenarios considered, whereas the viability of two Mexican spotted owl populations was projected to decline substantially as a function of climate change. Viability in the San Bernardino Mountains did not decline largely because reproduction is lower in cold, wet nesting seasons, and such conditions are expected to attenuate under climate change. At least two important caveats need to be mentioned regarding the findings of this study. First, neither changes in wildfires, which may increase in frequency and severity, nor other agents of disturbance (e.g., insects and diseases) were modeled. Second, expected changes in temperature under climate change exceeded the variability that occurred during the period used to develop demography-weather relationships. Thus, the authors assumed that relationships between weather and owl demography will hold under a novel climate space, an assumption that may not be valid.

Although milder nesting conditions may improve reproductive success (Peery et al. 2012), the owl's bioclimatic niche will almost certainly move to higher elevations in southern California. It is unclear whether suitable owl habitat will be able to track elevational changes in the owl's bioclimatic niche within the timeframe needed to avoid mismatches between needed forest conditions and suitable climate. Moreover, the spotted owl's bioclimatic niche will likely occur over more narrow elevational gradients in southern California as the climate warms, which could cause a contraction in the distribution (and reduction in abundance) of owls in the region. Finally, low intermountain dispersal rates in southern California suggest that spotted owls may not be able to track latitudinal shifts in their bioclimatic niche (LaHaye et al. 2001).

Chapter Summary

The status of the spotted owl in southern California is, if not dire, significantly more deteriorated than when it was evaluated as part of CASPO (Verner et al. 1992c). Most information stems from the largest population of owls in southern California, which should have the highest potential for self-sustaining viability. If this population is undergoing substantial decline (50 percent; see footnote 2) (LaHaye et al. 2004), we can assume other populations in southern California are declining as well. The large number of threats, concomitant with no apparent remedies to them, suggests that every effort be made to maintain the integrity of existing suitable forests. Minnich (1980) indicates that canyon live oak/bigcone Douglas-fir forests may have declined in the past century as a result of fire. Canyon live oak/bigcone Douglas-fir forests are often surrounded by highly flammable chaparral and scrub cover types and therefore could be a priority for fire treatments. However, the tenuous nature of the metapopulation makes active management to reduce fire risk arguably a more risky activity than in other regions. Regardless, maintaining all habitat elements known to be used by owls, especially large trees (both conifers and hardwoods), diverse forest structure, snags, and high canopy cover in mature forests, appears to be a key factor in conserving owls. Areas at higher elevations are also likely to be of greater importance in the future given predictions of climate change and potential use of refugia at higher elevations (Jones et al. 2016, Peery et al. 2012). As noted by CASPO (Verner et al. 1992c), efforts to improve connectivity among mountain ranges and facilitate northerly movements to areas that may be resilient to climate change are important. A spatial population modeling exercise that incorporates climate change and evaluates functional connectivity could greatly facilitate such planning. Finally, assuming the San Bernardino population could first be stabilized and then increased, it may well be time to consider reintroducing owls from this population to other areas where populations have become extinct to provide artificial "rescue effects" in this metapopulation. However, if extinction of populations is from loss or fragmentation of habitat, translocations would not be beneficial.

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Chapter 9: Synthesis and Interpretation of California Spotted Owl Research Within the Context of Public Forest Management

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Introduction

In this chapter, we synthesize the information presented in the preceding chapters of this assessment of the California spotted owl (*Strix occidentalis occidentalis*) and provide a scientific appraisal of its implications for forest management and owl conservation. We focus on the key scientific findings since the 1992 California spotted owl technical assessment (CASPO) (Verner et. al. 1992) and discuss priorities for future research that could enhance the successful conservation of California spotted owls and their habitat. Throughout this chapter, we acknowledge when uncertainty limits well-founded conclusions and articulate differences in interpretation of the scientific literature, where such differences exist. The development of a spotted owl conservation strategy will require additional, careful analysis and deliberation to arrive at specific and scientifically defensible management guidelines (sensu CASPO; Verner et al. 1992).

Implications of Recent Research for Spotted Owl Conservation

The greatest challenge for managers charged with maintaining a viable population of spotted owls on National Forest System (NFS) lands in the Sierra Nevada may be to embed effective, long-term owl conservation practices within an overall management strategy aimed at restoring resilient forest structure, composition, and function. We discuss how and when spotted owl conservation and forest ecosystem restoration are compatible based on our current understanding of the

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scientific literature. Conversely, we identify circumstances in which reducing fuels and restoring desired forest structure and composition may pose significant risks to spotted owls so that managers and policymakers can make informed decisions about relevant tradeoffs.

A number of species of conservation concern exists within the Sierra Nevada in addition to California spotted owls, including American marten (*Martes americana*), northern goshawk (*Accipiter gentilis*), black-backed woodpecker (*Picoides arcticus*), great gray owl (*S. nebulosa*), and particularly Pacific fisher (*Pekania pennanti*). The cumulative effects of meeting the current habitat conservation needs of each of these species may increase the challenge of achieving ecosystem management and ecological restoration objectives. However, a comprehensive old-forest management strategy that promotes large trees and canopy complexity within a landscape-scale mosaic of forest conditions could benefit many species of conservation concern, not just the California spotted owl.

Conservation of Spotted Owls in the Context of Ecosystem Restoration

Meeting the dual objectives of conserving spotted owls and promoting resilience of Sierra Nevada forests will require restoring some semblance of historical wildfire regimes without endangering already declining spotted owl populations. Conserving spotted owl populations and restoring ecosystem resilience are complementary objectives when management activities reduce the loss of old forest and owl habitat to drought and large high-severity fires. To do so will require reducing small-tree densities and promoting "natural" fire regimes in Sierra Nevada forests while maintaining a sufficient amount and distribution of suitable habitat to support viable owl populations (a key uncertainty is the amount and distribution of habitat that is sufficient). Thus, a reasonable guiding philosophy is to manage Sierra Nevada forests in ways that combine the objectives of spotted owl conservation, fuels management, and drought resilience while also recognizing that forests are dynamic ecosystems that will support a range of vegetation types and structures that vary over space and time. In practice, however, implementing effective fire management and ecosystem restoration programs that do not also pose risks to spotted owls will be challenging. In some cases, conserving habitat elements known to be important to spotted owls may lead to dense stands with high fuel loadings that are at risk from high-severity fire and other stressors such as drought, insects, pathogens, and air pollution (chapters 5 and 7). Conversely, fuel reduction and forest restoration strategies that reduce canopy cover, the complexity of forest structure, or large-tree density can potentially affect spotted owl populations negatively in both the short and long term (chapters 2, 3, 4, and 7). Determining the appropriate pace, scale, and intensity of treatments as well as the type of treatment is complicated by scientific uncertainty of the potential impacts of a suite of threats including some types of mechanical treatments on spotted owls (chapters 3 and 7; see also the "Research Implications" section below).

Two different paradigms emerged as part of this assessment regarding tradeoffs between the potential short-term negative impacts and possible long-term benefits of fuel and restoration treatments on spotted owls. One paradigm holds that treatments within spotted owl habitat pose risks to spotted owls because owls have declined significantly on some NFS lands in the Sierra Nevada and southern California over the past two decades (chapters 4 and 8). Although the cause of these recent declines is uncertain, the large reduction in abundance observed on the Eldorado National Forest study area cannot be attributed to barred owl (*Strix varia*) or fire, as estimated declines occurred before the King Fire, and very few barred owls have been detected on the Eldorado. Certainly non-habitat-related factors (e.g., climate) could have contributed to recent declines (Jones et al. 2016a), but there is concern that habitat features known to be important to spotted owls (e.g., forests with vertical structure and complex canopies) have declined during demographic studies as a result of forest management activities on both public and private lands, recognizing that these potential effects have been difficult to detect as part of demographic studies (chapters 4 and 7). There is also concern that the removal of large trees as hazards (e.g., road- and trail-side tree removal) and salvage logging affect owl habitat suitability and could be affecting spotted owl populations in the Sierra Nevada. Finally, and perhaps most importantly, pre-CASPO changes to owl habitat from historical even-age timber harvesting and the selective removal of large and "defect" trees may be contributing to recent population declines (via long-term "legacy" effects) as well as longer term (unmeasured) declines.

The conclusion from this interpretation of the published literature is that current spotted owl populations may be small relative to historical levels and limited by the spatial extent of old forest and forests containing legacy elements in the Sierra Nevada (chapter 4). There is recognition that high-severity fire and other ecosystem stressors pose threats to California spotted owls (Jones et al. 2016b), but there is also concern that the expansion of treatments that simplify forest structure and decrease forest tree canopy cover in owl habitat could exacerbate population declines and increase the probability of extirpation of owls from the region. Moreover, whether fuel treatments will protect spotted owl habitat from high-severity fire sufficiently to compensate for potential short-term impacts to populations is unknown. This paradigm suggests that conserving and promoting a sufficient amount of forest dominated by large trees, complex forest structure, and closed canopies at sites known to be used by spotted owls—particularly in owl nest stands, activity centers, and territories—is likely to enhance owl habitat and populations. Nevertheless, fuels and restoration treatments are considered to be an important component of an overall strategy intended to restore resilience to Sierra Nevada forests at larger spatial scales (chapter 5). Thus, under this paradigm, treatments would occur primarily in areas of the landscape dominated by younger forests with high small-tree density and be designed to enhance foraging habitat and foster growth rates of larger, retained trees to enhance resilience to fire when possible. Finally, it is a well-established principle of wildlife management ("Declining Population Paradigm") that halting and reversing substantial recent population declines of a species of concern, like the spotted owl, is an essential component of a conservation program (Caughley 1994). Doing so will be challenging, likely requiring restoration of habitat conditions as well as the implementation of studies carefully designed to identify the cause of recent population declines more precisely (and thus facilitate effective and specific management actions; see below).

The alternative paradigm that emerged from the assessment holds that increases in the spatial extent of high-severity fire and other disturbances to forests (e.g., prolonged drought, insects, and disease), resulting from over a century of fire suppression and now climate change, pose the primary proximate threat to spotted owl population persistence, owl habitat, and forest ecosystems in the Sierra Nevada. Current fuels and other restoration treatments are intended to retain and promote large-tree development, but their pace and scale is small (on national forests in the Sierra Nevada <12 141 ha/year (<30,000 ac/year) of mechanical thinning and <3642 ha/year (<9,000 ac/year) of prescribed fire occur, compared to 196 677 ha/year (486,000 ac/year) that historically burned [North et al. 2012]) such that any detrimental effects to owls are likely to be local and short lived. In contrast, recent and projected wildfire and drought-related mortality, exacerbated by the fire deficit, affect a significantly greater area, and often kill the largest trees while also drastically reducing canopy cover. Actions consistent with this paradigm could include, for example, fuel- and density-reduction treatments strategically placed with less consideration of owl habitat impacts and an emphasis placed on reducing the spatial extent of high-severity fire effects and drought-induced mortality.

This paradigm suggests that working with dynamic forest processes would be more effective for reducing risks to owls and the forests upon which they depend than a strategy focused on conserving and enhancing existing owl habitat. Underlying this interpretation of risk is uncertainty about historical (i.e., pre-Euro-American) spotted owl populations when forest conditions were significantly different than they are today. Recent analyses of historical datasets and efforts to reconstruct stand structure prior to the fire-suppression era (chapter 5) suggest that average canopy cover was lower in landscapes with an active fire regime. Modern forests, by contrast, have far fewer large trees, and defect structures have declined while high canopy cover conditions have become more widespread. It is unclear how these changes have influenced owl population declines that have been documented in three of the four Sierra Nevada demographic studies. Furthermore, it is uncertain whether and to what degree observed population declines may be a result of either recent management practices that created a more homogeneous forest, a legacy of more extensive and intensive management practices in previous decades (e.g., the logging of large trees and snag removal), or a change in a population that is currently higher than was supported under historical forest conditions. In light of these uncertainties, it is possible that restoring forest conditions where high canopy cover conditions are aligned with productive sites will support an owl population equilibrated to forest conditions and resilient to dynamic processes even as the climate changes.

The underlying uncertainties associated with past, present, and future conditions will present challenges to spotted owl conservation and forest management. However, there was consensus about new findings presented in this assessment that are relevant to both owl conservation and forest restoration in the Sierra Nevada. These include:

- Spotted owls have declined in abundance on some NFS lands in the Sierra Nevada over the past two decades (chapter 4).
- The density of large and defect trees has declined in Sierra Nevada forest as a result of historical (pre-CASPO) timber harvesting (chapter 5), and these habitat elements may well be contributing to recent spotted owl population declines.
- A century of fire exclusion has led to an increase in the size of high-severity fires owing to the accumulation of surface and ladder fuels (chapter 5). Habitat loss resulting from large high-severity fires and other stressors poses an increasing risk both to spotted owls and forest ecosystems, and these risks will likely increase with climate change over coming decades (Jones et al. 2016b).
- Restoring low- to moderate-severity fire regimes to the mixed-conifer zone could help achieve both spotted owl conservation and forest restoration goals.

- Habitat conditions in some spotted owl territories may not be viable in the long term because they are located in areas that have high burn probabilities or low drought tolerance. Conservation and restoration of owl habitat (large trees, moderate stem density, and canopy cover) in areas that could support these conditions (i.e., higher actual evapotranspiration and lower climatic water deficit rates) may align the distribution of owl habitat with forest restoration goals.

These key findings and points of consensus suggest that the viability of spotted owls in the Sierra Nevada depends on carefully balancing fuel and restoration treatments with the maintenance and enhancement of existing owl habitat. However, as discussed above, developing a specific set of management guidelines as part of owl conservation efforts that will simultaneously achieve these objectives will be complicated by scientific uncertainty about the potential risks and rewards posed by fuel and restoration treatments. Thus, conservation planning efforts would benefit from a quantitative risk assessment, which would require close coordination among wildlife ecologists, forest and fire ecologists, and remote-sensing scientists, as well as the development of an integrated model that links fire behavior, forest conditions, and spotted owl habitat/demography at the appropriate spatial and temporal scales. Moreover, the success of future conservation planning efforts also would benefit from the development of a robust feedback loop that generates and incorporates new information and learning through implementation, for example by monitoring the impacts of management actions on both forest structure and owl population response. Possible approaches for evaluating the short- and long-term impacts of fire and restoration treatments, as well as possible components of an adaptive management strategy, are described in more detail below.

Desired Conditions for Areas of Ecological Importance

Research summarized in chapters 2 through 8 indicates that different ecological (e.g., habitat) features are important to spotted owls at each of several spatial scales, and that considering these scale-specific requirements will facilitate the development of forest conditions that minimize risk to owls and promote resilient forest ecosystems. The scales of greatest importance are the owl’s activity center, territory, and home range, embedded within the broader forested landscape. In general, owl territory occupancy and demographic rates are likely to fare better with a gradient of less intensive to more intensive forest management activities within owl habitat as a function of distance from activity centers. Maintaining key habitat elements within activity centers and territories will likely promote population growth in the short term, whereas reducing risk from high-severity fire and other threats within owl home ranges and the broader landscape could promote population viability in the long term. Given that owls are central-place foragers and exhibit strong nesting site fidelity (see chapter 2), and new nesting habitat (primarily old forest) develops over long time scales, maintaining existing nesting habitat (particularly at sites that have a history of use) is likely to promote viable populations while forest and restoration treatments designed to reduce risks from high-severity fire and other environmental stressors are implemented at larger spatial scales. The retention of large trees (particularly old trees with structural defects) and the accelerated development of additional large trees is likely to be beneficial at all scales, given that such trees have declined on the landscape and are important for both forest resilience and spotted owls. Desired conditions for each scale of ecological importance, as well as the implications of recent research for achieving these conditions via forest management, are described as follows:

- **Activity-center scale**: Maintaining high-quality nesting and roosting habitat (i.e., old forest) at known spotted owl activity centers (defined as the areas of long-term nesting and roosting use within an owl territory) will likely enhance occupancy and demographic performance. Forest structural characteristics known to be important at this scale are more likely to be maintained or even enhanced through low-intensity vegetation treatments when forest management is implemented with the intent of reducing the risk of high-severity fire and drought-induced large tree mortality.
- **Territory scale (outside of activity centers)**: Within territories, spotted owl occupancy and fitness appear to be positively related to the acreage of high-quality habitat (i.e., forests dominated by large trees and particularly high canopy cover), and a landscape populated by territories containing a sufficient amount of these habitat conditions will likely promote viable spotted owl populations. However, given climate change predictions and the likely increase in large high-severity fires and drought-induced tree mortality, reducing these risks to forests within territories will likely benefit spotted owl populations.
- **Home range scale (outside of territories)**: Spotted owl home ranges characterized by heterogeneous forests containing a mosaic of vegetation conditions, including patches of old forest and a mix of stand ages will likely confer sufficient high-quality nesting, roosting, and foraging habitat. At this scale, there is an opportunity to place greater emphasis on fuels management and forest restoration, particularly approaches that enhance

forest resilience, landscape heterogeneity, and spotted owl foraging habitat. Maintaining and increasing the prevalence of large trees could be particularly effective for restoring forest resilience and improving owl foraging habitat at this scale.

