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Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species

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Abstract. Fuels-reduction treatments are commonly implemented in the western U.S. to reduce the risk of high-severity fire, but they may have negative short-term impacts on species associated with older forests. Therefore, we modeled the effects of a completed fuels-reduction project on fire behavior and California Spotted Owl (*Strix occidentalis occidentalis*) habitat and demography in the Sierra Nevada to assess the potential short- and long-term trade-offs. We combined field-collected vegetation data and LiDAR data to develop detailed maps of forest structure needed to parameterize our fire and forest-growth models. We simulated wildfires under extreme weather conditions (both with and without fuels treatments), then simulated forest growth 30 years into the future under four combinations of treatment and fire: treated with fire, untreated with fire, treated without fire, and untreated without fire. We compared spotted owl habitat and population parameters under the four scenarios using a habitat suitability index developed from canopy cover and large-tree measurements at nest sites and from previously derived statistical relationships between forest structure and fitness (λ) and equilibrium occupancy at the territory scale. Treatments had a positive effect on owl nesting habitat and demographic rates up to 30 years after simulated fire, but they had a persistently negative effect throughout the 30-year period in the absence of fire. We conclude that fuels-reduction treatments in the Sierra Nevada may provide long-term benefits to spotted owls if fire occurs under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. However, we only simulated one fire under the treated and untreated scenarios and therefore had no measures of variation and uncertainty. In addition, the net benefits of fuels treatments on spotted owl habitat and demography depends on the future probability that fire will occur under similar weather and ignition conditions, and such probabilities remain difficult to quantify. Therefore, we recommend a landscape approach that restricts timber harvest within territory core areas of use (~125 ha in size) that contain critical owl nesting and roosting habitat and locates fuels treatments in the surrounding areas to reduce the potential for high-severity fire in territory core areas.

Key words: California Spotted Owl; fuels treatment; habitat; Sierra Nevada; *Strix occidentalis occidentalis*; territory fitness; territory occupancy; wildfire.

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Introduction

The management of fire-adapted forests in the western U.S. is increasingly challenged by the need to consider the ecological impacts of wildfire and fuels-reduction treatments intended to modify wildfire behavior (Stephens et al. 2013). Historic fire regimes in many of these forests were characterized by fires burning at intervals of less than 20 years and having primarily low- and moderate-severity fire effects but interspersed with some areas of high-severity effects (Agee 1993, Skinner and Chang 1996), and some high-severity fire apparently occurred with regularity (Collins and Stephens 2010, Hanson and Odion 2014). This type of fire regime resulted in highly heterogeneous landscapes in which vegetation conditions were governed by complex interactions between topography, site productivity, and disturbance (Collins et al. 2015, Stephens et al. 2015). However, decades of fire exclusion have disrupted historic fire regimes, altered forest structure and landscape vegetation patterns, increased forest fuel loads, and led to increases in the frequency of large fires (Westerling et al. 2006), as well as increases in proportions and patch sizes of high-severity fire (Miller et al. 2009, Miller and Safford 2012). In addition, further increases in fire activity are expected under most climate change scenarios (Westerling and Bryant 2008, Liu et al. 2013). High-severity fire effects (defined by >75% mortality of overstory trees) can impact ecosystem processes such as erosion rates, stream sedimentation, and carbon sequestration (Benavides-Solorio and MacDonald 2001, Breshears and Allen 2002), as well as modify forest structure and wildlife habitat. While some wildlife species become more abundant after high-severity fire (Smucker et al. 2005, Fontaine and Kennedy 2012), other species, particularly those associated with older forests, may be negatively impacted by habitat loss resulting from large patches of high-severity fire (e.g., Lee et al. 2013). Old-forest species with large home ranges are typically rare and preventing their populations from reaching critically small sizes is widely regarded as an important policy objective (e.g., National Forest Management Act of 1976), in part because meeting the habitat needs of such species might protect broader old-forest communities (Temple 1997).

To reduce the potential for large patches of high-severity fire, forest managers are implementing fuels-reduction treatments in many western U.S. forests (e.g., USFS 2004). Fuels-reduction treatments primarily remove duff, downed wood, shrubs, and smaller trees (i.e., surface and ladder fuels), and fire models suggest that these treatments can reduce potential fire spread and intensity across landscapes (Ager et al. 2007, Finney et al. 2007). However, these treatments also reduce canopy cover and vertical forest structure, which could have negative short-term impacts on old-forest-associated species such as the spotted owl (*Strix occidentalis*). Hypothetically, such short-term negative impacts would be outweighed by the longer-term benefits from reductions in the amount of habitat lost during future wildfires, as has been suggested by previous simulations (Ager et al. 2007, Roloff et al. 2012). Similarly, the current management plan for the national forests in the Sierra Nevada posits that fuels-reduction treatments will result in long-term increases in the amount of suitable California Spotted Owl (*S. o. occidentalis*) habitat while acknowledging the potential for short-term negative impacts (USFS 2004). Indeed, a recent study found that fuels-reduction treatments can negatively impact spotted owl populations over shorter time frames (<10 years) if they reduce the amount of high-canopy-cover (≥70%) forest dominated by trees ≥30.5 cm diameter at breast height (dbh) within owl territories (Tempel et al. 2014*a*). However, whether short-term impacts of fuels treatments to spotted owls and their habitat in the Sierra Nevada will be offset by long-term gains resulting from reductions in high-severity fire is unknown.

Here, we used fire and forest-growth models to simulate how fuels treatments might alter the effects of fire on spotted owl habitat and demographic rates at the "fireshed" scale over a 30-year period in the Sierra Nevada. Firesheds are contiguous areas with similar fire histories and have been identified by the U.S. Forest Service as useful landscape units for fuels-treatment planning and effective fire suppression (Bahro et al. 2007, North et al. 2015). Firesheds are commonly delineated by sub-watershed boundaries and range in size from ~3,200 to 16,200 ha within the Sierra Nevada (North et al. 2015). We chose this spatial scale because of its management relevance (i.e., project planning) and because our field-based vegetation sampling would not have been feasible at larger spatial scales. In contrast to previous studies that relied upon simulated treatments (Ager et al. 2007, Roloff et al. 2012; but see Stephens et al. 2014), our study involved actual fuels-reduction treatments implemented by the U.S. Forest Service and was intended to assess the efficacy of existing management guidelines governing forest management at a bio-regional scale. We intensively sampled the vegetation within field plots before and after the implemented treatments and coupled this fine-scale vegetation data with LiDAR data to quantify changes in forest structure and parameterize fire and forest-growth models. Finally, we linked spotted owl demographic rates to changes in vegetation conditions resulting from fuels treatments and wildfire using data from a long-term demography study, as few previous studies have simulated the short- versus long-term trade-offs of fuel treatments on wildlife population dynamics (however, see Scheller et al. 2011). We specifically considered two demographic parameters at the scale of an owl territory: (1) fitness, which we defined as the population growth rate (λ) conferred on resident owls by habitat conditions within the territory (Franklin et al. 2000); and (2) equilibrium occupancy, which is the level at which occupancy probability at a territory will stabilize when colonization and extinction probabilities remain constant (MacKenzie et al. 2006).

We hypothesized that fuels treatments would result in a short-term loss of owl habitat, but in the event of simulated wildfire, these treatments would result in a long-term increase in owl habitat (relative to the untreated landscape) by reducing owl habitat loss to fire. Thus, if a fire was simulated under extreme weather conditions shortly after treatment implementation, we predicted the treatments to reduce the amount of habitat lost during the fire and to result in greater habitat amounts 30 years post-fire because forest growth would be insufficient to compensate for the loss of overstory trees during this timeframe. If no fire was simulated after treatment implementation, we expected that the amount of habitat would initially decline, but that similar amounts would be present on treated and untreated landscapes after 30 years because of forest regrowth (Collins et al. 2011). Because owl demographic rates are strongly and positively correlated with the amount of high-canopy-cover ($\geq$70%) forest within owl territories (Tempel et al. 2014*a*), we predicted that owl demographic rates would follow similar patterns as habitat amount. Thus, we hypothesized that fuels treatments would reduce territory fitness and occupancy in the short-term, but result in higher fitness and occupancy after 30 years in the event of simulated fire.

Materials and Methods

Study area

Our 13,482-ha Last Chance Study Area (LCSA) was located within the Tahoe National Forest in the central Sierra Nevada, California (Fig. 1). Elevations ranged from 600 to 2,200 m. The vegetation was primarily mixed-conifer forest dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*), with lesser amounts of other forest types and montane chaparral. The LCSA had a Mediterranean climate with an average of 1,182 mm of precipitation, most of which fell as snow, from 1990 to 2008 (Hell Hole Remote Automated Weather Station). The historic fire regime in this region mainly consisted of frequent, low-to moderate-severity fire occurring every 5–15 years (Stephens and Collins 2004).

As part of the experimental design for SNAMP, the study area was composed of a central treatment fireshed (4,293 ha) and two adjacent watersheds to the north and south that together served as a control 'fireshed' (5,658 ha; Fig. 1). We further expanded the study area by an

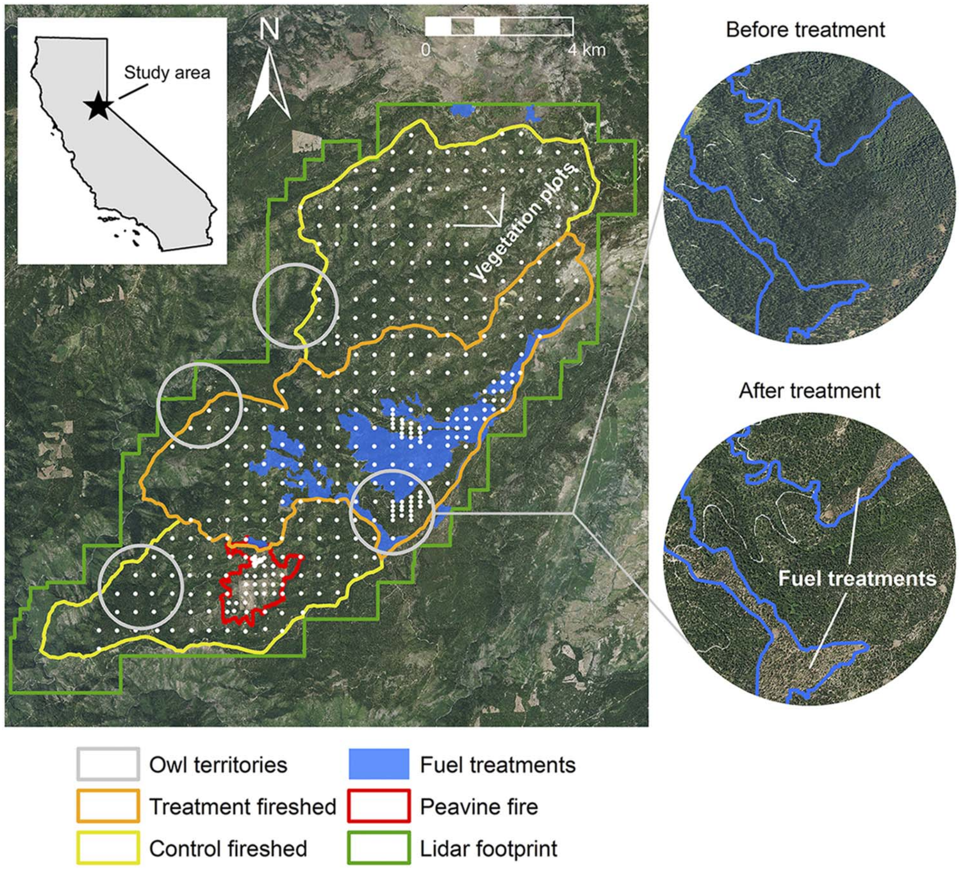

Fig. 1. Map of the Last Chance Study Area in the central Sierra Nevada, California, showing the delineation of treatment and control firesheds, the locations of four California Spotted Owl (*Strix occidentalis occidentalis*) territories used in our demographic analyses, fuel treatments conducted in 2011–2012, the plot network for ground-based sampling of forest vegetation before and after the fuel treatments, and an aerial overview of part of the treated area before and after the fuel treatments.

additional 3,531 ha of untreated landscape covered by the LiDAR footprint to incorporate additional owl territories (Fig. 1). Fuels-reduction treatments were implemented within the treatment fireshed by the U.S. Forest Service during 2011–2012 as part of the Sierra Nevada Adaptive Management Project (SNAMP; Sierra Nevada Adaptive Management Project 2014). The fuels treatments, also known as Strategically Placed Landscape Area Treatments (SPLATs), followed the guidelines specified in the 2004 management plan for national forests in the Sierra Nevada (USFS 2004). The management plan specified that no trees $\geq$76.2 cm can be harvested, at least 40% canopy cover must be retained, and at least 40% of a stand's basal area must be retained. Treatments were implemented on 942 ha (7.0% of the total study area) as follows: 561 ha of mechanical thinning (tractor and cable), 247 ha of prescribed fire, and 134 ha of mastication of shrubs and small trees. Although no treatments were implemented in the control fireshed, the 2008 Peavine Fire burned 268 ha within the southern unit of the control fireshed (Fig. 1). Collins et al. (2011) modeled treatments and hazardous fire potential in the same study area, but focused on the treatment fireshed only.