- **Landscape scale (matrix between home ranges)**: A landscape of heterogeneous forests containing a mosaic of vegetation conditions including patches of old forest will likely provide opportunities for recruitment of new spotted owl territories in the context of dynamic forest conditions and confer broad-scale ecosystem resilience. Thus, fuels and restoration treatments—in conjunction with prescribed and managed fire—that promote landscape heterogeneity in forest conditions and reduce risks for high-severity fire and other stressors will likely benefit spotted owls and forest resilience in the longer term.

The Science Behind Scale-Specific Desired Conditions: Implications for Forest Management

Here, we review the scientific basis for the above-described desired conditions and discuss how the knowledge accumulated about California spotted owls and forest ecosystems in the Sierra Nevada since CASPO could inform forest management at each of these scales in more detail.

Activity-center scale—

California spotted owl activity centers are typically characterized by old-forest conditions (i.e., large trees, complex structure; chapter 3) and maintaining such conditions within activity centers is likely important for promoting owl reproduction and population viability. Protected activity centers (PACs) were designed as part of the CASPO strategy to protect 120 ha (300 ac) of the "best available" nesting and roosting habitat (i.e., activity centers) within known spotted owl territories and appear to have been a useful management construct based on research demonstrating long-term use of these areas by owls (Berigan et al. 2012; chapter 2). Moreover, Blakesley et al. (2005) demonstrated that reproductive success in California spotted owls was correlated with vegetation types characterized by high-canopy and medium/large trees at the approximate scale of a PAC (see chapter 4 for more details). These observations, coupled with observed significant declines in owl populations on NFS lands (chapter 4), suggest that fuels and restoration treatments that substantially affect these habitat attributes within spotted owl activity centers could affect spotted owl populations adversely. Limiting treatments to approaches designed to avoid impacts to existing spotted owl habitat such as prescribed burning and hand removal of small trees are more likely to provide a balance between habitat conservation and fuels management than prescriptions that appreciably affect forest overstory structure at this scale.

Territory scale—

The quality of nesting, roosting, and foraging habitat at the territory scale is inevitably a complex function of many variables such as the density of large trees (including snags), vertical forest structure, canopy complexity, and large woody debris, as well as forest heterogeneity (chapter 3). Consideration of the range of forest conditions the literature suggests is important to owls at this scale will facilitate management of spotted owl habitat in a manner that promotes viable populations (chapter 5). Many of these characteristics, however, have proven difficult to map with sufficient accuracy and resolution at the territory scale, particularly with a large enough sample size of territories to understand how they affect owl occupancy and fitness, and thus population viability (chapter 6). In contrast, canopy cover has been relatively tractable to map at this scale and has proven to be a reasonably strong predictor of spotted owl territory occupancy and fitness (chapter 4). Recent research on the Eldorado study area indicates that occupancy and territory fitness (i.e., λ or annual population growth rates at the territory scale) (Franklin et al. 2000) are higher in territories (400-ha [988-ac] circles centered on activity centers) that contain relatively large extents of closed-canopy forest (≥70 percent cover) (Tempel et al. 2014), and that owls occupying high-elevation territories appear to be more sensitive to reductions in this forest type (Jones et al. 2016a). To date, these studies provide the most rigorous quantitative assessment of the association (particularly the directionality and the shape of the relationship) between the acreage of high-canopy forest and spotted owl demographics and provide the best available information for management of owl habitat at the territory scale. Although from a management perspective it would be valuable to understand what acreage of high-canopy cover forest is expected to lead to stable population growth at the territory scale, the absolute estimate of territory fitness (see fig. 4 in Tempel et al. 2014) is biased low owing to territory switching by owls and because recruitment into territories was not considered in the analysis by Tempel et al. (2014). As a result, decisions about how much high-canopy cover forest to retain within territories, based on this analysis, will be, to a certain extent, subjective (but see below). Tempel et al. (2014) suggested that 100 to 150 ha (247 to 370 ac) of high-canopy cover forest might provide a reasonable balance between perceived tradeoffs associated with maintaining owl habitat quality and promoting forest resilience. However, the mean area of high-canopy-cover forest in the declining Eldorado "population" was about 137 ha (338 ac), and thus a population of territories each containing only 100 ha (247 ac) of high-canopy-forest is expected to decline even more rapidly given the association between high-canopy-cover forest and spotted owl population growth rates. By extension, a landscape populated by territories containing only 50 ha (123 ac) of forests >70 percent canopy cover—the mathematical inflection point in the nonlinear relationship between territory fitness and the area of high-canopy-cover forest—will likely lead to even more rapid population declines, at least in the short term. Importantly, ongoing research based on all four demographic study areas will provide more precise estimates of how much high-canopy-cover forest (as well other canopy cover types) is required to yield stable population growth rates at the territory scale.

Although consistent empirical evidence supports the short-term conservation value of retaining high-canopy-cover forest (i.e., most owls are found in these forests), the amount of canopy cover necessary to allow owl persistence remains uncertain. The topography and past, active fire regimes of the Sierra Nevada created a diverse array of patches at different scales (i.e., patchy tree patterns within patches; successional patchworks within local landscapes; and life form, cover type, and structural patchworks within ecoregions). Consequently, many existing stands having high canopy cover are likely the result of past logging and fire suppression rather than locations that would normally support high canopy cover with a historical fire regime (chapter 5). For mixed-conifer forests, historical estimates of canopy cover generally ranged from 15 to 30 percent for forests with active fire regimes (Collins et al. 2011, 2015; Lydersen et al. 2013; Stephens et al. 2015), 19 to 49 percent for modern old growth with restored fire regimes (Lydersen and North 2012), and 60 to 65 percent for modern forests having fire-suppressed regimes (Lydersen et al. 2013), with lower values for pine-dominated stands (Stephens and Fry 2005, Taylor 2010). Particular locations, such as a group of tall trees or a grove of large trees supporting a dense cluster of codominant trees within the grove matrix, may have high canopy closure, but a stand-level average canopy cover of 70 percent appears to have been rare in historical forests (Collins et al. 2015, Stephens et al. 2015). Thus, although 70-percent canopy cover may be a desired condition for owls, in some locations it will be difficult to achieve and harder to maintain because such stand conditions usually have high surface and ladder fuel loading, high stem density, and associated water stress that increases large tree mortality.

Our assessment of the scientific literature indicates that reconciling perceived differences in desired conditions for spotted owls and Sierra Nevada forests at the territory scale—particularly with respect to canopy cover—is one of the more significant challenges facing management intended to maintain viable owl populations and promote resilient forests. However, at least three general principles for simultaneously achieving both objectives are emerging from ongoing scientific research. First, aligning high-canopy-cover stands with locations capable of supporting these forest types (e.g., north-facing slopes and drainage bottoms) will likely increase the resilience of both forest ecosystems and owl habitat to predicted increases in fire and drought severity under climate change. While desired conditions for the distribution of high-canopy-cover areas within spotted territories are uncertain, ongoing research using light detection and ranging (LiDAR) and studies of actual evapotranspiration and climatic water deficit are investigating these issues from a forest-restoration perspective. Second, if other attributes of spotted owl habitat, such as the prevalence of large defect trees, can be enhanced via forest management, it may be possible to maintain viable owl populations with less high-canopy forest present within territories than has been estimated in recent studies (Tempel et al. 2014). Third, emerging research suggests that once a certain amount of high-canopy forest is present within territories (presumably to meet nesting and roosting requirements), gains in medium (40 to 70 percent) canopy forest provide similar benefits to expected territory occupancy rates as gains in high canopy cover forests (Tempel et al., in press). While additional research is needed to develop desired conditions likely to confer both resilient forests and high-quality spotted owl habitat at the territory scale, these findings collectively suggest that achieving seemingly incompatible objectives may be possible.

When developing management guidelines based on studies of spotted owl demography and canopy cover conditions at the territory (and other) ecological scales, it is important to recognize that canopy cover is often estimated using different techniques in research and management applications. For example, canopy cover was estimated using aerial photointerpretation in Tempel et al. (2014) and Landsat imagery in Tempel et al. (2016), both mapping products being informed by ground-based vegetation measurement taken with spherical densitometers. By contrast, many forest management applications use Forest Vegetation Simulator-derived canopy cover values (Dixon 2002), which generally yield lower estimates (particularly when canopy cover is high) and do not necessarily indicate that desired conditions are not being met (Fiala et al. 2006). Determining whether desired conditions are being met requires developing appropriate calibration equations or “cross-walking” exercises.

Home range scale—

Heterogeneous forests containing a mosaic of vegetation conditions within spotted owl home ranges (but outside of the territory scale) could both enhance the resilience of Sierra Nevada forests and benefit owl populations (chapters 3 and 5). In particular, forest restoration practices that promote the maintenance/recruitment of old-forest conditions within a heterogeneous matrix of other forest and vegetation types would likely increase resilience to changing climate and other stressors. Moreover, the promotion of wildfire regimes characterized by a range of burn severities and that produce a mosaic of vegetation conditions, including unburned refugia, can potentially enhance spotted owl foraging habitat and prey resources (chapter 3). Mast-producing trees, particularly oaks, within mixed-conifer forests may also benefit owl prey species, particularly woodrats (*Neotoma* spp.) (chapter 3). However, diet studies of California spotted owls suggest that management intended to benefit prey populations would ideally be tailored to specific elevations (chapter 2). Shrubs and early seral stage forest may benefit the primary prey species at lower elevations (woodrats), whereas at higher elevations, older forests will more likely benefit the primary prey species (flying squirrels). Promoting woodrat habitat at the expense of suitable spotted owl nesting habitat (e.g., converting older forest to brush or early seral stands) could adversely affect owls. Moreover, as is current practice, we suggest that the scale at which spotted owl home range areas are managed vary along a latitudinal gradient because home ranges are smaller in the southern Sierra Nevada than in the northern Sierra Nevada.

Identifying spotted owl home ranges (as well as sites within individual home ranges) that would most benefit from fuel and restoration treatments would help balance the potential short-term impacts and long-term benefits of such treatments. Specifically, treatments in home ranges containing relatively poor spotted owl habitat and dominated by dense stands of shade-tolerant trees species on south slopes or ridgetops (i.e., fire prone) could be particularly beneficial (chapters 3 and 5). Conversely, treatments in home ranges containing habitat conditions known to promote reproduction, survival, and territory occupancy, and where forests did not depart appreciably from the “natural range” of variability are likely to be more detrimental to owl populations. An important issue to resolve when developing an owl habitat management strategy is that California spotted owl fitness appears to benefit from prevalent closed-canopy forests, conditions that can also increase the risk of high-severity fire and susceptibility to climate change and related stressors. A key issue is that home ranges that contribute disproportionately to population growth and stability may not be readily identified. It might be possible to mitigate this uncertainty, to some extent, by emphasizing the retention and promotion of other habitat features known to be important to spotted owls in all home ranges, such as large and old trees (especially ones with defects that are used as nest sites), large oaks, large coarse woody debris, and other features in treated areas. Emerging remote sensing technologies will likely improve the ability to characterize spotted owls habitat features at home range (and landscape) scales and thus provide opportunities to develop habitat targets based on more than simply canopy cover (chapter 6 and see below).

Landscape scale—

Similar to the home-rangescale, landscape-scale heterogeneity in forest conditions, shaped by a range of burn severities, could increase both the resilience of Sierra Nevada forests and spotted owl population viability. Thus, restoration activities intended to promote historical fire regimes and forest heterogeneity at broad spatial scales would be consistent with owl conservation objectives, particularly when implemented in areas where fire risk is high and the density of owl sites is low. Wildland fire (managed wildfire and prescribed fire) is an option, in conjunction with mechanical treatments to reduce fuel loads, for reducing risk of high-severity fire in the broader landscape. In addition to restoring historical fire regimes, landscape-scale fuel and restoration treatments could be designed to reduce risks to owl territories, particularly in highly productive ones. Nevertheless, some “protected” habitat will inevitably be lost to high-severity fire and the recruitment of nesting habitat outside of home ranges (e.g., via the protection and enhancement of large trees) through strategic management approaches will likely be needed to maintain a well-distributed spotted owl population. Such an approach explicitly recognizes and embraces the inherent spatial and temporal variability of forest conditions that is characteristic of a dynamic forest landscape. A habitat monitoring program, similar to the one developed for Pacific fisher, and discussed in more detail below, could be an effective means to account for the losses and gains in suitable habitat and to increase confidence that sufficient habitat is being maintained or restored at landscape scales to promote viable owl populations.

Landscape-scale conservation of spotted owl habitat is complicated by the fact that climate change will continue to alter the structure and composition of forests, as well as other environmental factors (e.g., microclimates and prey communities) that may affect California spotted owls (chapters 5 and 7). Projections of future climate suggest that pine-oak, mixed-conifer, and red fir forests, which comprise the majority of spotted owl habitat, are expected to shift upward in elevation but remain in locations where soils and topographic features maintain relatively suitable growing conditions and microclimates (chapter 5). Thus, the conservation, restoration, and promotion of old-forest conditions at appropriate sites on north-facing slopes and in steep drainages within the current range are likely to benefit spotted owls in both the short and long term. In addition, spotted owl habitat may develop at sites where it is currently not present (e.g., by promoting old-forest characteristics at higher elevations in montane conifer and red fir forests), and these sites could be particularly important in the future if owl populations track suitable climate conditions and that of the forests they tend to occupy. The establishment and growth of large-diameter trees at sites where they presently do not occur will take many decades and perhaps centuries depending on current forest conditions. Long-term planning would be required to identify such sites and implement management activities that will promote habitat features required by owls in a timely manner.

Postfire Management

Recent research indicates that California spotted owls persist in territories that experience low- to moderate- severity and mixed-severity (i.e., low to moderate fire regimes with inclusions of high-severity fire patches) wildfire and that small patches of high-severity fire may enhance foraging conditions for spotted owls (chapters 3 and 7). Salvage harvesting within such landscapes, particularly high-intensity salvage (removal of most snags), could negatively affect spotted owl habitat via the removal of snags and ultimately the reduction of coarse woody debris on the forest floor (chapter 5 and 7). However, site occupancy after fire is more likely to be affected when large areas of forest are burned at high severity (chapters 3 and 7). While salvage harvesting may have few short-term (<10 year) ecological benefits in such landscapes, over the long term (>30 years), judicious salvage practices (e.g., leaving some snags) followed by reforestation based on goals for desired restoration of historical conditions may help promote a return to mature conifer forest more quickly than an intensively burned area that is not harvested or replanted. Replanting trees in intensively burned landscapes, particularly large burns far from seed sources, will likely increase the rate at which spotted owl habitat is regenerated (chapter 5). However, forests resulting from reforestation efforts will be a function of planting design (e.g., density of tree planting) and subsequent management; large areas planted using conventional plantation prescriptions (i.e., high densities of equally spaced seedlings and homogeneous thinning) (chapter 5) could lead to delayed or poor habitat conditions for spotted owls, high risk to wildfire, and a reduction in landscape-scale diversity in vegetation conditions. In sum, spatial scale and planting practices are both important considerations when balancing tradeoffs among salvage harvesting, restoration, and spotted owl conservation. Salvage within low-moderate and mixed-severity burned areas can potentially affect spotted owls negatively, whereas the inability to replant large patches of high-severity burned forest could result in the long-term loss of owl habitat (chapter 5).

Barred Owl Range Expansion, Monitoring, and Control

Barred owls have recently expanded their range into the northern Sierra Nevada, and a small but increasing number of barred owls are being detected in the central and southern Sierra Nevada (chapter 7). Given the apparently profound impacts that they have had on northern spotted owls (*S. o. caurina*), control measures would likely be most effective while barred owls still occur at low densities in the Sierra Nevada (Dugger et al. 2016). As is the case generally for invasive species, the momentum of range expansion and abundance is expected to increase exponentially once barred owls have reached a critical, as yet unknown, density. The control of barred owls throughout forest areas in the Sierra Nevada will be difficult, if not impossible, when such a critical density is reached. If barred owls reach a critical density, as they have in the range of the northern spotted owl, we can expect a rapid increase in their numbers, interspecific competition, predation, and other impacts to spotted owls (Gutiérrez et al. 2007).

The primary control strategy for barred owls being tested in the range of the northern spotted owl is lethal removal. Barred owls are easy and cost-effective to remove from known locations (Diller et al. 2014). In the southern Cascades and Sierra Nevada, known barred owls could likely be removed in one or two field seasons by small crews of technicians using current techniques (Diller et al. 2014). An effective regional strategy could include a comprehensive survey and removal protocol that targets some specified degree of coverage and detection probability, and then the removal of barred owls wherever they occur in the Sierra Nevada. The success of such a program could be gauged based on how effectively it maintained barred owl numbers near their current low levels and prevented the rapid and sustained increases that were observed within the range of the northern spotted owl.

The development of barred owl monitoring and control measures could be an important topic for the conservation of the California spotted owl. Development and implementation of these measures would likely benefit from an integrated effort by several natural resource agencies, including the USFS, U.S. Fish and Wildlife Service, National Park Service, and California Department of Fish and Wildlife, as well as the cooperation of private landowners with property in the forest matrix.

Establishing Benchmarks for Conservation Success

Conservation of California spotted owls in the Sierra Nevada will require maintaining a well-distributed population of owls of sufficient abundance that the population will be resilient to the effects of climate change and other environmental stressors. A set of "conservation benchmarks" would be valuable to indicate the status of California spotted owl populations; such benchmarks could be used to evaluate monitoring results and gauge whether management activities have accomplished their intended objective of conserving spotted owls, or whether additional conservation measures need to be implemented, within an adaptive management framework. Establishing population and habitat benchmarks could reduce conflicts in interpretation of monitoring results and improve management responsiveness, at least to the extent that stakeholders agree on a set of predefined conservation benchmarks. Potential demographic metrics of spotted owl population status upon which conservation benchmarks could be based include abundance, population trends, and geographic distribution. Demographic metrics of population status could be feasible and cost effective to monitor and are generally indicative of the viability of California spotted owls in the Sierra Nevada. Habitat-based metrics, such as those currently under development as part of the Pacific Fisher Conservation Strategy, also have merit (see above) particularly at regional scales that are outside of existing spotted owl demographic study areas. However, such metrics cannot replace population-based metrics because spotted owls may decline for many reasons (e.g., barred owls, disease, etc.). In contrast, changes in habitat metrics only reflect changes in distribution and abundance of habitat.

Quantifiable benchmarks based on demographic metrics could include, for example: (1) the number (n) of spotted owls that represent different levels of probability of long-term persistence in the Sierra Nevada; (2) population trends that represent stable, increasing, or declining populations with given degrees of confidence; and (3) the number of owl territories that must be occupied in each geographic zone (perhaps as defined by clusters of ranger districts) to achieve different levels of probability of long-term persistence. Establishing scientifically defensible benchmarks for demographic metrics is challenging, and the minimum viable population size (MVP) concept, for example, has been criticized on the grounds that no single "magic" population size guarantees population persistence and that modeling frameworks for estimating MVPs are not exact (Flather et al. 2011). Nevertheless, as a practical matter, quantifiable conservation benchmarks are important to trigger management decisions—whether they indicate problems and trigger conservation “triage” efforts, or they indicate positive conditions and validate that management activities have had either a positive or neutral effect. Exploring extinction risk across a range of possible benchmarks and identifying thresholds below which extinction risk is increasingly likely can circumvent some of the perils associated with estimates of “absolute” conservation benchmarks. The California spotted owl is rare among species of conservation concern because there is a significant body of demographic data available to inform the development of conservation benchmarks for a population viability analysis perhaps guided by expert opinion. In addition, genetic analyses described below could provide historical context for conservation benchmarks developed as part of such a modeling exercise.

Progress on CASPO Uncertainties and Remaining Knowledge Gaps

Inventory

The CASPO technical assessment identified deficiencies in inventory (i.e., surveys to assess spotted owl occurrence and abundance) as one of the major uncertainties about California spotted owls (Verner and Taylor 1992). Specifically, they mentioned three parts of the owl’s range where basic information on owl locations and habitat use is needed: (1) the mountains of southern California; (2) the foothill woodlands of the western Sierra Nevada; and (3) the Coast Ranges, particularly the region from the Santa Cruz area northward to San Mateo County. Extensive surveys in southern California were conducted on the San Bernardino demographic study area (San Bernardino and San Jacinto Mountains) from 1987 through 2000 and as part of a regional U.S. Forest Service (USFS) monitoring program from 2003 through 2012 (see chapter 8). The information gained from these surveys suggests that owl populations in southern California have declined in the past 20 years and that little, if any, connectivity exists between owl populations in the various mountain ranges in southern California. However, based on an inspection of the California spotted owl databases from the California Department of Fish and Wildlife (CDFW) and the Pacific Southwest Region of the USFS (see figs. 4-1 and 4-2), it appears that very few spotted owl surveys have been conducted in other mountain ranges of southern California, the foothills of the western Sierra Nevada, and the Coast Ranges (particularly north of Monterey Bay) since CASPO. Some surveys may have been conducted on private timberlands within these geographic areas, but not incorporated into the CDFW database. Nonetheless, considerable uncertainty remains about the owl’s distribution and winter ranges in these areas, and the significance of these local and regional owl populations to the species’ rangewide persistence.

Monitoring

The CASPO recommendations included the formal adoption of demographic approaches for monitoring California spotted owls in the Sierra Nevada by continuing and expanding four demographic studies recently established at that time. The rationale for a demographic, as opposed to an occupancy-based, strategy stemmed from concern over potentially low statistical power to detect declines in territory occupancy using methods developed for northern spotted owls. Moreover, demographic studies provide more insight into the mechanisms behind changes in populations, and they are likely better able to contend with lag effects associated with the owl's long lifespan. These ongoing demographic studies have now yielded reasonably precise estimates of population trends and indicate that two of three study populations occurring primarily on national forests are declining in abundance, and the third is likely declining (chapter 4).

From a statistical perspective, conclusions about population trends are limited to the areas encompassed by the four demographic study areas because the areas were not randomly selected. However, because study areas are large, span the length of the Sierra Nevada, have long-term (20+ years) data, and have similar study designs, they likely reflect the trends in California spotted owl populations throughout NFS lands on the west side of the Sierra Nevada. To achieve a regional-scale inference based on sampling of owls, monitoring would have to occur at a much larger scale using a lower intensity approach that did not sacrifice the statistical rigor of the demography study areas. Subsequent to CASPO, formal approaches based on presence/absence data (i.e., occupancy analysis) were developed to provide a statistical framework for estimating changes in occupancy over space and time while accounting for imperfect detection probabilities. For example, a recent analysis of territory occupancy data for the Eldorado Study Area found that annual rates of change in occupancy were similar to rates of change in abundance estimated with demographic methods (reverse-time mark-recapture models). Although this congruence is encouraging, developing an occupancy-based monitoring program outside of the demographic studies (i.e., a regionwide scale of monitoring) would involve beginning a new monitoring program with no prior information. Moreover, given the species' long lifespan, detecting trends in spotted owl populations can take many years, even decades (as was the case with the existing demography studies). Nonetheless, a regional-scale, occupancy-based monitoring program would be highly complementary to the information provided by the demographic monitoring and would facilitate the assessment of barred owl impacts and serve as a valuable component of a barred owl management strategy (see below).

Research

One major knowledge gap identified in CASPO involved "habitat capability" as little to no information existed on relationships between fitness (survival and reproduction) and habitat features. As described in chapter 4, significant progress has been made in this regard as several studies have investigated correlations between habitat features and owl demographic rates such as reproduction, survival, and occupancy across a range of spatial scales. A general picture has emerged where individual fitness and territory occupancy appear to be linked to the availability of closed-canopy forest with complex vertical structure. Other vegetation types (e.g., montane chaparral) distributed within a mosaic of forest types may constitute important foraging habitat, particularly when juxtaposed with closed-canopy forests, and may confer fitness benefits to spotted owls; however, such linkages have not been demonstrated conclusively for California spotted owls.

Priority Research Needs

The synthesis of information in each chapter, as well as progress made on knowledge gaps identified as part of the CASPO process, indicate that a paradox exists with respect to our understanding of the California spotted owl's ecology and life-history needs. On the one hand, many aspects of its ecology have been studied intensively, and consequently, we have a reasonable understanding of population trends within specific demography study areas as well as habitat associations at a variety of spatial scales. On the other hand, many important uncertainties remain; two of the most important being (1) the environmental and anthropogenic causes of observed population declines, and (2) the short- and long-term effects of forest fuels and restoration management and wildfire regimes on spotted owls. Reducing these two uncertainties, as well as others described below, would be facilitated by creative research approaches that integrate emerging advances in animal tracking technology, remote sensing-based habitat mapping, and population genomic and other molecular approaches. Below, we highlight priority research needs for the coming years and briefly point to possible new research approaches that could be employed to reduce outstanding uncertainties.

Identifying Environmental Causes of Population Declines

Spotted owls are declining in abundance on some NFS lands in the Sierra Nevada (chapter 4). The identification of environmental factor(s) responsible for population declines is essential for halting and reversing wildlife population declines. Understandably, much research on California spotted owls has focused on habitat associations and, more recently, the influence of habitat quality and wildfires on populations in an effort to inform managers of forest lands (see chapters 2, 3, and 4). However, studies explicitly attempting to diagnose causes of the decline and discriminate among candidate environmental factors are lacking given the inherent challenges in conducting such work, and mechanism(s) behind observed declines thus remain uncertain. Tempel et al. (2014) suggested that reductions in the amount of closed-canopy forests may have contributed to observed declines in spotted owl abundance in the central Sierra Nevada, but the study area-level decline in owl habitat (about 8 percent) was considerably less than the decline in owl numbers (about 50 percent) over a two-decade period. The population decline may have exceeded the recent reduction in habitat because of lag effects related to historical habitat change, nonlinear effects of habitat loss, and changes in other, unmeasured habitat elements. However, factors unrelated to habitat could also be contributing to the decline (see chapter 7), and carefully designed studies are needed to understand the relative importance of potential threat factors. Moreover, multiple environmental factors could be responsible for observed population declines, and they could be acting synergistically (interacting) such that cumulative effects exceed the impacts of stressors when considered individually and even additively. Clearer understanding of these processes would facilitate the effective allocation of conservation resources and improve the likelihood of halting and reversing declines.

Several conceptual frameworks have been developed to diagnose causes of decline in species of conservation concern (e.g., Peery et al. 2004). These frameworks can include comparing populations experiencing different levels of potential threat factors, comparing population trends before and after a threat factor emerges, and direct experiments designed to manipulate threat factors and measure an appropriate response. Carefully designed experimental studies constitute the most rigorous way to test hypotheses about causes of declines (e.g., effects of forest treatments) in spotted owls (chapter 7), but are challenging to implement because of the owl’s long lifespan and large spatial requirements, and previous attempts have met with limited success. Controlling the many factors influencing owl population performance, while testing specific hypotheses, is immensely difficult on landscapes with significant environmental variability and diverse historical conditions. Moreover, the owl is currently declining, and additional losses of habitat under the auspices of “experimentation” need to be carefully vetted with consideration for potential detrimental effects on the species. Successful research would also require experimental control over large geographic areas, something that has proven to be very difficult to execute.

Comparing populations experiencing different levels of threats (e.g., amounts of habitat loss, disease incidence, prevalence of barred owls) is a potentially powerful approach. For instance, comparisons of population growth rates among the four Sierra Nevada demographic study areas (owls on the three NFS study areas are declining, whereas owls on the National Park Service [NPS] study area appear stable; chapter 4) suggest that past and current management differences between NFS lands and NPS lands could be responsible for spotted owl declines in the former. However, ecological and other anthropogenic differences between NFS and NPS lands could be responsible for differences in population trends between land ownerships. For example, the NFS study areas contain a large amount of private land managed for commercial timber production, whereas the NPS study area does not. Inference about causes of declines can be strengthened by considering individual owls or territories as the sampling unit and relating spatiotemporal variation in demographic parameters (e.g., survival, reproduction, and occupancy) to variables that reflect potential threat factors. In fact, population-level research has thus far shown that the individual/territory is the key sampling level for attempting to partition the complex and interacting mechanisms behind the observed population declines in the long-term and spatially extensive monitoring demographic study areas. However, a key gap here involves a dearth of individual- and territory-level information (other than relatively coarse-scale habitat metrics) that can be used to explain variation in the demographic rates. Greater emphasis on collecting information about prey availability, competitor and predator abundance (particularly barred owls—at this time they are only a potentially important consideration within the Lassen Study Area), and diseases within the demographic study areas could help elucidate the causes of declines. Some of this information can readily be collected as part of captures (e.g., health parameters) or surveys (e.g., presence/absence of predators or competitors) that are already part of the monitoring activities conducted for each demographic study. Although correlative associations (i.e., observational studies) between owl demographic rates and environmental variables do not necessarily identify causative mechanisms behind population declines, concordance in results across study areas greatly strengthens inferences about causes. Moreover, once reasonably well-supported correlations between environmental factors and demographic rates have been identified, simple population models can be used to estimate the sensitivity of population growth to each variable. Environmental variables with a strong influence on population growth (i.e., high sensitivity) and that are amenable to manipulation would then be likely candidates for management intervention. Although some information (notably prey availability) may be impractical to collect at a sufficiently large number of territories, there are smaller scale opportunities and indirect methods for studying prey as a limiting factor (see below). The research approach described here would benefit from maintaining the three demographic study areas on NFS lands and restoring the NPS study area (Sequoia and Kings Canyon), as doing so would facilitate both broad- and fine-scale assessment of relationships between owl population and changes in environmental conditions.

Effects of Fuel Treatments and Wildfire on Population Viability

Greater understanding of the effects of fuel and restoration treatments and wildfire on California spotted owls is needed to inform forest management that is intended to recover owl populations and restore ecosystem resilience in Sierra Nevada forests (chapters 3 and 7). Fuel and restoration treatments may confer long-term benefits to spotted owls by reducing the risk of large high-severity fires (chapter 5), but it is unknown under what circumstances potential long-term benefits outweigh more certain short-term impacts to owls if treatments substantially change forest structure. In short, for fuel and restoration treatments to confer a net benefit to spotted owls, the following conditions all must be met:

- Large high-severity fires have a negative effect on owl habitat and populations.
- Fuel and restoration treatments effectively reduce the frequency and size of high-severity fires and water-stress mortality that are detrimental to spotted owl habitat.
- Treatment changes to forest structure do not lead to the extirpation of spotted owls or to such low abundances that owls cannot recover to realize the benefits of restored fire regimes.

High-severity fires—

Until recently, the effects of high-severity fire on spotted owls has remained uncertain, in part, because studies had been predicated on a limited number of territories experiencing extensive high-severity fire, potential fire effects have been confounded by the effects of salvage logging, and the lack of marked individuals makes it difficult to interpret the occupancy status of territories (chapters 3 and 7). However, the King Fire of 2014 provided an unprecedented opportunity to understand the impacts of a large high-severity fire on California spotted owls given its impact on the Eldorado demography study area in the form of a natural “before, after, control, impact” experiment. Spotted owl occupancy declined markedly at severely burned sites 1-year postfire, and the large patch of severely burned forest was strongly avoided for foraging by global positioning system (GPS)-tagged individuals whose territories were at the perimeter of the fire (Jones et al. 2016b). Because fire impacts were not confounded by salvage harvesting, this study thus provided compelling evidence that high-severity fire can negatively affect spotted owls when burn patch size is large. In contrast, occupancy did not appear to decline in the first breeding season following the Rim Fire (Bond and Lee 2015); however, caution is advisable when interpreting results after only 1 year given the high site fidelity of spotted owls and without knowledge of the distribution, size, and severity of burned forest patches. Caution is also appropriate because owls were not individually marked and movements among territories by unmarked individuals can give the appearance of occupancy in vacant territories. Additional opportunities will likely emerge for studying the effects of severe fire on spotted owls by taking advantage of these opportunities through monitoring responses after fires and using radiotelemetry or GPS tagging when feasible to augment our understanding of owl responses to fire.

Fuel treatments—

In terms of fuel treatment effectiveness, model-based and empirical evidence indicate that fuel treatments can reduce fire severity and spread, and that combining fuel treatments (e.g., Strategically Placed Landscape Treatments [SPLATs] or topography-based variable-density reduction) with prescribed and managed fire can effectively reduce the extent of high-intensity fires in the Sierra Nevada under most conditions (chapter 5). In some recent wildfires (e.g., Rim, King, Valley, Butte), fire behavior has exceeded current model predictions, producing large patches of high-severity effects, including areas with recent (<15 years) fuels treatments. It is not always clear what is driving this extreme behavior, but some observations and early analyses (Lydersen et al. 2013) suggest two likely factors: (1) heavy fuel loads sufficient for the wildfire to generate its own extreme weather, and (2) increasingly efficient early suppression of past fires, which has effectively selected for fewer, high-severity large wildfires that “escape” containment during more extreme weather than occurred historically (North et al. 2015). Fuels treatments, such as some combination of mechanical thinning, prescribed burning and managed wildfire, will likely only be effective in the absence of extreme fire behavior.