Development of vegetation map

We developed a pre-treatment vegetation map using a combination of LiDAR, high-resolution digital color-infrared (CIR) aerial imagery, and an intensive network of field plots. First, we used LiDAR and CIR data to create an initial polygon-based map where the polygons represented areas of homogeneous vegetation in terms of species, vertical structure, basal area, and canopy cover. The mean polygon size was 9.4 ha (range = 0.9–72.6 ha). We collected the LiDAR and CIR data before the fuels-reduction treatments, and we sampled vegetation at the field plots before and after treatment. We then used the field-plot data to impute detailed attributes (e.g., tree lists and fuels models) for each polygon. Thus, we derived two different maps (with and without treatment), which we used in fire and forest-growth modeling. We used field-plot data to assess the accuracy of the pre-treatment and post-treatment maps in terms of canopy cover and large tree density, which were the variables we used to identify spotted owl habitat (see *Materials and methods: Assessing effects of fuels treatments and fire on spotted owl habitat*). We found that values for percent canopy cover and large tree density were similar for field plots and their associated map polygon, although on average the field plot values were slightly lower than the map values. For percent canopy cover, the average difference for the pre-treatment map was −5.42% canopy cover (SE = 1.12), and for the post-treatment map the average difference was −2.05% canopy cover (SE = 1.21; Appendix A). For large tree density, the average difference for the pre-treatment map was = −7.05 large trees per hectare (SE = 1.51), and for the post-treatment map the average difference was = −4.30 large trees per hectare (SE = 1.55; Appendix A).

We contracted with the National Center for Airborne LiDAR Mapping (National Center for Airborne Laser Mapping 2011) to collect small-footprint, multiple-return airborne LiDAR data with a point density of 6–10 points/m^2 in September 2008, and we obtained 1 × 1 m^2 resolution CIR data collected by the National Agriculture Imagery Program (NAIP) in 2005. After initial processing of the LiDAR and CIR data, we used an object-based segmentation approach to delineate polygons of homogeneous vegetation types. We then applied an unsupervised classification strategy to label the different vegetation types based on the Bayesian Information Criterion algorithm, which is used to automatically determine the optimized number of vegetation groups. We identified 8 vegetation types on our study area—low shrub, high shrub, open true fir, pine forest, cedar forest, young mixed-conifer forest, and mature mixed-conifer forest. The dominant vegetation type on the study area was mixed-conifer forest (56% mature, 19% young); the other forest types were present in lesser amounts (13% cedar, 7% pine, 4% open true fir). Chaparral (low and high shrubs) covered only 1% of the study area. Post-treatment LiDAR was collected in 2013 and was used to delineate actual treatment areas based on a change-detection algorithm to identify where forest structure noticeably changed between the two LiDAR acquisitions. This approach was employed because there can be inconsistencies between agency-generated treatment polygons and actual treatment extent on the ground.

We sampled forest vegetation at field plots that were spaced at 500-m intervals across the LCSA, except the southwest corner of the LCSA where extreme topography precluded sampling (Fig. 1). We sampled more intensively at 125- and 250-m spacing around instrument locations for a separate hydrological study. In August 2008, we also intensively sampled the area burned by the Peavine Fire. In total, we sampled 408 plots in 2007–2008 (pre-treatment) and 369 plots in 2013 (post-treatment). We briefly summarize the vegetation sampling here, but refer the reader to Collins et al. (2011) for greater detail. We sampled within 0.05-ha circular plots and recorded information on individual trees using three different sampling intensities based on tree size: (1) throughout the entire plot for trees ≥19.5 cm dbh; (2) within a random one-third of the plot (167 m^2) for trees 5.0–19.4 cm dbh; and (3) along a random belt transect (76 m^2) for trees <5.0 cm dbh. We recorded tree species, vigor, crown position, dbh, total height, and height to live crown base (live trees only) for all trees in the upper two size classes, and species and dbh for trees in the smallest size class. In addition, we sampled downed wood, litter, duff fuels, and woody shrub cover on three randomly chosen transects within each plot. We used the line-intercept method to sample downed woody fuels (van Wagner 1968, Brown 1974), and we recorded percent cover and average height for woody shrubs intersecting each transect.

We then used the field-plot data to impute detailed vegetation attributes for each polygon of the vegetation map for use 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. The definition of the gradient nearest neighbors for each polygon (sensu Ohmann and Gregory 2002) included topographic variables (e.g., slope, aspect, elevation), canopy structure (percent canopy cover and an index of large tree density), and vegetation type. To maintain some of the fine-scale heterogeneity observed in the field, we identified all plots in the 95th percentile in terms of nearest neighbor distance for each stand and then randomly assigned three of those plots to the stand. Our pre-treatment map represented conditions after the Peavine Fire occurred (see *Materials and methods: Study area*) because we collected the remotely sensed data and sampled additional field plots within the burned area after the fire. The treatment scenario differed from the no treatment scenario in what field-plot data were used to impute vegetation attributes for polygons where treatments occurred. For the treatment scenario, we used post-treatment tree lists from treated plots ($n = 49$) for polygons that experienced noticeable structural change based on LiDAR change detection or were confirmed on-the-ground to have been burned by prescribed fire.

Modeling forest dynamics and fire

We considered four scenarios when modeling forest dynamics and wildfire: (1) with treatments and with fire; (2) without treatments and with fire; (3) with treatments and without fire; and (4) without treatments and without fire. For the "with fire" scenarios, we used FARSITE (Finney 1998) to simulate a single fire for both the treated and untreated landscape based on the weather conditions during the 2001 Star Fire, which burned 6,817 ha, including 314 ha on the northeast edge of our study area (Fig. 2). Approximately 39% of this fire burned at high severity (www.mtbs.gov; accessed on 4 February 2015). 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. Topographic inputs such as slope, aspect, and elevation were obtained from the LiDAR-derived surface elevation model at 30-m resolution. We derived forest structure map layers for canopy cover, canopy bulk density, canopy base height, and canopy height using the imputation procedure previously described. We calculated fuel-model assignments using a selection logic based on surface fuels and forest structure measured at the plots (Collins et al. 2011, 2013). This approach has proven sufficient at assigning fuel models based on actual fuel loads rather than relying on the Forest Vegetation Simulator (FVS; Dixon 2002), which has been shown to use fuel models that underestimate fire behavior (Collins et al. 2013). This approach for assigning fuel models was different for treated and untreated stands. For untreated stands, we used a regression tree analysis with several response variables representing surface fuels: shrub cover, litter, 1- to 100-hour woody fuels, and 1000-hour woody fuels. Forest structure and stand vegetation classification were used as independent variables. Model fits were moderate ($R^2 = 0.3$–0.6), but given the known variability in surface fuels in mixed-conifer forests (Lydersen et al. 2015), we deemed the assignments to be sufficient in describing the generalized fuel conditions represented by surface fuel models (Collins et al. 2011, 2013). For treated stands, post-treatment fuel models were based on treatment type and post-treatment fuel measurements. Prescribed-burn plots were assigned a moderate-load timber-litter fuel model (Scott and Burgan 2005). We assigned a low-load, timber-understory model to initial post-treatment masticated stands based on observed fire behavior from Knapp et al. (2011). There were two types of tree-harvest treatments: thinning and cable logging. Prescriptions for the cable-logging units indicated that the slash was to remain on site, so we used a moderate-load, timber-slash model followed by timber-understory models. Thinning treatments used whole-tree removal in which slash typically was removed, so we used the same selection logic for these treatments that we used for untreated stands.

We obtained weather information from the Duncan Remote Automatic Weather Station, limited to the active burning period of the Star

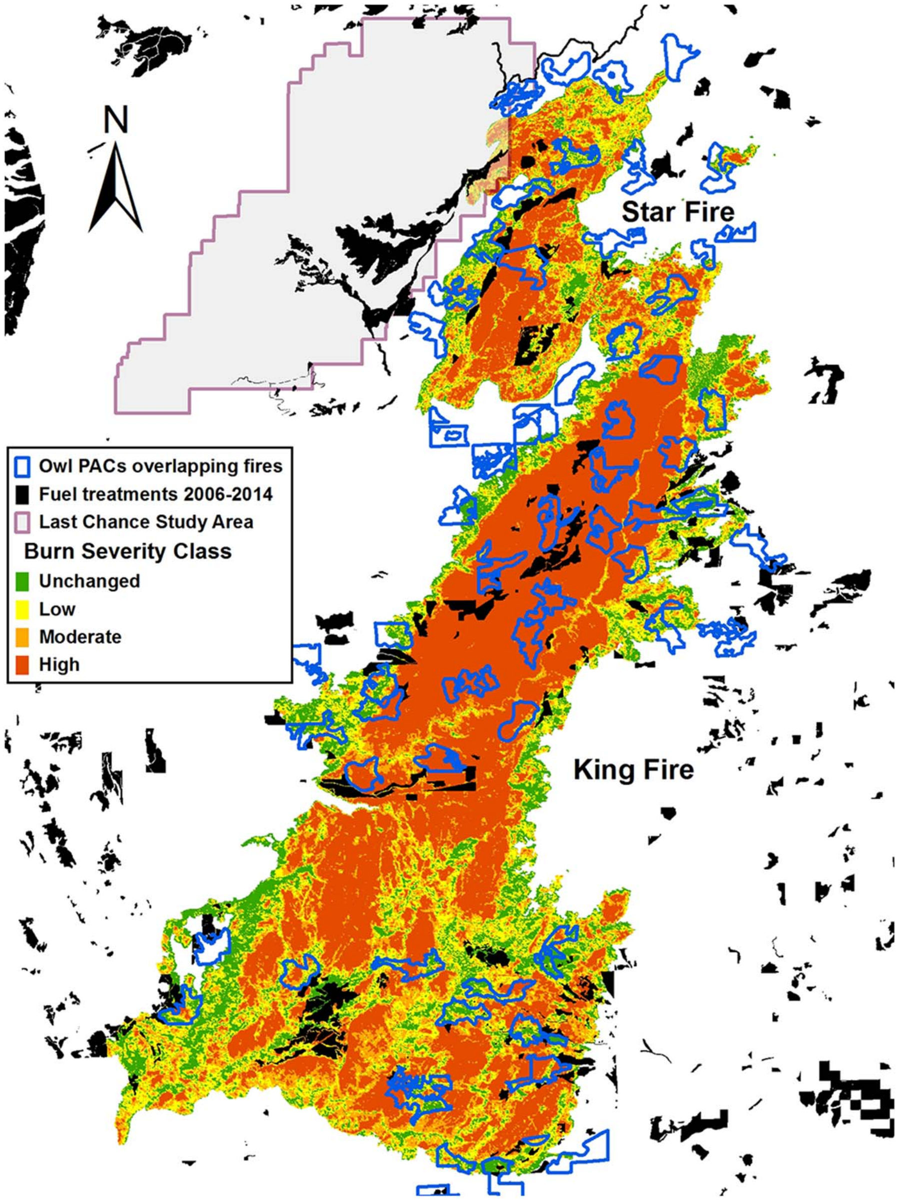

Fig. 2. Burn-severity map of the 2001 Star Fire and 2014 King Fire that burned near the Last Chance Study Area in the central Sierra Nevada, California. The burn-severity maps were created by the U.S. Forest Service (USFS) as detailed in Finco et al. (2012). We also show the spotted owl Protected Activity Centers (PACs) that were affected by these fires, and fuels-reduction treatments that were implemented by the USFS from 2006 to 2014.

Fire (August–September 2001), which served as the basis of our fire modeling. Moisture content for live and dead woody fuels and live herbaceous fuels used in the model were equivalent to 97th percentile weather conditions. Winds were generally easterly in the morning, switching to southwest to west during the day, with an average of 8 km h^{-1} (range = 0–15 km h^{-1}). Our ignition location was established in the northeast corner of the study area where the Star Fire perimeter overlapped our study area boundary. There were other wildfires that burned into the study area (2008 Peavine Fire, 2013 American Fire), but the 2001 Star Fire location and the conditions it burned under yielded the highest potential to burn a large portion of our study area, and in doing so impact more known owl sites. The simulation duration was set to allow the fire perimeter to expand through the entire study area.

We used the tree list databases associated with the 2008 pre-treatment field plots when simulating fire under the "no treatment" scenario, and we used the 2013 post-treatment field plots when simulating fire under the "treatment" scenario. Stand average flame lengths and proportion burned by fire type (surface fire, conditional crown fire, and active crown fire) were calculated for both scenarios and used as inputs for fire effects simulation using the keyword SIMFIRE in FVS with the Fire and Fuels Extension (FFE; Reinhardt and Crookston 2003).

For all four scenarios, we then simulated 30 years of forest growth on the study area in 10-year time steps using FVS with FFE. The simulations were performed using the integrated platform ArcFuels (Ager et al. 2006, Vaillant et al. 2011), which runs FVS-FFE to produce the forest structure inputs needed for FARSITE. We used the western Sierra variant of FVS to simulate forest dynamics over the simulation periods. Because this variant does not include a "full-establishment model," users must set parameters for tree regeneration by identifying number, species, and frequency of establishment. Following the methods of Collins et al. (2011, 2013), we used a random-number generator, within defined bounds, to set the number of seedlings at each time step in FVS while regulating height-growth rates to simulate realistic conditions in a mixed-conifer forest.

Assessing effects of fuels treatments and fire on spotted owl habitat

We identified canopy cover and large trees as the most important predictors of spotted owl habitat because nest locations were characterized by greater amounts of these elements in the central Sierra Nevada (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997, Williams et al. 2011). To determine a biologically meaningful definition of a large tree, we examined 101 spotted owl nest trees on the nearby Eldorado Demography Study Area (EDSA). The size distribution of these nest trees was not significantly different from a normal distribution at $\alpha = 0.05$ (Shapiro-Wilk test, $p = 0.052$), so we estimated the standard deviation of the 101 nest tree diameters and used the 10% quantile value of a normal distribution to identify the minimum size of a large tree as 71.3 cm dbh. Thus, 90% of owl nest trees on our study area were expected to be $\geq$71.3 cm dbh. We then performed a logistic regression (Hosmer et al. 2013) of owl nesting habitat as a function of canopy cover and large tree density using data collected by Bond et al. (2004) within 0.02-ha plots at 25 nest trees and 36 random locations within potentially suitable owl nesting habitat on the EDSA (Fig. 3). We identified the following logistic regression equation for canopy cover (CC; percent) and large tree density (LT; ha^{-1}) using SAS (SAS Institute, Cary, North Carolina, USA):

$$\begin{aligned} logit(Pr[nesting\ habitat]) &= -4.141 \\ &\quad + 0.026 \times CC \\ &\quad + 0.052 \times LT. \end{aligned} \tag{1}$$

The parameter estimate for large tree density was statistically significant at $\alpha = 0.05$ ($p < 0.01$, Wald chi-squared test statistic $[Q_W] = 8.71$, df $= 1$), but the parameter estimate for canopy cover was not ($p = 0.19$, $Q_W = 1.72$, df $= 1$). However, we elected to include CC in the model given that canopy cover is known to be an important component of spotted owl nesting habitat (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997).