Treatment changes to forest structure do not lead to the extirpation of spotted owls—

Little direct information exists about the short-term influence of fuel treatments on owls. Tempel et al. (2014) found a small negative effect on reproductive output related to “medium-intensity” timber harvests that included, but was not limited to, SPLATs and SPLAT-like thin-from-below prescriptions with relatively even spacing among the remaining trees and found no effect on territory occupancy or individual survival. Stephens et al. (2014) reported a decline in the number of territorial owl sites 3 to 4 years following implementation of a landscape fuels management strategy primarily consisting of defensible fuels profile zones and forest thinning treatments. The potential effects of actual SPLATs or “newer” fuels reduction and restoration treatments that vary forest conditions with topography (North et al. 2009) have not been assessed. Further, studies of the potential long-term benefits of restoring historical fire regimes (reducing the extent of high-severity fire) to spotted owls have remained in their infancy. Recently, the Sierra Nevada Adaptive Management Project (SNAMP) investigated this question at the “fireshed” scale (tens of square kilometers) within an interdisciplinary framework. Results from this project suggest that SPLATs can reduce the risks of high-severity fire to spotted owls on the fireshed scale over a 30-year timeframe (Tempel et al. 2015). In the absence of fire, SPLATs had a persistent negative effect on spotted owl fitness over the modeling period (Tempel et al. 2015). Thus, additional research will be needed that incorporates absolute risks of fire into model-based evaluations of fuel treatments effects in order to examine relative risks in greater detail. Moreover, similar studies conducted at landscape scales will be needed to fully assess the effects of implementation of fuel treatments on the spotted owl population throughout the Sierra Nevada. Ultimately, rigorous characterization of the short- and long-term effects of fuel and restoration treatments on spotted owls will be possible with the development of a spatially explicit population model that could be used as a decision-support tool to help evaluate the potential effects of alternative forest management actions (see above).

Historical (Pre-Euro-American) Abundance of California Spotted Owls

The California spotted owl is unusual among species of concern because more than 20 years of detailed demographic data have been collected at multiple sites, whereas most threatened species do not have such a wealth of information to guide managers. However, our insight into factors affecting population trends is limited to recent decades although wildfire suppression and timber harvesting have altered the composition and structure of Sierra Nevada forests since the late 19th century (chapters 4 and 5). As discussed above, unavoidable uncertainty exists about population trends over the past 150 years and the full suite of factors that influenced populations. Several hypotheses have been suggested about this early history of owls, but these cannot be tested with information from demographic studies, and existing genetic information does not provide definitive information regarding historical population size. However, emerging genetic-based methods provide exciting opportunities to evaluate demographic history in California spotted owls (chapter 4). Populations that have dramatically declined (i.e., effective population size) tend to lose genetic diversity (e.g., heterozygosity and allelic diversity) because of genetic drift. When historical specimens from museums are available, direct comparisons of genetic diversity (and thus effective population size) can be made between historical and modern sampling times, but few such samples are available for California spotted owls. However, the recent advent of next-generation-sequencing (NGS) has revolutionized researchers' ability to characterize demographic history using genetic samples collected at a single point in time (chapter 4). Indeed, NGS approaches now allow for the screening of tens of thousands of loci (as opposed to tens of loci) and thus the evaluation of competing models of demographic history (e.g., population expansion or contraction over relatively short periods of time) and estimation of important population parameters (e.g., pre-Euro-American population size and subsequent trends in population size). As such, "genomic" methods could provide considerable potential for understanding the combined effects of forest management activities on spotted owls in the 20th century. Answering the question of whether spotted owls are more abundant currently or historically would provide insight into how resilient owl populations might be to future population perturbations as a function of climate, fire, management, or combinations thereof.

Enhancing Foraging and Prey Habitat

Evidence is mounting that California spotted owls forage in heterogeneous forests containing a mosaic of vegetation types and seral stages (including patches of old forest) because complex landscapes support a diversity and abundance of small mammal prey (chapter 3). Indeed, the juxtaposition of mature conifer forests containing a hardwood component with other vegetation types may enhance foraging opportunities and confer fitness benefits to owls (chapter 3). However, greater understanding of the vegetation conditions that shape the abundance and distribution of important prey species in the Sierra Nevada would facilitate the development of effective stand- and landscape-scale forest management strategies to enhance spotted owl foraging habitat. Pairing such forest management activities with carefully designed field studies (ideally within an experimental framework) could provide a rigorous means for evaluating the potential benefits of efforts to enhance spotted owl prey and foraging habitat. Assessments of forest management intended to improve foraging habitat quality would also benefit from the integration of pellet-based diet analyses, prey and vegetation sampling, as well as the use of fine-scale tracking of radio- or GPS-marked owls. Ultralight GPS loggers are now sufficiently small (5 to 10 g [0.2 to 0.4 oz]) to be deployed safely on owls, can generate precise locations at rapid intervals, and would provide an effective tool for determining the use of different vegetation types for foraging. Such studies could be enhanced by the use of isotopic tracers applied to prey occurring in the target patches, which would allow for the estimation of the contribution of prey captured in different habitats to the total biomass of prey consumed by marked owls.

Impacts of Climate Change to Spotted Owls and Their Habitat

Climate change will inevitably alter the structure and composition of Sierra Nevada forests and thereby the suitability and configuration of spotted owl habitat (chapter 5). Thus, it will be important to identify sites that are most likely to continue to support suitable habitat, as well as sites that are likely to transition into suitable habitat as the climate changes, and to actively manage and conserve priority sites (e.g., by reducing fire risk and promoting old-forest conditions). Existing habitat areas that are likely to retain suitability into the future are generally predicted to occur in cooler, north-facing areas with high topographic relief, and existing models of forest vulnerability provide a tool for predicting the specific locations of likely refugia on the landscape (chapter 5). Although plants and animals in montane systems are generally expected to make upslope shifts in distributions as the climate warms, novel vegetation communities are likely to emerge, and changes in the distribution of owl habitat and prey will likely be influenced by soil conditions and topographic features (chapter 5). A recent climate change-modeling study based on 20 years of spotted owl occupancy data from the Eldorado demography study area suggests that maintaining viable spotted owl populations is most likely to be achieved by managing for owl habitat at high-elevation territories (Jones et al. 2016a). This analysis constitutes a novel and useful first attempt to project the effects of climate change on spotted owl distribution in the Sierra Nevada; however, it does not explicitly consider projected changes in forests or fire regimes in this region. Future studies could further our understanding of potential climate change effects by linking expected changes in owl distribution to shifts in vegetation communities and change in fire dynamics—an effort that would benefit from integrative efforts involving wildlife, forest, and fire ecologists.

Habitat Evaluation Tools

Accurate and high-resolution mapping of the California spotted owl habitat elements across landscapes will enhance the effectiveness of many aspects of owl habitat conservation, including monitoring the effect of management actions on habitat quality. As described in chapter 6, most previous map-based studies of California spotted owl habitat associations have made use of moderate-resolution Landsat imagery that cannot discern some key structural elements (e.g., high concentrations of residual trees or multilayered canopy) that are important to spotted owls. Emerging remote sensing methods such as LiDAR will continue to improve our ability to characterize habitat quality for spotted owl habitat at landscape scales and hopefully provide the spatiotemporal vegetation data needed to understand the effects of forest management and natural disturbance on owls. Despite improvements in habitat mapping provided by LiDAR and other high-resolution sensors, there are many outstanding needs for mapping of wildlife habitat, including the mapping of snags, large trees, and large broken-top trees; development of improved metrics to quantify vertical canopy structure; and development of tree species distributions in mixed-conifer forests. The integration of various LiDAR techniques with other optical imagery may overcome some of these hurdles and improve the mapping of wildlife habitat in the near future, particularly to the extent that simple, field-validated remote sensing metrics can be linked to management goals (chapter 6).

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Glossary

Clearcut—An even-age regeneration or harvest method that removes all trees in the stand producing a fully exposed microclimate for the development of a new age class in one entry.

Commercial thin—A harvest intermediate between planting and final harvest of a stand with the objective of reducing stand density to improve growth, enhance forest health, and other resources objectives. Treatment can recover potential mortality while producing merchantable material. Thinning can include application of the following techniques to achieve objectives: chemical (killing of unwanted trees by herbicide application); crown (removal of trees from dominant and co-dominant strata); free (no consideration to crown position); low (removal of trees from lower crown classes); mechanical or row (removal of trees either in row, strips by using a fixed spacing interval); selection (removal of the crown class to favor those in the lower crown classes.)

Conversion (forest)—Alteration of timber-growing lands to a use or uses other than the growing of timber.

Core area—A management term used to refer to the area within an owl's home range that receives concentrated or disproportionally high use by an owl.

Cover type—A category within a classification scheme defined by the user that distinguishes among different landscape conditions (e.g., vegetation types, water, talus slopes).

Damaged timberland—An area of timberland where wildfire, insects, disease, wind, flood, or other disturbance has occurred that has resulted in a reduced stocking of trees below "minimum stocking requirements."

Fuel break—An area where the cutting or removal of trees eliminates the vertical continuity of vegetative materials and the horizontal continuity of tree crowns for the purpose of reducing flammable materials and maintaining an open space to reduce fire spread, duration, and intensity.

Foraging habitat—The cover types an owl uses to forage for food and that are found within each owl's territory and home range.

Group selection—An uneven-age regeneration method in which trees are cut in small groups to establish a matrix of new age classes. The width of groups is commonly less than about twice the height of the mature trees. Individual trees in the matrix may or may not be harvested to provide improved growing conditions for remaining trees. Multiple entries of this activity ultimately results in an uneven-aged stand of three or more age classes.

Habitat quality—The capacity of the habitat to provide resources and conditions suitable for individual and population persistence.

Home range—The area used by an individual to meet its requirements for survival and reproduction.

Landscape matrix—The mosaic of cover types in a landscape outside of specified areas recognized as supporting spotted owls (i.e., designated territories and home ranges), which may or may not include areas of suitable habitat.

Nest stand—The forest stand containing the location of a nest (note: nests can occur on the edge of forest stands).

PAC—protected activity center. A management area designation on National Forest System lands. A (123-ha) 300-ac area of the best available habitat around a known nest site or center of activity within which specified habitat protective measures are applied.

Overstory removal cut—The cutting of trees within the upper canopy layer with the purpose of "releasing" (i.e., removing competition from dominate trees) understory trees. The primary source of regeneration is advance reproduction. A minor (less than about 10 percent of full stocking), live component of the upper canopy may be retained for reasons other than regeneration.

Rehabilitation (forest)—Activities undertaken for the purposes of restoring and enhancing the productivity of commercial timberlands which do not meet minimum stocking standards. Activities may include harvest or clearing of the site followed by site preparation and restocking.

Salvage cut—An intermediate harvest that removes trees that are dead or dying because of injurious agents other than competition for the purpose recovering economic value, as well as to improve forest health.

Sanitation cut—An intermediate harvest removing trees to improve stand health by stopping or reducing the actual or anticipated spread of insects and disease, but not necessarily to recover economic value.

Seed-tree cut—A type of logging where all trees are removed except those needed for seed production. Prepares the seed bed and creates a new age class in an exposed microenvironment. Additional trees may be retained to provide a minor (less than about 10 percent of full stocking) live component after the removal cut, for reasons other than regeneration.

Shelterwood cut (includes prep and removal)—The shelterwood logging method results in regeneration of a stand via a series of harvests (preparatory, seed, and removal). The shelterwood regeneration method is normally used when some shade canopy is considered desirable for the establishment of regeneration.

single-tree selection cut—An uneven-age logging method where individual trees of any size classes are removed more or less uniformly throughout the stand creating or maintaining a multiage structure to promote growth of remaining trees and to provide space for regeneration. Multiple entries of this activity ultimately results in an uneven-aged stand of three or more age classes.

Territory—The area of the home range from which an owl excludes (i.e., defends other owls. Presumably such areas are most important for nesting, roosting, and foraging. The territory is commonly represented for the purposes of habitat analysis as a 1,000-ac circle (1.5-mi radius) around the nest site or half the average nearest neighbor distance of owls within a population.

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F^3: simulating spatiotemporal forest change from field inventory, remote sensing, growth modeling, and management actions

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Abstract

Contemporary forest management requires highly-detailed, spatially-contiguous, multi-temporal, and scenarios-comparable forest conditions. Field inventories and individual-tree models often contain highly-detailed data and allow for long-term complex scenarios comparison, but the information is only at sampled locations and lacks complete spatial coverage. Forest landscape models (FLMs) provide landscape-level spatiotemporal data, but the details that are important to land managers are often lost in the generalized outputs. We developed a modeling framework, F^3, to integrate FIA (Forest Inventory and Analysis) plots, the Forest Vegetation Simulator (FVS), and FastEmap (Field And SatelliTe for Ecosystem MAPping) to simulate spatiotemporal forest change under natural succession and vegetation management. F^3 extrapolates the details of forest inventory plots and individual-tree model outputs to a spatially-contiguous landscape by fusing tree-list field measurements, individual tree growth and yield models, remote sensing and environmental geospatial datasets. F^3 allows for area-specific management action simulations. F^3 compares FVS results with field measurements for temporal accuracy assessment and uses a leave-one-out cross-validation for spatial accuracy assessment. F^3 adopts parallel computation techniques to implement the modeling in an automatic and efficient manner. The proof of concept of F^3 was demonstrated in Tahoe National Forest (TNF) showing spatiotemporal changes on six forest structural metrics (quadratic mean diameter, basal area, biomass, habitat suitability index, canopy cover, and coarse woody debris) under natural succession, regeneration-cut, and thinning scenarios for the years 2014-2114 at a 30 m resolution. F^3 can be used for initializing FLMs and for analyzing a wide range of ecosystem services; however, the under-representation of certain forest types in the FIA plot data set, the modeling bias from FVS, and choice of FastEmap covariates contribute to major uncertainties in the framework.

Keywords: Forest Inventory Analysis, Forest Vegetation Simulator, forest landscape models, ecosystem service, species distribution model

1. Introduction

1.1 Forest information requirements

Forests are a complex ecosystem that provide an array of benefits and services beyond marketable commodities. With increased interests in old growth conservation, wildlife habitat management, carbon sequestration, forest restoration, fuel reduction, biomass energy, and wildfire risk assessment, in addition to maintaining a sustainable timber supply, forest managers and policymakers have to compare alternative management actions in order to achieve multiple and sometimes conflicting objectives (Sharik *et al.* 2010; Zald *et al.* 2014; Binder *et al.* 2017). During this process, integrating various data from field measurements, remote sensing, and modeling exercises to project future forest conditions associated with specific management actions across multiple temporal and spatial scales is essential (Taylor *et al.* 2009; Shifley *et al.* 2017). For this purpose, the information is best to meet five characteristics (Crookston and Dixon 2005; Zollner *et al.* 2008; *Zald et al.* 2014; Huang *et al.* 2017; Shifley *et al.* 2017). First, the information needs to compare multiple management scenarios to answer "what if" questions. Second, the information needs to be spatially-explicit, permitting landscape-scale analysis. Third, the information needs to cover long time periods as the management effects may last several decades. Fourth, the information needs to incorporate sufficient details about forest conditions for many forest management and research applications. Fifth, the information should be delivered in a timely manner for operational usage.

1.2 Individual-tree models

To meet these demands, many efforts have been attempted to project forest conditions across spatial and temporal domains with different management scenarios considered. The first effort is the empirical, individual-tree growth and yield models favored by forest managers (Gálvez *et al.* 2014). These models describe the stand with a list of tree records where each record reflects the current tree information such as stem diameter, height, and crown length. Then they predict growth and survival over time for individual trees, as well as the corresponding cumulative change for the stands and landscapes represented by the inventory plots (Binder *et al.* 2017; Shifley *et al.* 2017). Because the dimensions of hundreds or even thousands of trees in a stand can be explicitly projected by individual-tree simulators, a detailed picture of stand structure and composition over time can be revealed, which facilitates the simulation of many forest-related functions and processes such as wildlife habitat and carbon sequestration (Crookston and Dixon 2005; Binder *et al.* 2017). In the U.S., many individual-tree simulators in different regions have been incorporated into the Forest Vegetation Simulator (FVS) (Crookston and Dixon 2005; Binder *et al.* 2017).

The FVS is the U.S. Forest Service's (USFS) nationally supported framework and a widely used growth and yield modeling platform in the U.S. (Dixon 2002). The FVS operates at the individual-tree level and simulates growth, mortality, and regeneration based on empirical studies to depict forest vegetation change in response to natural succession and proposed management actions. FVS is based upon a body of scientific knowledge developed from decades of natural resources research and experience. FVS uses 22 "variants" to represent different geographic areas across the country. FVS is a mature modeling technology that is documented, validated, and supported by a permanent USFS staff serving private and public land managers (https://www.fs.fed.us/fvs/). Forest managers link FVS to forest inventory data bases to summarize and predict current and future forest stand conditions under different management alternatives. The FVS is capable of simulating a wide range of customized silvicultural treatments and has the capability to model growth across a wide array of forest species compositions and structures (i.e., single to mixed species, even-aged to uneven-aged stands and single- to multi-story stands) (Dixon 2002). At present, FVS is routinely and extensively applied throughout the U.S. to support on-the-ground forest planning and silvicultural decisions (Crookston and Dixon 2005; Gálvez *et al.* 2014; Shifley *et al.* 2017). Despite its details of modeling each individual tree, one principle shortcoming of FVS is that it does not operate in a spatially-explicit analysis framework (Falkowski *et al.* 2010; Gálvez *et al.* 2014); this weakness is reflected in the "California Climate Investments" program (California Air Resources Board, 2017). In this program, FVS is used to estimate the net greenhouse gas benefit from reforestation, forest pest management, fuels reduction, forest conservation, and biomass utilization. Users need to model the "baseline" and "project" scenarios using FVS for 50-80 years. Since on-the-ground activities are conducted at landscape level (more than several hectares), it is desirable to program managers to upgrade FVS to function at the landscape scale, which is the incentive of our study reported here.