We used Eq. 1 to estimate the probability that each forest stand (i.e., map polygon) on our study area contained suitable owl nesting habitat under each of the four treatment/wildfire scenarios at four points in simulated time (years 0, 10, 20, and 30). Using the values for canopy cover and large tree density from each map polygon, we calculated the probability that the polygon contained suitable nesting habitat and obtained an average probability (weighted by the area of each map polygon) for the entire study area, which we refer to hereafter as the habitat suitability index. We also obtained separate habitat suitability indices for the control and treatment fireshed within the study area (see *Materials and methods: Study area*) because we expected the direct and indirect (i.e., through modification of fire behavior) effects of fuels treatments to be more pronounced near the treatments.

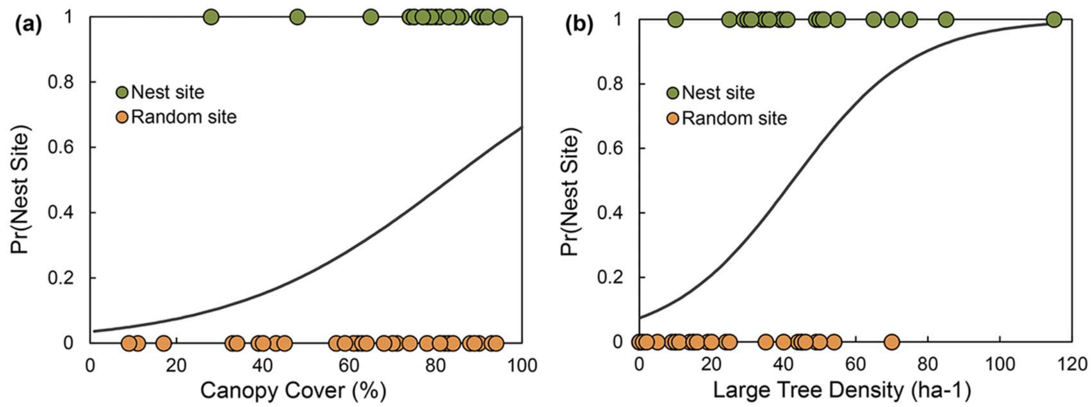

Fig. 3. Comparison of (a) canopy cover (percent) and (b) large tree density ($\geq$71.3 cm dbh; ha^{-1}) for 25 California Spotted Owl (*Strix occidentalis occidentalis*) nest locations and 36 random locations in potentially suitable owl nesting habitat on the Eldorado National Forest in the central Sierra Nevada, California. These data were used to develop a logistic regression model to estimate the probability of forest being suitable as spotted owl nesting habitat; best-fit logistic regression lines are shown on each graph.

Assessing effects of fuels treatments and fire on spotted owl demography

Under each of the four treatment/wildfire scenarios, we projected how changes in owl habitat were expected to affect fitness and equilibrium occupancy (ψ_{Eq}) at the spatial scale of a spotted owl territory. We defined an owl territory as the area contained within a 1,128-m radius (400-ha) circle around each owl territory center; this radius was equal to one-half the mean nearest neighbor distance between owl territory centers on the EDSA (Tempel et al. 2014*a*). We estimated the territory center as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year; otherwise we used the mean of the roost locations for that year. We located nests and roost sites during surveys conducted annually from 2007 to 2013 during the spotted owl breeding season (April–August; see Tempel et al. [2014*a*]), and we found no barred owls (*Strix varia*) on our study area. We limited this analysis to four spotted owl territories that were largely within our study area ($\geq$80% of the 400-ha territory). Three of the territories were occupied by an owl pair every year from 2007 to 2013, and the other was occupied in all but one of those years. For the demographic analyses, we defined owl habitat as high-canopy-cover forest dominated by trees $\geq$30.5 cm dbh because previous analyses showed that this vegetation type had a strong positive relation with λ and ψ_{Eq} (Tempel et al. 2014*a*). On the 2008 pre-treatment map, forest stands with $\geq$70% canopy cover always contained a substantial number of trees $\geq$30.5 cm dbh (mean density = 55.8 ha^{-1}, range = 16.0–130.7 ha^{-1}), so we considered all of these stands to be dominated by trees $\geq$30.5 cm dbh. Although our inferences were limited by the small sample size of four territories, the amount of high-canopy-cover forest within these territories (mean = 154 ha, range = 102–207 ha) was typical of the amount found in 70 other territories near our study area (mean = 132 ha; Tempel et al. 2014*a*).

To assess how changes in the amount of high-canopy-cover forest impacted fitness and ψ_{Eq} at each of the four territories, we used the habitat maps developed under each scenario at four points in simulated time (years 0, 10, 20, and 30) to quantify the proportion of each territory consisting of high-canopy-cover forest. We estimated territory fitness and equilibrium occupancy following the methods of Tempel et al. (2014*a*). For fitness, where we used a stage-based, Lefkovitch matrix model parameterized with fecundity and survival rates to represent changes in the female population size

$$\begin{bmatrix} N_{J,t+1} \\ N_{S1,t+1} \\ N_{S2,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \varphi_{S,t} b_{S,t} & \varphi_{S,t} b_{A,t} & \varphi_{A,t} b_{A,t} \\ \varphi_{J,t} & 0 & 0 & 0 \\ 0 & \varphi_{S,t} & 0 & 0 \\ 0 & 0 & \varphi_{S,t} & \varphi_{A,t} \end{bmatrix} \begin{bmatrix} N_{J,t} \\ N_{S1,t} \\ N_{S2,t} \\ N_{A,t} \end{bmatrix}$$

where $N_{J,t}$, $N_{S1,t}$, $N_{S2,t}$, and $N_{A,t}$, were the number of juvenile, first-year subadult, second-year subadult, and adult females at time t, respectively; $\varphi_{J,t}$, $\varphi_{S,t}$, and $\varphi_{A,t}$ were the apparent survival rates of juvenile, subadult, and adult females from time t to $t+1$, respectively; and $b_{S,t}$ and $b_{A,t}$ were the fecundity rates for subadult and adult females at time t, respectively. Fecundity was the number of female offspring produced per female in the population, assuming a 50:50 sex ratio for fledged owls. Based on previous analyses in Tempel et al. (2014*a*), we estimated survival at each territory as a function of female age and the logarithm of the hectares of high-canopy-cover forest (HCF)

$$logit(\varphi) = -0.005 + 0.557 \times age + 0.497 \times log([HCF/10] + 1) \quad (2)$$

where age = 0 for subadults and 1 for adults, and we divided the amount of HCF by 10 to facilitate model fitting. However, we estimated fecundity solely as a function of female age because high-canopy-cover forest was not a significant predictor of reproductive output,

$$b = 0.153 + 0.178 \times age \quad (3)$$

where age = 0 for subadults and 1 for adults. Using the territory-specific estimates of survival and fecundity, we then computed a territory-specific fitness (i.e., λ) as the dominant eigenvalue of the matrix. As noted in Tempel et al. (2014*a*), we expected our estimates of fitness to be biased low because (1) we did not incorporate immigration into the projection matrix, and (2) if an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history at the original territory (which lowered the estimates of annual survival) to avoid making assumptions about the owl's location during the intervening period. Nevertheless, differences in fitness allowed us to evaluate the relative simulated effects of fuels treatments and wildfire.