In summary, individual-tree growth and yield models such as FVS can ingest tree-list inventory and track the species, number, and size of each tree in a stand, and they are favored by forest managers for real and complex on-the-ground forest management and planning; however, individual-tree models are difficult to apply in a spatially-explicit manner over a large spatial extent. This weakness can be overcome by a second type of models: Forest Landscape Models (FLMs).

1.3 Forest landscape models

FLMs are applied to extensive forest areas by subdividing the landscape into cells (or polygons) and projecting attributes of the vegetation in each cell. There are many FLMs such as TreeMig (Lischke *et al.* 2006), LANDIS (Mladenoff *et al.* 1996; He and Mladenoff 1999; Yang *et al.* 2011), LANDIS PRO (Wang *et al.* 2013; Luo *et al.* 2015), and iLand (Seidl *et al.* 2012); these FLMs differ in the level of detail for each stand and/or the complexity of forest landscape processes (Shifley *et al.* 2017). FLMs have several limitations (Shifley *et al.* 2017). First, the widely available data for parametrizing initial forest conditions of FLM have to be transformed with additional assumptions to match the requirements of a given model. Second, FLMs typically simplify stand-scale processes (e.g. competition at the tree level) for landscape scenario analyses in order to reduce the massive computational load; simplifying stand-scale process loses the details about forest conditions required for contemporary forest management. Third, it is especially problematic to calibrate and validate FLMs to address large-scale forest change scenarios. Considering these problems, Wang *et al.* (2013) concluded that a FLM that is capable of invoking an established individual-tree-based simulation model such as the FVS to simulate tree and stand scale forest change for each raster cell at each time step is highly desirable.

1.4 Research objectives

Considering the advantage and disadvantages of individual-tree and FLMs, we sought to combine the advantages from both model types into a new modeling framework. With access to the detailed U.S. Forest Inventory Analysis (FIA) dataset (U.S. Forest Service 2017a), the mature individual-tree growth and yield FVS (U.S. Forest Service, 2017b), and the recent development of the point-to-surface mapping tool "Field And SatelliTe for Ecosystem MAPping (FastEmap)" (Huang *et al.* 2017), the objective of this research was to develop and demonstrate a modeling framework that can simulate spatiotemporal forest change from highly-detailed tree-list inventory data under different vegetation management scenarios. This framework uses FIA to initialize forest conditions, then uses FVS for multi-temporal scenario projections, and finally uses FastEmap for point-to-surface extrapolation. We abbreviate the modeling framework as F^3 (i.e., **F**IA, **F**VS, and **F**astEmap). F^3 has the following four characteristics. First, it uses FIA inventory data sets as input to drive the individual-tree forest growth and yield FVS model; therefore, it keeps the high detail of FIA and FVS. Second, it enables users to explore spatially-contiguous forest change rather than point-specific inventory plots. Third, it allows the comparison among different forest management scenarios applied to specific areas to address "what if" questions. Fourth, it allows temporal and spatial accuracy assessment. Taking the heterogeneous Tahoe National Forest (TNF) as an example, we demonstrate how F^3 simulated the change of six metrics at 30 m resolution for 100 years under three scenarios of natural succession (no management), regeneration-cuts, and thinning.

2. Methodology

F^3 combines the details and capabilities of FIA, FVS, and FastEmap to project long-term forest conditions over a landscape and is described in detail in the next sections. The field inventory measurements from the FIA program are used for initializing forest conditions where sampled (2.1). The FVS is utilized to project multi-temporal forest dynamics for these point-specific stands (2.2). Point-specific projections are extrapolated to a spatially-contiguous landscape using FastEmap (2.3). These three elements are integrated to produce maps to assess the forest change (2.4). The accuracy assessment is included (2.5). We describe the details of technical implementation (2.6). The general workflow is shown in **Figure 1**. We applied our approach to the TNF as a proof of concept of the modeling framework (2.7).

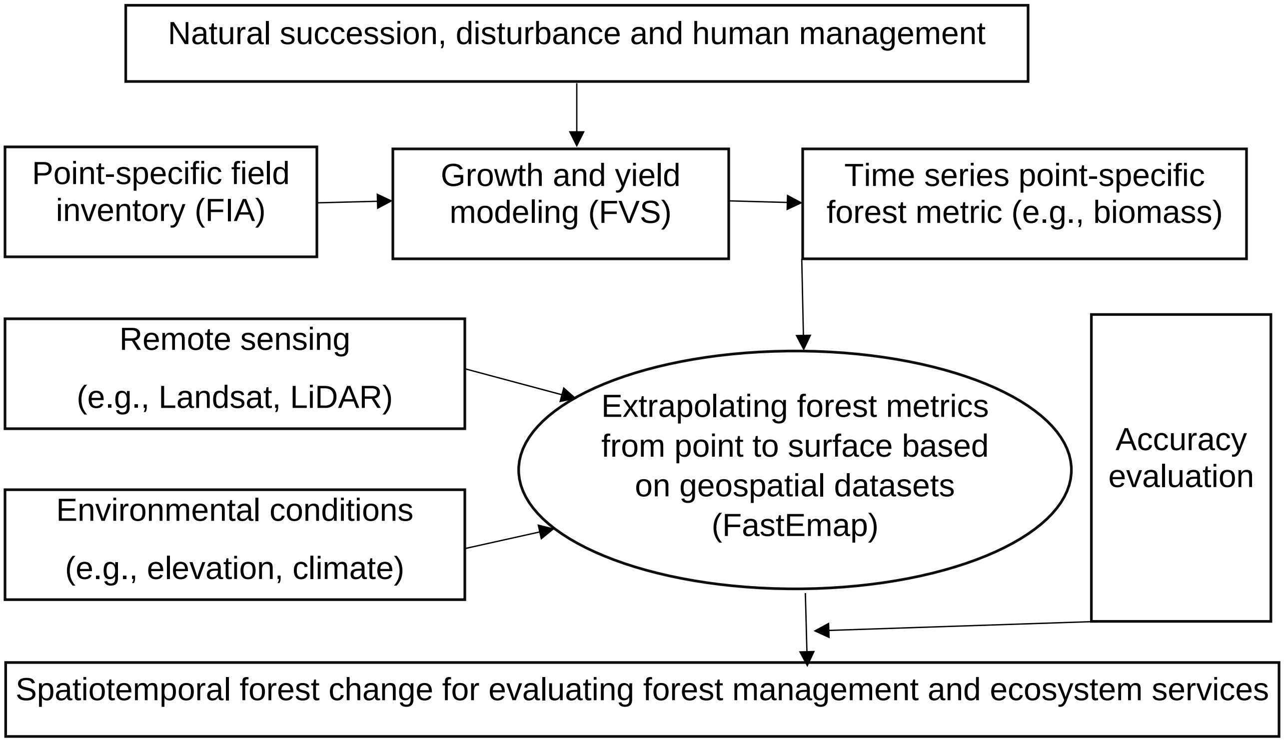

Figure 1. Flowchart of F^3 modeling framework

2.1. Field inventory FIA

The FIA program is the national forest inventory program implemented by the USFS to collect, compile, and archive data about the extent, condition, status, and trends of forest resources for predominately forested conditions throughout the U.S. in a consistent and compatible manner on the national grid (Smith 2002). More details of FIA annual inventory protocols can be found in the FIA national core field manual (U.S. Forest Service 2017c). The positions of FIA plots for public access are perturbed from their actual coordinates by U.S. law, but their actual coordinates are used in F^3. FIA data are used as inputs for FVS modeling.

2.2 Individual-tree model FVS

With tree-list data from inventory plots, the FVS model can project forest change caused by natural succession, disturbance, and management for each stand. We utilize the FVS's capability to simulate the temporal forest change for each individual FIA plot. FVS is a semi-distance-independent, individual-tree growth and yield model to predict changes in tree diameter, height, crown ratio, crown width, and mortality over time (Dixon 2002; Crookston and Dixon 2005; Hoover and Rebain 2011; Keyser and Keyser 2017). FVS projects each stand several decades at a resolution of 5–10 years.

A variety of stand-level variables, including slope, aspect, elevation, site index, and stand location, inventory design specifications, and other parameters are used in the FVS modeling process (Dixon 2002; Hoover and Rebain 2011). Necessary tree-level variables include species and diameter. Additional variables include tree count, diameter growth, height, height growth, crown ratio, and various other tree-level information. To account for the biotic and abiotic influences of different regions, FVS uses variants with each geographic region having various submodels that describe growth and mortality (Hoover and Rebain 2011). To compensate for the modeling bias, FVS contains a self-calibration feature that uses growth rates measured from the field to modify predictions for local conditions so that growth predictions are consistent with growth rates measured in the inventory; FVS also adjusts growth and mortality estimates for fire, insect, and pathogen impacts (Dixon 2002; Hoover and Rebain 2011). The projections of FVS are dependent on interactions among trees within each stand, and FVS can also account for competition-related mortality of individual trees (Crookston and Dixon 2005).

With all these capabilities combined, FVS has been extensively used by forest managers to summarize current stand conditions, predict future stand conditions, and update inventory statistics (Dixon 2002). FVS also allows users to simulate standard and customized forest management activities to see how they affect these forest attributes. This has been implemented by adding extensions to the core growth model (Dixon 2002; Hoover and Rebain 2011; Crookston and Dixon 2005). The drawback of FVS that the modeling is limited to the forested stand rather than complete landscape is addressed by the following FastEmap algorithm.

2.3 Point-to-surface extrapolation FastEmap

We adopt the FastEmap algorithm to extrapolate point-specific forest metrics to spatially-contiguous map products based on remote sensing and other auxiliary geospatial datasets (Huang *et al.* 2017). Remotely sensed data are ideally suited for mapping forest characteristics over large landscapes; however, the level of detail about forest composition and structure cannot be provided by satellite imagery alone (Zald *et al.* 2014). FastEmap was designed to integrate field inventory and environmental (e.g., topography, soils, and climate) data with remotely sensed data to generate maps with the spatial coverage of remotely sensed imagery and the ecological detail of field plots, with the details reported in Huang *et al.* (2016, 2017). FastEmap consists of four major components in an automated production line, which are briefly summarized as follows.

The first step of "creating virtual plots" assigns the attribute of a field plot to those pixels that are "almost identical". This means 1) the remote sensing values (e.g., reflectance) of these pixels are extremely similar to the remote sensing value of the corresponding field plot; and 2) all these pixels fall in the same ecological zones of soil, elevation, aspect, slope, precipitation, and temperature. In this way, the training sets can be expanded in spatial coverage to more climatic, topographic, soil, and forest representative classes. The original plots and the virtual plots are combined for use in the subsequent steps.

The second step of "stepwise regression" provides a map prediction on selected attributes to capture the general distribution of forest attributes. Stepwise regression helps users determine which variables are more significant than others. But most importantly, the stepwise regression map prediction will be subsequently used to calculate weighting coefficients, which aims to reduce the influence of outliers caused by spatial errors, in the following third step of "group imputation".

The third step of "group imputation" is similar to the well-known "stratum mean" technique, where the stratum boundaries are superimposed on the field plots and then the average from plots falling within stratum boundaries are calculated (Muinonen *et al.* 2001; McRoberts 2008). FastEmap uses the binning approach to divide remote sensing channels and derived metrics (e.g., NDVI) into different classes, then the classified remote sensing data are integrated with auxiliary geospatial datasets to create unique combinations. In this way, FastEmap divides the study area into many groups composed of similar pixels (in terms of remote sensing values and environmental conditions). The weighted mean of plots falling within a specific group is assigned to the group. The weighing of a plot is inversely proportional to its difference between a stepwise regression result and its measurements; the main purpose is to reduce the influence of outliers caused by spatial registration errors (Huang *et al.* 2017). After the first imputation, it is possible that some groups cannot be assigned a value because of no or insufficient plots. FastEmap ignores the least important auxiliary variable or reduced the binning for a new imputation. Therefore, the imputation process in FastEmap is an iterative procedure, starting from highly homogeneous groups gradually to less homogeneous groups. From the procedure mentioned above, we can see that the "group imputation" differs from traditional "stratum mean" technique in three aspects. First, the "group" is an arbitrary cluster and not necessarily geographically connected. Second, a weighted mean instead of a simple mean is used. Third, the task is completed in an iterative manner instead of only one time.

The fourth step of "local interpolation and strata median filling" is to assign values to the remaining pixels that have not been filled by the "group imputation" mentioned above. This is based on the mean of "local window interpolation" and "strata median" (Huang *et al.* 2017).

In general, FastEmap is nonparametric; it does not rely on any assumptions that the suite of variables has a specific distribution (e.g., multivariate Gaussian distribution). FastEmap is flexible enough to allow for the use of multisource data, including field survey data, satellite images, and environmental data (e.g., soil, climate, and topography). FastEmap is integrated with an automated suite of tools to efficiently process a high volume of geospatial data over a large area (Huang *et al.* 2017).

2.4 Integrating FIA, FVS, FastEmap into F^3

The F^3 modeling framework integrates tree-list FIA inventory data, individual-tree FVS modeling, and the extrapolation tool, FastEmap, to produce spatiotemporal forest change over a landscape. Assuming different management actions are applied to specific area, F^3 utilizes the keyword component (KCP) files, which are used in FVS for defining management scenarios (Dixon 2002), and implements the modeling through three primary steps.

The first step is the natural succession modeling. When no forest management is applied, the forest will change following successional pathways, which is modeled well by FVS. In this case, the tree-list data of each individual FIA inventory plot are used directly to drive the FVS model. Subsequently, for each individual year, the point-specific projections (no human management but only natural succession) are ingested into the FastEmap tool and extrapolated into landscape surfaces. The FastEmap parameters, including the predictor variables and weighting coefficients, are consistently used among metrics, years, and management scenarios. The reason for using the consistent parameters is to avoid unrealistic combinations of forest metrics (e.g., a stand with very high biomass, but with very sparse small trees).

The second step is the management scenario modeling. For a scenario of interest, an FVS KCP file is created to simulate the actions. For each FIA inventory plot, the tree-list data along with this KCP file are used to drive the FVS model to project the change in forest conditions. Subsequently, all the point-specific projections (with management considered) are extrapolated into spatially-contiguous maps. This is repeated for every scenario.

The third step is the spatial mosaicking, which combines natural succession and management scenarios across the whole study area. For a specific area (defined with GIS polygons or raster cells) where a specific management action is applied, the modeling results from the corresponding scenario are extracted. This extraction procedure is repeated for all management scenarios. For those remaining areas where no management is applied, the results from natural succession are extracted.

After the time series spatially-explicit map products are produced, a post-processing module in F^3 can help users analyze and visualize the results. The following functions are implemented: 1) maps with legend, scale, and title can be automatically created, and animations from time-series maps are produced; 2) time series values for each raster cell can be statistically calculated for maximum, minimum, mean, sum, and standard deviation; and 3) statistics for user-defined zones can be exported to a standardized database from which F^3 can create Microsoft Excel-like graphics automatically for users.

2.5. Accuracy evaluation

The protocol or algorithm have been well documented for FIA inventory (U.S. Forest Service 2017a), FVS modeling (U.S. Forest Service 2017b), and FastEmap extrapolation (Huang *et al.* 2017), where readers can gain information on how these three essentials work. Especially, FVS has a distinguishing feature of using actual measurements for internal calibration to improve the modeling (Dixon 2002; Hoover and Rebain 2011); however, spatial and temporal validation of model forecasts are still necessary (Shifley *et al.* 2017). We quantify the F^3 uncertainties through two steps. First, for assessing F^3 temporal forecast, we compare FVS modeling results with field measurements for evaluating FVS accuracy. Assuming a FIA plot is measured four times in 1999, 2005, 2010, and 2016, respectively, then we have 6 pairs of comparison if there is no disturbance between t_1 and t_2 (**Table** 1). This comparison is repeated for every plot. Second, for evaluating F^3 spatial forecast, we use leave-one-out cross-validation, which means N-1 plots are used for calibration and only one plot is held for validation and this is repeated for N times. Assuming in a specific year the number of plots used for FastEmap extrapolation is N, then we have N pairs of comparison.