We calculated equilibrium occupancy (ψ_{Eq}) from the territory extinction (ε) and colonization (γ) rates at each territory where $\psi_{Eq} = \gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006). Again, based on previous analyses in Tempel et al. (2014*a*), we estimated extinction probability at each territory as a linear function of the hectares of HCF

$$logit(\varepsilon) = -1.944 - 0.058 \times (HCF/10), \quad (4)$$

and we estimated colonization as a function of the logarithm of the hectares of HCF

$$logit(\gamma) = -3.528 + 2.149 \times log([HCF/10] + 1). \quad (5)$$

As we did when estimating survival, we divided the amount of HCF by 10 to facilitate model fitting.

Results

Effects of fuels treatments on forest structure

We compared pre- and post-treatment measurements at 49 field plots located within the fuels-treatment network (Table 1). Fuels treatments reduced the mean canopy and woody shrub cover by ~10% and reduced mean total tree density from 540.8 to 263.6 trees/ha. Mean large tree density increased slightly from 20.8 to 22.8 trees/ha, perhaps because of tree growth during the five years that elapsed between pre- and post-treatment measurements. Fuels treatments decreased the amount of 1–1000 hour woody fuels from 31.5 to 24.9 Mg/ha, whereas duff fuels increased from 64.2 to 67.2 Mg/ha.

Fire modeling

The simulated fire spread across nearly all of the study area for both scenarios (with and without treatment) because of the prevailing winds (Fig. 4). Fuels treatments reduced the intensity of the fire, as evidenced by the predicted flame lengths, with the greatest reductions occurring within treated areas. Overall, when fire occurred on the untreated landscape, 70.2%, 16.6%, 9.3%, and 3.9% of the study area experienced flame lengths of <2, 2–4, 4–8, and >8 m, respectively. In contrast, when fire occurred on the treated landscape, 76.2%, 14.3%, 6.8%, and 2.7% of the study area burned at these flame lengths. Collins et al. (2011) noted that flame lengths >2 m often corresponded to areas with crown fire initiation (i.e., torching). Differences in fire behavior between the two scenarios (i.e., a greater proportion of the fire

Table 1. Comparison of pre- and post-treatment canopy cover (percent), total tree density (ha^{-1}), large tree density (≥71.3 cm dbh; ha^{-1}), shrub cover (percent), duff fuels (Mg/ha), and woody fuels (1–1000 hour; Mg/ha) at 49 field plots located within a fuels-treatment network on the Last Chance Study Area in the central Sierra Nevada, California. Standard errors are shown in parentheses.

Vegetation attribute	Pre-treatment	Post-treatment
Canopy cover	56.6 (3.2)	45.8 (2.7)
Total tree density	540.8 (31.6)	263.6 (21.1)
Large tree density	20.8 (4.4)	22.8 (4.6)
Shrub cover	31.6 (4.0)	22.2 (3.3)
Duff fuels	64.2 (5.4)	67.2 (5.6)
Woody fuels	31.5 (4.9)	24.9 (4.1)

burned at <2 m after fuels treatments) also generally held true for the land encompassed by the four owl territories. Interestingly, the one territory where this pattern did not hold true was at the territory located within the fuels-treatment network (the territory in the southeastern part of the study area; Fig. 4) where 29.3% of the territory burned at flame lengths >2 m under the treatment scenario compared to 19.7% under the no treatment scenario. This result may have been influenced by differences in the direction of fire spread and time-of-day that the territory burned, which would influence burning conditions via fuel moisture, relative humidity, and air temperature.

Effects of fuels treatments and fire on spotted owl habitat

When we applied Eq. 1 to the habitat maps under the four treatment/wildfire scenarios, we found that fuels treatments had a persistent, slightly negative effect on the owl habitat suitability index for the entire study area when no wildfire occurred (Fig. 5). Implementing fuels treatments immediately decreased the habitat suitability index (0.25 for 2008 pre-treatment map compared to 0.23 for 2013 post-treatment map), and this small difference was still present after 30 years of simulated forest growth (0.37 without treatment versus 0.36 with treatment). Conversely, we found that fuels treatments had a

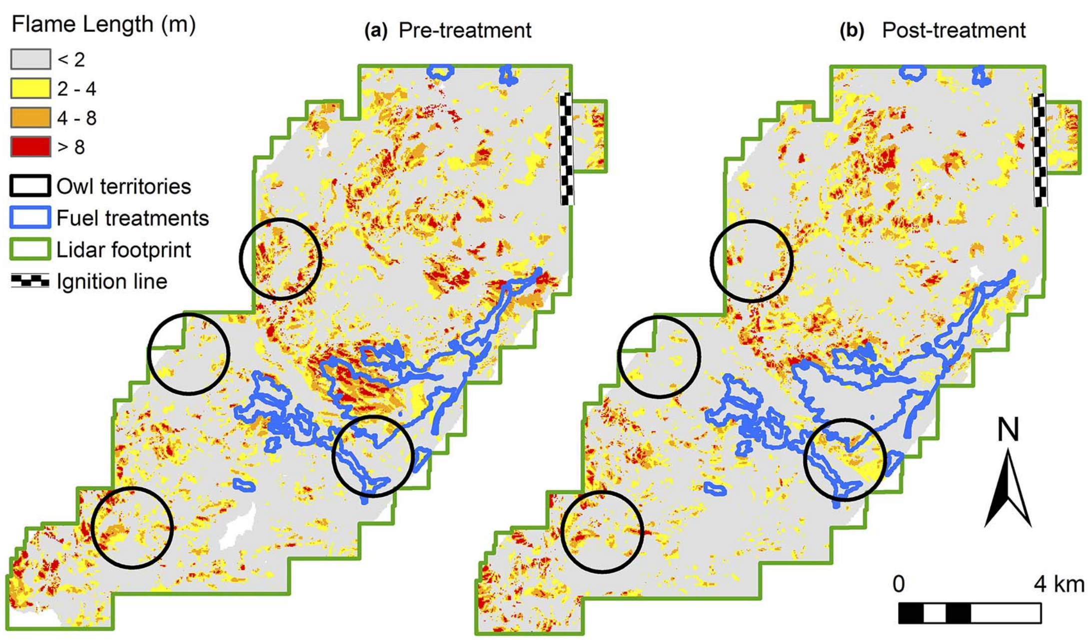

Fig. 4. Flame lengths (m) of simulated fires on the Last Chance Study Area under two scenarios: (a) on an untreated landscape; and (b) after implementation of fuels treatments. We show the location of treatment polygons in (a) for ease of comparison, but treatments were not implemented in (a). Four California Spotted Owl (*Strix occidentalis occidentalis*) territories within the study area are also shown. Fire occurred in all areas within the "< 2 m" category (gray shading).

persistent, slightly positive effect on the owl habitat suitability index for the entire study area after wildfire was simulated (Fig. 5). After 30 years of simulated forest growth following fire, the habitat suitability index under the treatment scenario was 0.20 compared to 0.17 under the no treatment scenario. The results were very similar when we summarized habitat suitability indices separately for the control and treatment fireshed (Appendix B).