Table 1. FVS modeling comparison with field measurements for a FIA plot surveyed in 1999, 2005, 2010, and 2016

FIA in year t_1	FVS in year t_2 projected from t_1 FIA	FIA in years t_2	Comparison pair
1999	2005	2005	FVS in 2005 vs FIA in 2005

1999	2010	2010	FVS in 2010 vs FIA in 2010
1999	2016	2016	FVS in 2016 vs FIA in 2016
2005	2010	2010	FVS in 2010 vs FIA in 2010
2005	2016	2016	FVS in 2016 vs FIA in 2016
2010	2016	2016	FVS in 2016 vs FIA in 2016

For these two comparisons, the root-mean-square error (RMSE) (**Equation 1**), mean absolute error (MAE) (**Equation 2**), and bias (**Equation 3**) are reported as:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n}} \tag{1}$$

$$MAE = \frac{\sum_{i=1}^{n}|y_i - \hat{y}_i|}{n} \tag{2}$$

$$Bias = \frac{\sum_{i=1}^{n} y_i - \hat{y}_i}{n} \tag{3}$$

where y_i is the predicted value and $\hat{y}_i$ is the input value for comparison.

2.6 Technical implementation

With the high-detail forest inventory datasets, large-volume remote sensing archives and other geospatial datasets, a variety of forest metrics of interest, multiple management scenarios, and long-term simulations over a large geographical area, the computational load is tremendous. F^3 is mainly programmed in a multi-core processor parallel computing environment. A multi-core processor is a single computing component with two or more independent actual processing units (called "cores"). Parallel computing is a type of computation in which many calculations or the execution of processes are carried out simultaneously, thus significantly improving the computation efficiency. The programming languages include fortran, python and the associated modules of arcpy, scipy, numpy, multiprocessing, and matplotlib. The general functions include: 1) filtering and removing the fire-, harvest-, or insect-disturbed plots; 2) creating KCP files based on management scenarios; 3) preparing FVS-ready data from FIA; 4) running FVS with FVS-ready data and KCP files; 5) creating virtual plots; 6) stepwise regression and weighting calculation; 7) iterative group creation and imputation; 8) local interpolation and stratum filling; 9) FVS projection validation and leave-one-out cross-validation; 10) maps and animation creation; 11) time series pixel-wise statistics; and 12) time series zone-wise statistics. Among these functions, steps 1-4 are for FIA and FVS; steps 5-8 are for FastEmap; step 9 is for accuracy assessment; and steps 10-12 are for post-processing modules.

2.7 F^3 demonstration in Tahoe National Forest, California

2.7.1 Pilot area of Tahoe National Forest

We selected the TNF as a pilot study area to demonstrate our F^3 approach. The TNF is located in northern California with a total area of 3,526.82 km^2. The elevation in this area ranges from 1500 feet (457 m) above sea level on the western edge of the forest to over 9400 feet (2865 m) on mountain tops along the crest of the Sierra Nevada. The study area generally experiences warm, dry summers and cold, wet winters, but the elevational gradient plays a major role in temperature and precipitation. Winter temperatures below zero and summer temperatures above 37.8 ºC indicate the normal seasonal spread. Precipitation typically falls from October through April, but it comes mostly in the form of snow at higher elevations. The TNF is home to a large variety of flora. The dominant coniferous species include red and white fir (*Abies magnifica and A.*

concolor), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana)*, Jeffrey pine (*P. jeffreyi*) and incense-cedar (*Calocedrus decurrens*).

2.7.2 Datasets for TNF

2.7.2.1 FIA plot

All of the available FIA plots that were surveyed from 2003 to 2014 in TNF were selected. The actual, rather than the perturbed locations, were used to locate the plots. We chose 2014 as the initial year and we discarded those plots disturbed by mortality events of fire, insect, and drought, resulting in a total of 305 plots for the analysis. For those plots that were surveyed prior to 2014, we used the FVS to adjust the plot condition to 2014.

2.7.2.2 Landsat and LiDAR data

We chose a Landsat 5 Thematic Mapper (TM) image (path 43 and row 33 acquired on 27 September 2011) surface reflectance (Masek *et al.* 2006) and some derived indices such as Normalized Difference Vegetation Index (Huang *et al.* 2017); they are sensitive to the forest canopy layer. In addition, a wall-to-wall LiDAR dataset was collected during 2013-2014 with the resulting return density ranged from 7 to 10 points per square meter. We generated 1 m canopy height models (CHMs), which represented the height above ground of the upper surface of the forest canopy. We upscaled the 1 m CHMs to create five map products at 30 m. The first was CHM_CanopyCover, which computed the percentage of the pixels greater than 2m in a 30 m x 30 m window as the proxy for stand canopy cover. The second was CHM_MeanHeight, which computed the mean CHM from those pixels greater than 2 m in a 30 m x 30 m window as the proxy of stand canopy height. The remaining three were 90th, 95th, and 99th percentile of CHM. These LiDAR metrics are widely used to depict forest structure.

2.7.2.3 Environmental conditions of climate, topography, and soil

Forest ecology is influenced by climate, topography, and soil; therefore, we compiled three ecological classifications to represent these factors. For climate, 52 climate zones were classified from downscaled 270 m actual evapotranspiration (AET), climatic water deficit (CWD), January mean temperature (T_{jan}), and July mean temperature (T_{jul}). For topography, six classes were derived from a 4 m DEM. For soil, productivity classes were compiled from the Soil Survey Geographic (SSURGO) database. These datasets were described in Huang *et al.* (2016).

2.7.3 Management experiments

To demonstrate forest change under different management scenarios that were applied to specific areas, we conducted three experiments (**Figure 2**). The first was natural succession (i.e., no human intervention). The second was a regeneration-cut scenario (only targeting trees with DBH greater than 12.7 cm) applied to the yellow polygons (Y1, Y2, and Y3) in year 2019. The third was a thinning scenario applied to red polygons (R1 and R2) in 2019. The thinning scenario was defined as “in year 2019, if forest canopy cover is greater than 50%, those trees that are from 15.24 to 76.2 cm in DBH will be cut, but all oak (*Quercus*) species remain untouched.” KCP files were created for these two scenarios. Note the regeneration-cut and thinning scenarios were not practical real-world management strategies applied to these arbitrary areas; they were utilized only for demonstration purposes as part of the experiment. In practice, one can target specific locations for treatment such as topographic positions with certain forest types that may be more vulnerable to mortality from a warmer and/or drier climate. For example, a management area could be defined as “10 km buffer area along a road with slope < 25 degree and elevation higher than 500 m where pines grow.”

In this demonstration, three scenarios from 2014 to 2114 at an interval of 5 years were modeled for the following six metrics: 1) “QMD”, which was the quadratic mean DBH of the tree of average per tree basal area; 2) “DFB", which was the basal area of all live Douglas-fir (*Pseudotsuga menziesii*) with DBH ranging from 30.48 to 50.8 cm; 3) "AGB", which was the aboveground live tree total dry biomass; 4) "RHSI", which was the Pacific fisher (*Martes pennanti*) resting habitat suitability index (RHSI) ranging from 0 (not suitable) to 1 (highly suitable); 5) "CC", which was the canopy cover modeled from FIA using FVS; and 6) "DWD", which was the downed woody debris volume. These six metrics can be used for many applications such as timber management, wildlife habitat, carbon sequestration, and wildfire fuel. Please note that 1) RHSI was developed by Zielinski et al. (2006) using FIA data in the southern Sierra Nevada and may not be appropriate in TNF; its calculation was only used for the proof of concept experiment for assessing potential habitat suitability; 2) RHSI was an integrated index and it included not only tree canopy cover variable but also the variables of basal area of trees with DBH < 51 cm, average hardwood, maximum tree DBH, percentage slope, and the DBH of the largest conifer snag (Zielinski *et al.* 2006); and 3) resting habitat was an important component of fisher habitat, but was not the only one (Zielinski *et al.* 2006). There were more variables affecting fisher habitat (Niblett *et al.* 2015; Sauder *et al.* 2015) and an improved habitat index was beyond the current study.

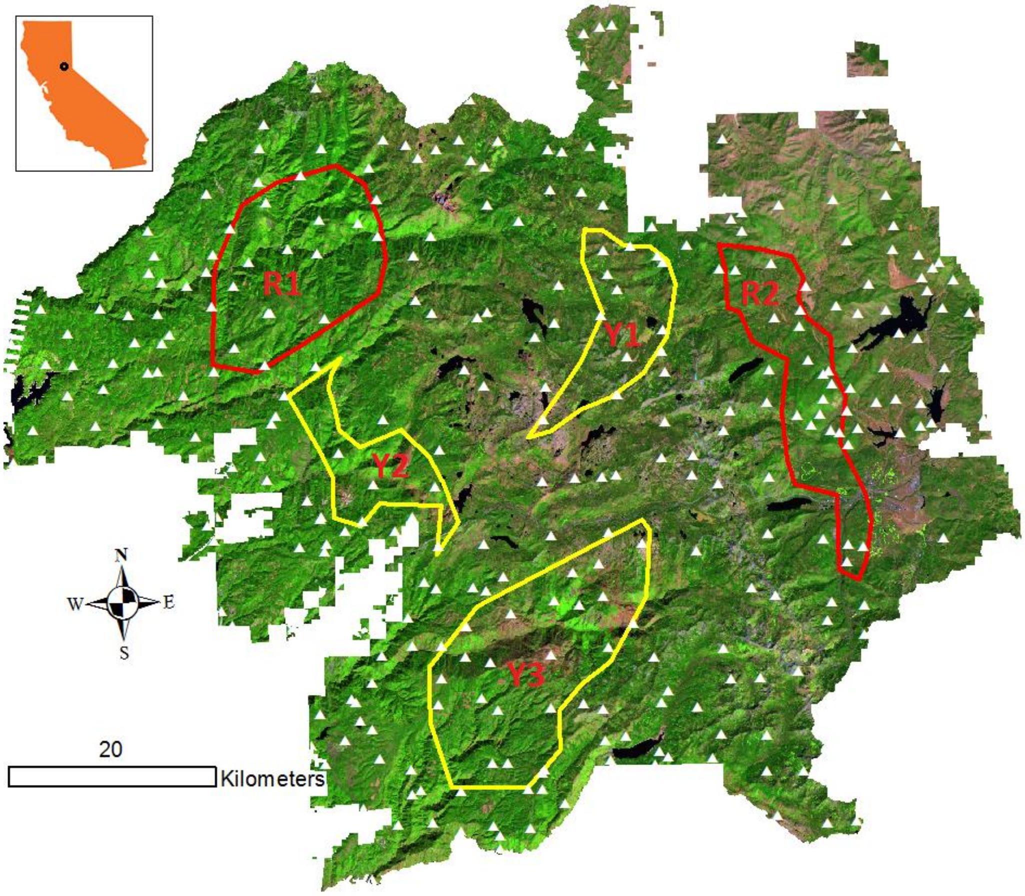

Figure 2. Thinning was applied to yellow polygons (Y1, Y2, and Y3) and regeneration-cut was applied to red polygons (R1 and R2) in 2019. Background is Landsat RGB (channels 5, 4, 3) composite covering Tahoe national Forest (TNF), and the white triangles are FIA plots whose locations are perturbed in this figure for demonstration purpose only. Upper left shows the approximate location of the TNF in California, U.S.A.

3. Results

The combination of 305 FIA plots, Landsat and LiDAR remote sensing data, and auxiliary geospatial datasets for six metrics under 3 scenarios from 2014 to 2114 at an interval of 5 years resulted in 6 x 3 x 20 = 360 digital datasets with columns of 3340 and rows of 2990 at 30 m resolution. Mosaicking three scenarios into annual maps across the whole study area resulted in 120 unique digital datasets. The results were further processed to create maps, animations, graphics, and tables. With a virtual machine of 16 cores and 9.96 GB memory, total processing time was approximately 1 day.

Figure 3 shows an example of spatiotemporal change of the species-specific and size-specific DFB (the basal area of all live Douglas-fir with DBH ranging from 30.48 to 50.8 cm). Because the regeneration-cut and thinning were applied in 2019, the baseline maps in 2014 (**Figure 3a, 3d, 3g,** and **3j**) are identical, which shows the Douglas-fir trees distribute in the west side of mountain commonly below 1800 m elevation. With vegetation management actions applied in 2019, the DFB of natural succession (**Figure 3b** and **3c**) diverges from that of regeneration-cut (**Figure 3e** and **3f**) and thinning (**Figure 3h** and **3i**), indicating the significant influence of management actions on forest condition. When considering the specific areas where management actions were applied, **Figure 3k** and **3l** show the landscape-scale DFB distribution under the combination of natural succession, regeneration-cut, and thinning. Our F^3 created four animation sequences (not shown here) for these three scenarios plus the scenario mosaic, enabling users to visually interpret the forest change. Similar animations were produced for the other five metrics (i.e., QMD, AGB, RHSI, CC, and DWD).

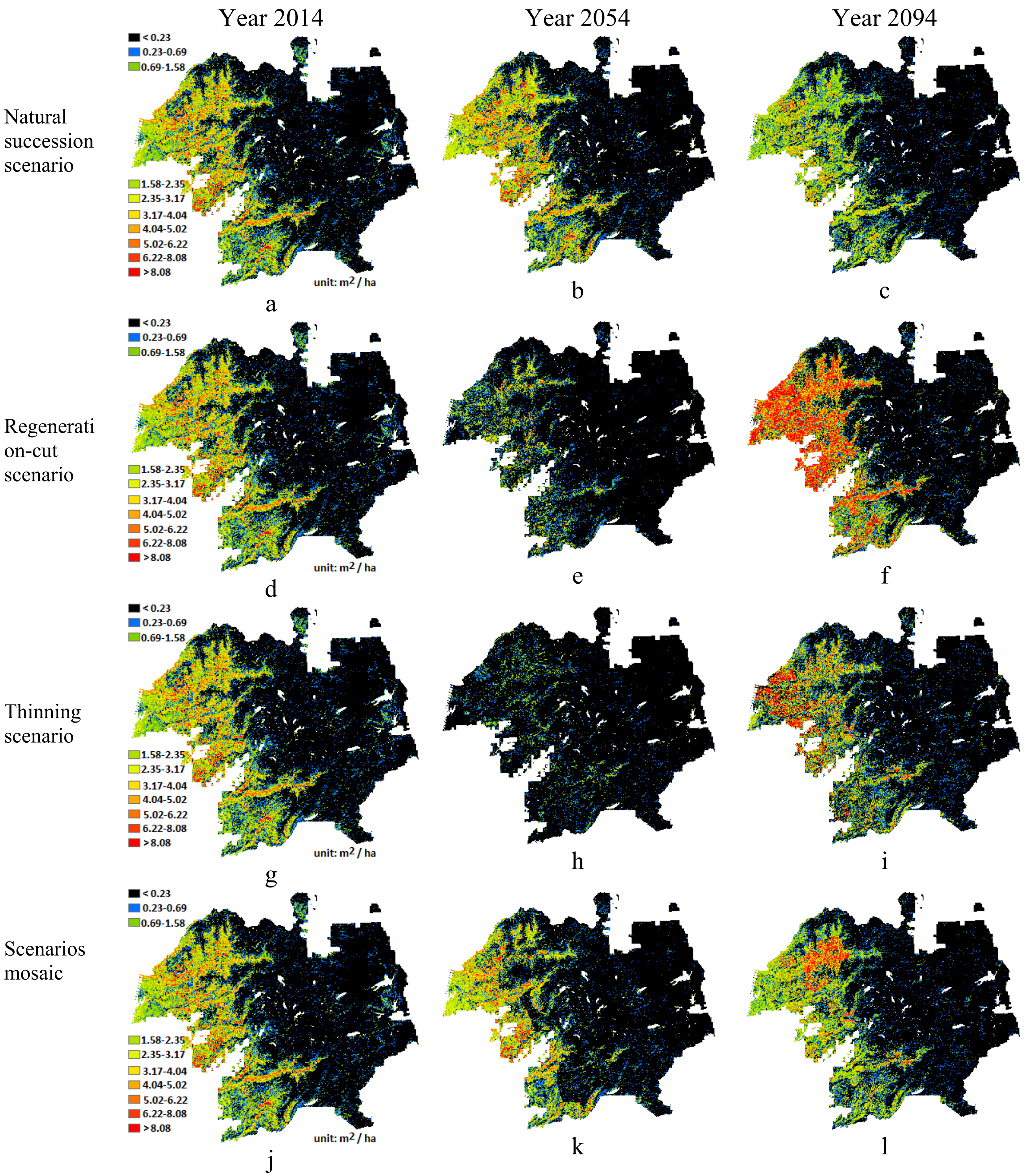

Figure 3. Three scenarios comparison of DFB (i.e., basal area of all live Douglas-fir with DBH ranging from 30.48 to 50.8 cm). Note 1) Regeneration-cut and thinning were applied in 2019;

and 2) Scenario mosaics were from the natural succession scenario, as well as the thinning and regeneration-cut management actions whose areas are shown in figure 2.

The pixel-wise statistics were automatically generated for further analysis. **Figure 4** shows the mean values of basal area, biomass, canopy cover, and QMD averaged from 2014-2114 for the scenario mosaic. The changes along the management boundaries (see **Figure 2** for management areas) indicate how the regeneration-cut and thinning management have a great effect on shifting the natural succession.

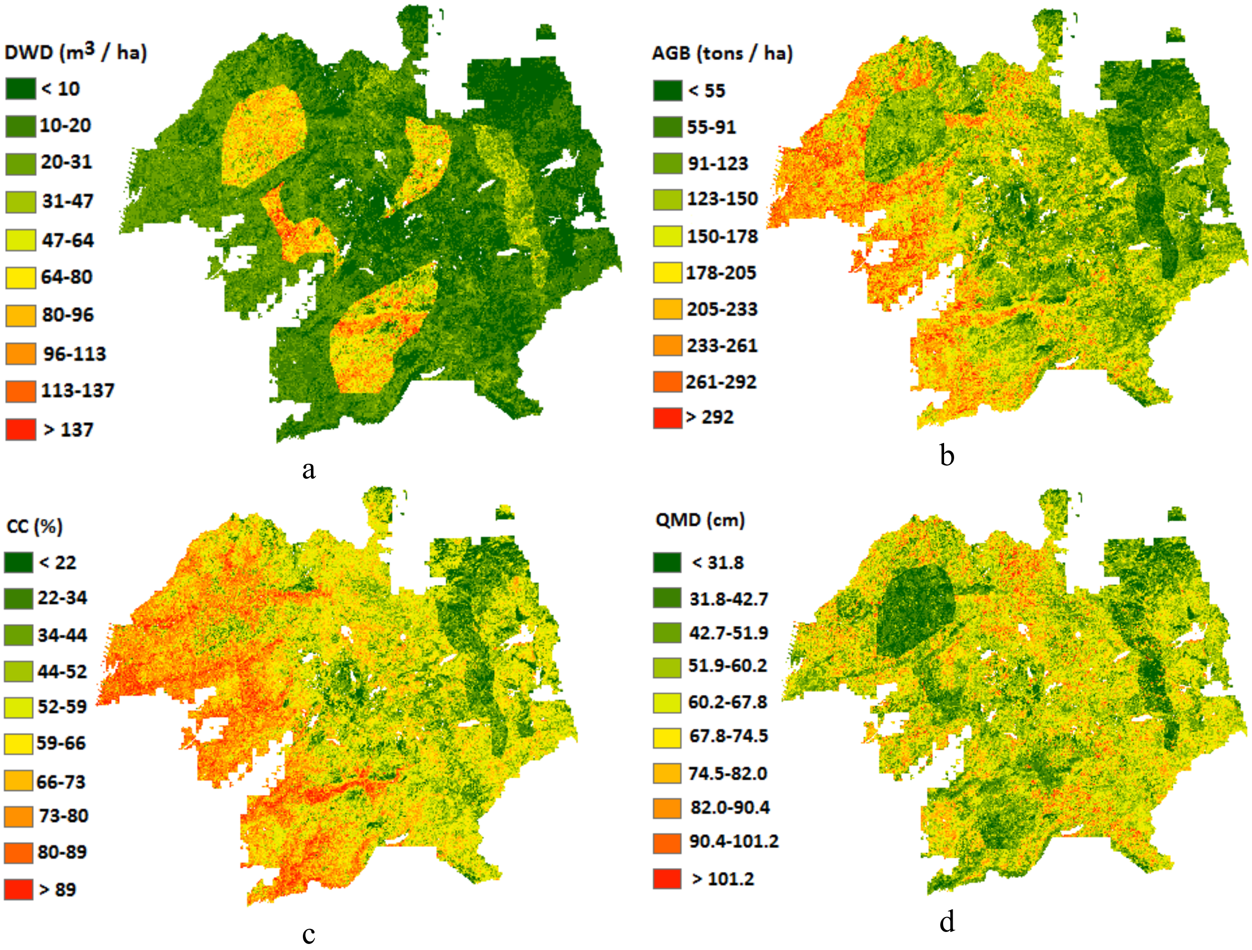

Figure 4. Pixel-wise 2014-2114 mean value for a) downed woody debris DWD, b) aboveground total live biomass AGB, c) canopy cover CC, and d) quadratic mean diameter QMD for the scenario mosaic. Note the distinguishing trajectory changes caused by the simulated management activities, as shown in figure 2.

The statistics of user-defined zones and the associated graphic and database generated from the post-processing module were especially helpful for end users. **Figure 5** shows the fisher RHSI for the specific areas under alternative management scenarios. It allows user to assess the long-term effect on fisher if alternative management actions were adopted for a specific area, thus addressing the “what if” questions.

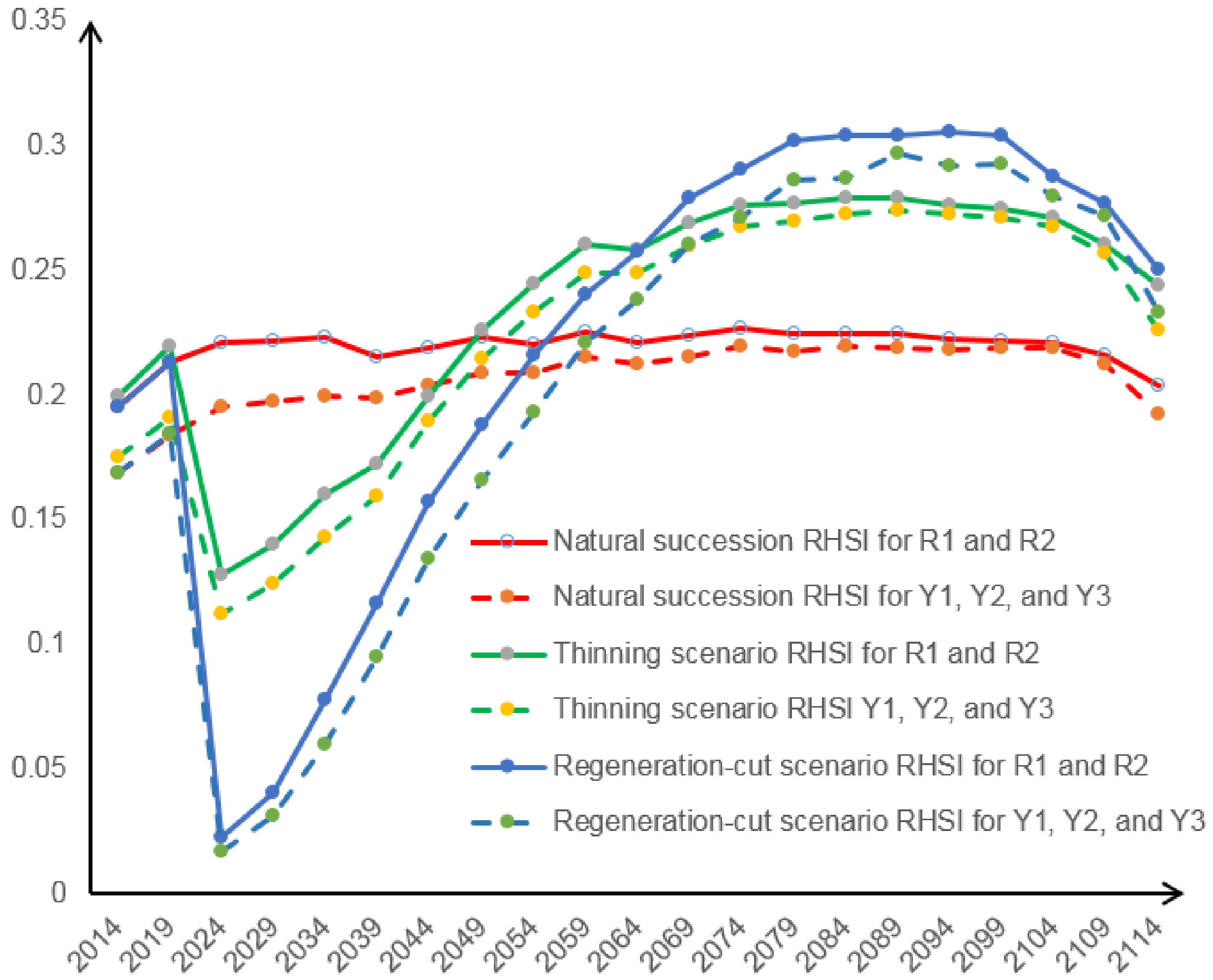

Figure 5. Time series fisher resting habitat suitability index (RHSI) comparison among natural succession, regeneration-cut, and thinning scenarios. R1, R2, Y1, Y2, and Y3 are management areas indicated in figure 2.

An example of the temporal accuracy assessment is shown for the comparison between field measurement and FVS modeling (**Figure 6**). An example of the spatial accuracy assessment is shown for the leave-one-out cross validation (**Figure 7**).

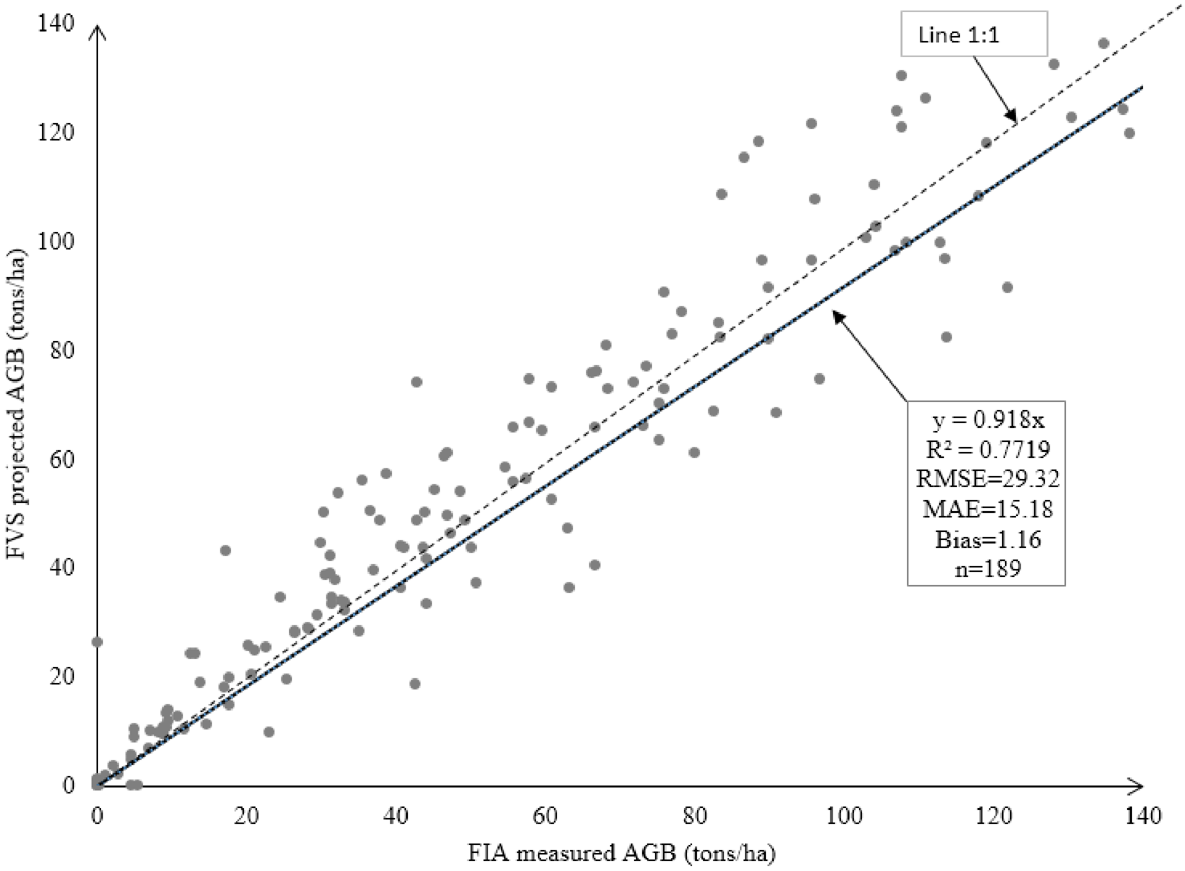

Figure 6. Comparison between measured aboveground total live biomass (AGB) by Forest Inventory and Analysis (FIA) and projected AGB by Forest Vegetation Simulator (FVS)

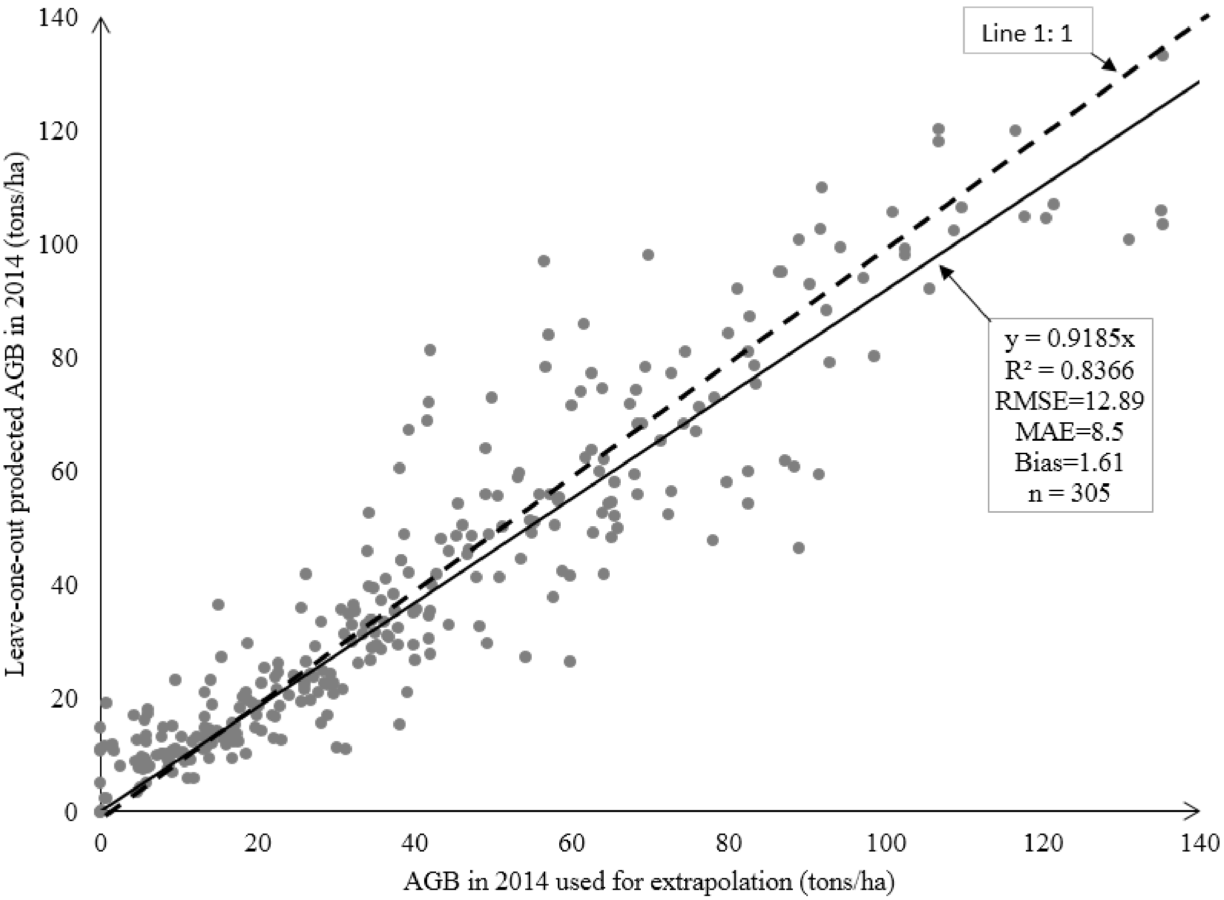

Figure 7. Leave-one-out cross validation for 2014 aboveground total live biomass (AGB)

4. Discussion

4.1 F^3 advantages

This paper presents a novel methodology for integrating tree-list forest inventories, individual-tree growth and yield modeling, and an extrapolation algorithm to reveal spatiotemporal forest change under natural succession and management actions over a large landscape. Specifically, the widely-available FIA data depicts the highly-detailed information of a forest stand as the initial condition, and the FVS model uses the tree-list as input to simulate the stand change. Several advantages of the existing FIA and FVS can be inherited. First, the growth, establishment, and mortality of each individual tree can be tracked through many years; this highly-detailed information is very useful for silviculturists and vegetation managers. Second, due to the details in FIA and FVS, complex treatments and silvicultural prescriptions, rather than broad management scenarios, can be defined (through KCP files in FVS) to assess the effects of on-the-ground forest management. Third, FVS is already calibrated and validated within each geographic variant throughout the U.S., allowing users to focus their resources in ecological analysis instead of model development. Fourth, the stable staff support of FIA and FVS benefits the potential application of our methodology throughout U.S. However, FIA and FVS are point-specific and cannot provide spatially-explicit information over a landscape; this prompts us to add the extrapolation algorithm of FastEmap. During the process of running the FastEmap model, remote sensing plays an important role in creating the "groups" composed of similar pixels (in terms of remote sensing and environmental conditions). An assumption behind this technique is that all the pixels in a specific "group" will experience a similar change of the plots falling in the group; therefore, a "group" serves a similar function of the "land type" used in LANDIS (Mladenoff *et al.* 1996; He and Mladenoff 1999; Yang *et al.* 2011). Once the "groups" are established from the current remote sensing data sets, the future projection does not rely on any additional remote sensing data sets. FastEmap allows the point-specific FIA conditions and FVS projections to be mapped for each raster cell, and alternative management options can be compared to support decision-making processes. To our knowledge, this is the first paper showing how the remote sensing datasets are fused with highly-detailed individual tree models for long-term impact assessment from different on-the-ground forest management alternatives.