Effects of fuels treatments and fire on spotted owl demography

We estimated that fuels treatments had a slight, persistent negative effect on fitness at four spotted owl territories within our study area when no wildfire occurred (Fig. 6). The mean fitness of owls at the four territories using the 2013 post-treatment map was 0.825 (SE = 0.012) compared to 0.839 (SE = 0.007) using the 2008 pre-treatment map. This difference was still present after 30 years of simulated forest growth (fitness with treatments = 0.850, SE = 0.008; fitness with no treatments = 0.856, SE = 0.005). In contrast, the simulations suggested that fuels treatments had a larger positive effect on territory fitness after wildfire (Fig. 6). Thirty years after the occurrence of fire, the simulations projected the mean territory fitness with treatments to be 0.796 (SE = 0.009) versus 0.776 (SE = 0.008) with no treatments.

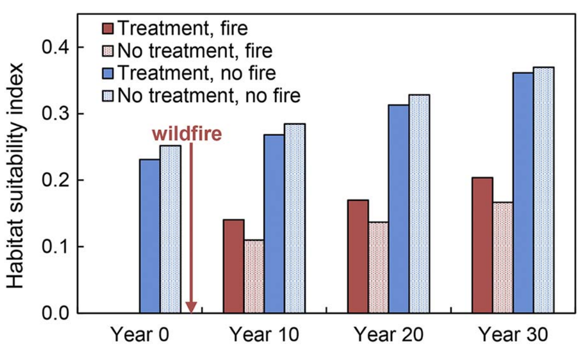

Fig. 5. California Spotted Owl (*Strix occidentalis occidentalis*) habitat suitability index for a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the "no treatment" scenarios was 2008, and year 0 for the "treatment" scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the "no treatment" and "treatment" scenarios, and post-fire effects were first assessed in year 10.

The general patterns for equilibrium occupancy were similar to those for territory fitness, but there was greater variation in ψ_{Eq} under the different scenarios (Fig. 6). Fuels treatments again had a slight negative effect if fire did not occur, but they had a larger positive effect if simulated fire did occur. When fire did not occur, the projected mean equilibrium occupancy for the four territories after 30 years was 0.883 (SE = 0.037) with fuels treatments and 0.911 (SE = 0.023) with no fuels treatments. In contrast, the projected mean equilibrium occupancy 30 years after fire was 0.577 (SE = 0.053) with treatments compared to 0.468 (SE = 0.042) with no treatments.

Discussion

Several studies have investigated the short-term and long-term impacts of fuel treatments on habitat availability for old-forest species using various treatment simulations (Lee and Irwin 2005, Ager et al. 2007, Thompson et al. 2011, Roloff et al. 2012), but ours was unique in several respects. First, we simulated the effects of actual (as opposed to hypothetical) fuels treatments that reflected an actual implementation of a region-wide strategy to reduce landscape-level fire spread and intensity on U.S. Forest Service lands, while conserving key forest structural attributes associated with old-forest species (i.e., large trees, high canopy cover; USFS 2004). Second, we combined field-collected vegetation data and LiDAR data to develop a detailed map of forest structure used to parameterize our fire and forest-growth models. The LiDAR data provided information on vertical structure that was unattainable with other sources of remotely sensed data (Lefsky et al. 2002) and allowed us to determine the actual extent of treatments. While the full potential of LiDAR data was not demonstrated here (e.g., the mapping of individual trees; Li et al. 2012, Jakubowski et al. 2013), the LiDAR data were critical in developing a more detailed and accurate vegetation map for use in fire modeling than what could have been

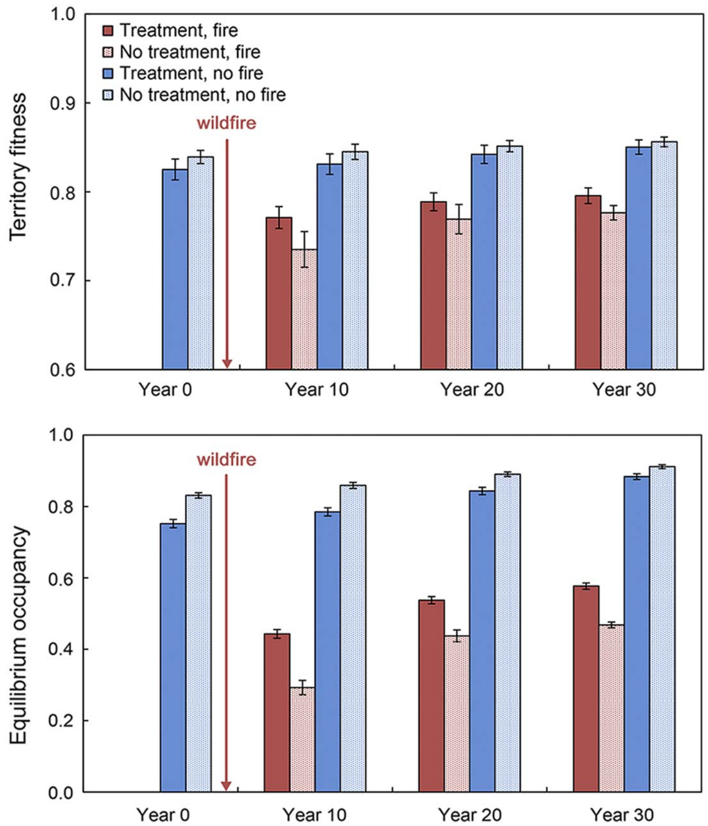

Fig. 6. The average territory fitness and equilibrium occupancy with standard errors at four California Spotted Owl (*Strix occidentalis occidentalis*) territories on a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the "no treatment" scenarios was 2008, and year 0 for the "treatment" scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the "no treatment" and "treatment" scenarios, and post-fire effects were first assessed in year 10.

solely achieved with lower-resolution satellite or optical imagery. Finally, in addition to projecting changes in habitat over time, we linked vegetation conditions under the different scenarios to territory fitness and occupancy within our study area using previously modeled relationships between forest structure and owl demography (Tempel et al. 2014*a*). For these reasons, we believe our study provided a rigorous simulation of the effects of fuels-reduction treatments on an old-forest species that has regional-scale implications for forest management.