With the integration of FIA, FVS, and FastEmap, our F^3 modeling provides foresters and vegetation management practitioners with the information that have the aforementioned characteristics: high-detailed, spatially-explicit, multi-temporal, and scenario-comparable. Nevertheless, FVS is mainly calibrated and validated in the U.S. For those countries with local forest inventory datasets accessible (Barrett *et al.* 2016) or for those users who are not satisfied with FVS, it will be necessary to replace FVS with their own forest growth and yield model or modify and calibrate FVS for their specific geographic area.

4.2 Potential applications of F^3

4.2.1 Species distribution and abundance for initializing FLMs

With the above information from the F^3 modeling framework, one application is to define initial landscape conditions for other FLMs. Landscape-wide estimates of tree species distributions and abundance is often of high interest for FLM initialization (Shifley *et al.* 2008; Wang *et al.* 2013; van Ewijk *et al.* 2014; Shifley *et al.* 2017). The capability is demonstrated in **Figure 3** that shows the time-series change of species-specific and size-specific distribution and abundance under natural succession and different management strategies.

4.2.2 A landscape version of FVS for ecosystem service evaluation

Our F^3 can be considered a landscape version of FVS that can potentially be used for evaluating many ecosystem services. Although only six metrics were demonstrated in our study, technically all the time-series forest metrics modelled from FVS for each point-specific can be extrapolated by our F^3 to landscape surface at a comparable resolution (e.g., 30 m). In addition to projecting remote sensing data forward in time, F^3 also includes management scenarios and models forest ecological dynamics, thereby linking on-the-ground management and forest ecology for policy-making decision support. The accuracy evaluation (i.e., spatial and temporal validation of model forecasts) helps the understanding on related bias for strategic forest planning. Linking the F^3 map products to models that use forest conditions to quantify forest-associated products and services such as wildlife habitat, biodiversity, fire effects, carbon sequestration, or air quality protection is straightforward in concept (Shifley *et al.* 2017). For example, for hydrological modeling, the quantity and quality of water are tightly correlated with the condition and proportion of forest cover in forested landscapes; therefore, our products enable examining the mechanism of how natural forest changes or alternative forest management scenarios are likely to affect water (Shifley *et al.* 2017). For wildfire studies, our products can be used by FARSITE, which was developed to make projections of fire growth patterns and rates under natural and anthropogenic conditions (Finney 2004). For wildlife conservation, our products such as **Figure 5** can be used to assess future wildlife habitat suitability to alternative forest management scenarios (Shifley *et al.* 2017). For climate change mitigation effort such as “California Climate Investments” program (California Air Resources Board, 2017), F^3 can be used for estimating greenhouse gas benefits from project-level forest management activities. For air quality protection, species-specific tree cover are important parameters for modeling the capability of forest to absorb air pollutants (Nowak *et al.* 2014). Moreover, users need to be aware that many different extensions have been developed for FVS, and increases in mortality from insects, pathogens, and fire are accounted for in the various FVS extensions, which can be directly utilized by F^3 (Dixon 2002). For example, the “Fire and Fuels Extension” predicts the effects of stand development and management actions on fuel dynamics, fire behavior, and fire effects, and it includes different biomass component of live tree, dead tree, down dead wood and forest floor, which can be used to estimate changes in carbon stocks over time. The “Insect and Disease extensions” simulate the effects on forest stands from insects and forest pathogens such as Western root disease and Douglas-fir Beetle. The “Economic Extension” calculates economic measures to aid evaluation of silvicultural alternatives. Especially, climate change effect on forest condition is not insignificant in long-term (e.g., 100 years) projections. When the FVS “Climate Extension (Crookston *et al.* 2010; Gálvez *et al.* 2014)” is incorporated, F^3 is able to capture the climate change effect. Furthermore, F^3 can be used over the entire U.S., but our demonstrative area is in California National Forest lands where wildfires, droughts, insects, and disease are interactively affecting forest conditions (Westerling 2016; Fettig *et al.* 2014; Negrón and Fettig 2014; Asner *et al.* 2016; Young *et al.* 2017), suggesting the inclusion of disturbances in F^3 is very critical. When the existing, customized or future-improved FVS extensions (e.g., “Fire and Fuels Extension” and “Insect and Disease extensions”) are incorporated, F^3 is able to simulate the effect of these confounding disturbances in California, which is our next target.

4.3 Major limitation and uncertainties

Although F^3 has an uncertainty quantification module, it is still worth mentioning major sources of uncertainties so that end users can be aware of how to appropriately use F^3 for their specific applications. The major sources include the inventory plot representativeness in FIA, growth modeling errors in FVS, and predictor variables in FastEmap.

4.3.1 Major uncertainty from FIA measurements

Plot location and how well the collection of plots captures the forest variation across the landscape, referred to here as its representativeness, have an effect on extrapolation performance (Huang *et al.* 2017). The positional accuracy of FIA plots averages 5–20 m, but sometimes exceeds 20 m (Zald *et al.* 2014; Huang *et al.* 2016). The spatial-mismatch issue is a challenging problem in traditional K-nearest-neighbor imputation approach (McRoberts 2010), but the influence can be reduced in our FastEmap algorithm which uses the inverse difference between regression results and measurements as a weight (Huang *et al.* 2017). More importantly, the FIA inventory plots are samples of forest conditions and thus by definition are an incomplete representation of reality (Bell *et al.* 2015). In areas that do not meet FIA's definition of forest, tree information is generally not collected (Riemann *et al.* 2010). This weakness will affect the performance of those “nonforest” areas containing trees; therefore, we suggest additional non-forest plots be added to avoid the overestimation in nonforest areas. In F^3, as reported in Huang *et al.* (2017), those areas where an FIA plot was sampled are imputed first, and those areas where no field plot was sampled are lastly filled. This implies that the sequence (i.e., the order of the pixel imputation in the iterative process during FastEmap) is an indicator of how well the area is represented by the field plots. Therefore, we adopt this sequence order to indirectly quantify the confidence of the results, as shown in **Figure 8** for TNF. For those areas that show low confidence, additional resources may be allocated to augment the field plot representativeness.

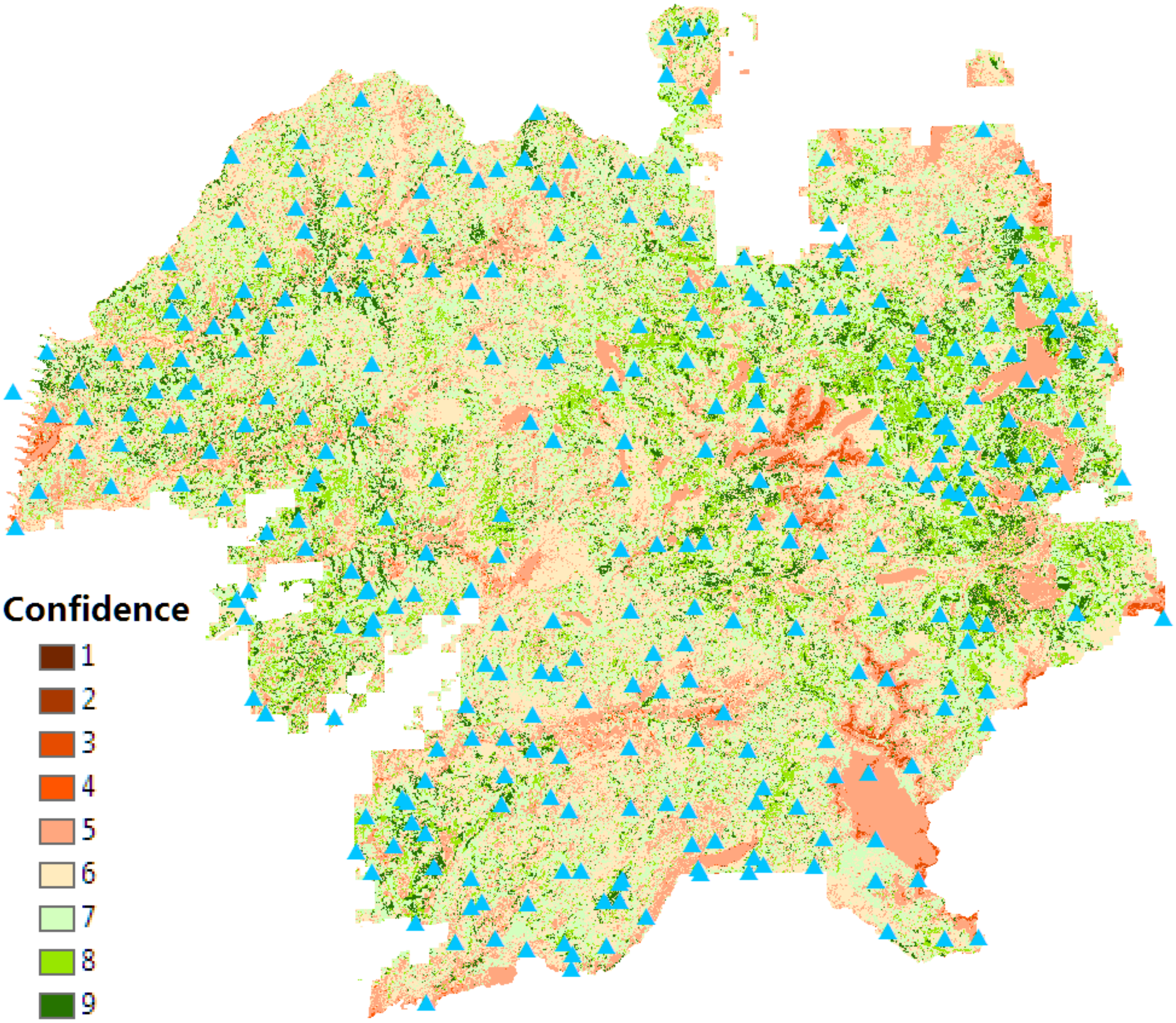

Figure 8. Confidence level with 1 meaning low and 9 meaning high. Blue rectangles indicate the perturbed FIA plot locations for demonstration purposes only.

4.3.2 Major uncertainty from FVS modeling

The underlying FVS growth model adopted by our F^3 has limitations (Crookston and Dixon 2005) and affects the F^3 results in at least three aspects. First, FVS has bias. For example, it was reported by Keyser and Keyser (2017) that 1) FVS produced biased estimates of percent canopy cover when trees were from stands with non-random spatial distributions (e.g., clumped or uniform); 2) FVS-Lake States over-predicted ten-year diameter increment slightly in undisturbed forests while under-predicted diameter increment in disturbed forests; and 3) the underlying equations driving the prediction of fire-related mortality for the vast majority of US tree species were derived from western conifer species, which might not be representative for the entire U.S. All of these relevant errors from FVS will propagate into F^3 results. However, much active research is still on-going to improve FVS modeling. Once updated modeling improvement is available, it can be promptly ingested by FVS (and therefore F^3) due to permanent USFS support. Second, inherited from FVS, F^3 does not include forest spatially-interactive processes (e.g., seed dispersal, fire spread, and insect/disease propagation) that FLMs usually do (He 2008; Shifley *et al.* 2017). This weakness can be partly addressed by using the F^3 outputs as the inputs of those spatially-interactive processes models such as FARSITE. Third, non-tree vegetation is represented in a limited way in FVS, so FVS is insufficient for detailed predictions of non-tree vegetation (Crookston and Dixon 2005). To improve the simulation capabilities in non-forested conditions and the characterization of understory conditions (herbaceous and shrub species) in the FVS, Reeves (2016) developed the Rangeland Vegetation Simulator (RVS). The next step in the F^3 development process is to incorporate RVS capabilities to improve the simulations.

4.3.3 Major uncertainty from FastEmap extrapolation

The extrapolation tool FastEmap does have deficiencies too. In any SDM and forest attribute predictions, predictor variables should ideally be significantly correlated with target attributes based on causal factors such as light, nutrients, water, temperature, disturbances, and biota (Austin and Van Niel 2011; Brosofske *et al.* 2014). When variables are difficult to quantify, proxies can be used (e.g., elevation as a proxy for temperature, and tree height, biomass or leaf area index as a proxy for light competition). In heterogeneous landscape, those predictor variables that can capture the fine-scale of climatic, topographic, edaphic, and biotic interactions need to be considered (Meier *et al.* 2010; Piedallu *et al.* 2013; van Ewijk *et al.* 2014). This also applies to the LANDIS model where the heterogeneous landscape is stratified into relatively homogeneous land types based on geospatial datasets such as land use data, classified TM imagery, and DEM. In each land type, the species establishment coefficients are assumed to be similar (Shifley *et al.* 2008; Wang *et al.* 2013; Luo *et al.* 2015). We repeat that the predictor variables chosen for F^3 modeling system must be sensitive and correlated to forest growth and yield, which was already pointed out in FastEmap (Huang *et al.* 2016, 2017). In the TNF, we used climate, topography, and soil data as well as Landsat and LiDAR data. Optical Landsat reflectance are good indicators of prevailing conditions in the forest stand, and the amount of chlorophyll information obtained from Landsat is closely related to forest growth and plant spectrum traits (Ung *et al.* 2001; Huang *et al.* 2016). However, optical sensors have limited sensitivity to vertical and below-canopy vegetation structure and they saturate in forests with high biomass and leaf area index (Zald *et al.* 2016). These limitations pose problems for those forest attributes such as stand density, snags, and down woody material (Zald *et al.* 2014). LiDAR-derived variables have strong relationships to fine-scale tree species' abundance properties to represent biotic and disturbance processes, and they are also sensitive to forest structure (van Ewijk *et al.* 2014). These are the main reasons why we chose both Landsat and LiDAR data for TNF. When F^3 is adopted for other applications, we suggest users choose LiDAR and/or long-wavelength radar data, if available, in addition to the widely-available optical data, because LiDAR and long-wavelength radar data are good at depicting forest structure characteristics (Huang *et al.* 2009). Following the same line of reasoning, for those species that do not have strong relationships with either biotic or abiotic factors, our F^3 will not perform well. Also for those non-ecological field plot attributes such as ownership, our F^3 will be problematic because of the lack of correlation to predictor layers, as stated by Wilson *et al.* (2012). In addition, FastEmap extrapolates poorly beyond the ranges of the reference data and may lose the variance of observed data (Huang *et al.* 2017), further implying the importance of field data representativeness as mentioned above.

5. Conclusion

Addressing real and complex on-the-ground forest management and planning problems requires highly-detailed, spatially-explicit, multi-temporal, and timely modeling system that allows for multiple scenarios comparison for decision-making and policy options. The point-specific tree-list inventory data can drive individual-tree models to project highly-detailed forest change under natural succession and human management; however, one weakness is the lack of spatial completeness over a landscape. In contrast, FLMs can model spatiotemporal forest change, but the details are typically simplified and scarce. The F^3 modeling framework we demonstrate here combines the advantages of individual-tree models and FLMs. F^3 uses highly-detailed FIA and FVS for point-specific projection under complex management scenarios, but it further utilizes the FastEmap algorithm to extrapolate the modeling results to spatially-contiguous land surface. FIA data with the details into each single tree have been widely available and will continue in the future. FVS tracks each individual tree and has been calibrated and validated throughout U.S. and is permanently supported. FastEmap takes full advantage of remote sensing and auxiliary geospatial datasets and extrapolates point-specific forest metrics to land surface in an automatic manner. F^3 integrates FIA, FVS, and FastEmap in a parallel computing system to increase the computation efficiency. F^3 further provides an accuracy assessment module and a post-processing module, facilitating users to analyze the modeling results.

F^3 can be used for initialing FLMs, and it can also be used for evaluating a variety of ecosystem services such as hydrological modeling, wildfire simulation, wildlife habitat, carbon sequestration, and air quality protection. However, users need to be aware of three sources of major uncertainties. First, FIA may not be representative of landscape heterogeneity, especially in the non-forest areas. Second, FVS model may provide biased estimates and is insufficient in non-tree vegetation simulation. Third, FastEmap requires the predictor variables be sensitive and correlated to forest metrics. Bearing these in mind, we expect F^3 will be accepted by forest managers and the science community for operational usage.

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