We modeled the behavior of a fire (both with and without fuels treatments) parameterized using actual conditions during the 2001 Star Fire; this fire burned large areas at high severity (2,677 of 6,817 total ha; Fig. 2). We then simulated forest growth 30 years into the future under four landscape scenarios: treated/fire, untreated/fire, treated/no fire, and untreated/no fire. As predicted, we projected that fuels-reduction treatments had a negative short-term impact on spotted owl habitat and demographic rates in the absence of fire, but contrary to our expectations, a very slight negative effect was still evident after 30 years. Conversely, treatments had a projected long-term positive effect on owls up to 30 years later when we simulated a fire that burned 30% of our study area at high severity (i.e., >2 m flame length). Thus, our findings were in general agreement with previous modeling efforts for the Northern Spotted Owl (*S. o. caurina*) in the Pacific Northwest where treated landscapes contained more owl habitat after simulated fire than untreated landscapes, either immediately afterwards (Ager et al. 2007) or up to 75 years later (Roloff et al. 2012).

The observed differences in owl habitat and demographic rates under the different scenarios were modest. For example, the habitat suitability index on our study area 30 years after simulated fire was 0.20 and 0.17 for the treated and untreated landscapes, respectively. Within the four owl territories 30 years after fire, we estimated the mean territory fitness to be 0.796 and 0.776 for the treated and untreated landscapes, respectively. Only 7% of the study area was treated because we expanded our study area to include additional owl territories (Fig. 1), but previous fire modeling studies suggested that at least 20% of the landscape should be treated to significantly reduce fire spread and intensity (e.g., Ager et al. 2007, Finney et al. 2007, Moghaddas et al. 2010). Thus, our finding of fairly modest differences in predicted flame lengths outside of the "treatment" fireshed for the treated and untreated scenarios (Fig. 4) was likely related to the low overall proportion of the study area treated. Based on the original study design, 18% of the area (i.e., the treatment fireshed) was treated, which was shown to be effective at reducing hazardous fire potential across the treatment fireshed (Collins et al. 2011). Although the projected effects on owl fitness are relatively small, even small reductions in annual growth rates (a function of fitness parameters) can translate into large population declines over longer time periods (Tempel et al. 2014*b*). For example, if the annual growth rate is 1.00, then the population size remains unchanged after 30 years. In contrast, if the annual growth rate is 0.98, then population size would decline by 45% after 30 years. Importantly, California Spotted Owl populations have already declined by up to 50% throughout the Sierra Nevada in the past 20 years (Conner et al. 2013, Tempel et al. 2014*b*), and any further declines could jeopardize their long-term persistence.

We linked spotted owl demography to fuels treatments and fire behavior via their effects on high-canopy-cover forests because relationships between owl territory fitness/occupancy and this forest type have been well-established in the Sierra Nevada (Blakesley et al. 2005, Tempel et al. 2014*a*). Moreover, previous studies have shown that large (>50 ha) areas of high-severity fire within owl territories may reduce territory occupancy (Lee et al. 2013). In addition, territory extinction has been positively correlated with the combined area of early-seral forests, high-severity burn, and post-fire salvage logging within owl territories (Clark et al. 2013). As such, a reasonable ecological basis exists for inferring that simplification or elimination of high-canopy-cover forests by fuels treatments or high-severity fire will adversely affect spotted owl populations. However, the effects of wildfire on spotted owls are undoubtedly complex and owls may benefit from the presence of a mosaic of habitat types promoted by mixed-severity fire, and particularly from shrub patches and early-seral forests that harbor diverse prey assemblages (Roberts et al. 2015). For example, Bond et al. (2009) found that spotted owls in the southern Sierra Nevada selectively foraged in burned areas, even those that burned at high severity. We further note that not all previous studies of spotted owls have found reduced occupancy rates in burned areas relative to unburned areas (Roberts et al. 2011, Lee et al. 2012). Therefore, to the extent that low- or moderate-severity fire may benefit owls, the modeled declines in territory fitness and occupancy in our fire scenarios might be overestimated, and by extension the long-term (30-year) benefits of fuels reduction treatments overly optimistic. Clearly, additional empirical work is needed to assess the complex effects of wildfire on spotted owls, particularly longer-term studies of marked individuals in landscapes that have experienced a range of fire severities (with and without existing fuel treatment networks on the landscape) and that are not confounded by the effects of salvage logging.

Other Sierra Nevadan species of conservation concern have similar habitat needs as the spotted owl (i.e., mature forests with high canopy cover), particularly the Pacific fisher (*Pekania pennanti*) and Northern Goshawk (*Accipter gentilis*; Greenwald et al. 2005, Davis et al. 2007). Thus, similar forest-management trade-offs may exist for these species such that fuels-reduction treatments may reduce available habitat in the short-term but result in greater, long-term habitat amounts if fire occurs. Indeed, Thompson et al. (2011) performed an analogous study to ours, in which they modeled fire and forest growth under treatment and no treatment scenarios and assessed fisher habitat suitability in the southern Sierra Nevada. They projected that fuels treatments had slight negative effects on fisher habitat in the absence of fire, but provided significant positive benefits up to 37 years after simulated fire. Truex and Zielinski (2013) suggested that less fisher resting habitat was present immediately after mechanical fuels treatments were implemented in the Sierra Nevada. However, fishers consistently used areas in the southern Sierra Nevada where some timber harvest had occurred, so it may be possible to implement fuels-reduction treatments at an extent and rate that achieves fire-hazard-reduction goals (Zielinski et al. 2013). Therefore, we believe that our results, although specific to the spotted owl, have broader applicability to other species of management concern in the Sierra Nevada that selectively use forests characterized by large trees and high canopy cover.

We note, however, several caveats from our study when assessing the long-term effects of fuels treatments and wildfire on spotted owls. First, our projections were based on a single simulated fire for each treatment scenario (with and without treatment), and additional fire simulations may have suggested alternative fire patterns with differing effects on the components of owl habitat that we considered (canopy cover, large tree density). We used FARSITE to simulate 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. Second, our simulation was conducted at the relatively fine spatial scale of the fireshed (10s of km^2) because of its management relevance (North et al. 2015) and the difficulty of collecting detailed vegetation data for improved parameterization of fire models at larger spatial scales. However, conducting simulations such as ours at a larger spatial scale would increase the sample size of owl territories used to assess the potential effects of fire and fuels treatments on spotted owls. Future studies should carefully weigh the trade-off between collecting more accurate vegetation data at smaller spatial scales, and therefore deriving more accurate inputs for fire modeling, and increasing the number of owl territories by using larger spatial scales. Third, both of our simulated fires exhibited burn patterns that were substantially different than the burn patterns of the 2001 Star Fire that we attempted to simulate and the large 2014 King Fire (39,545 ha) that burned near our study area (cf. Figs. 2 and 4). Whereas our simulations resulted in relatively small, evenly distributed patches of high-severity fire, the Star Fire and King Fire burned large, contiguous areas at high severity. Indeed, our past experience suggests that existing fire models are generally incapable of replicating the burn patterns seen in the most extreme real fires. Thus, improved fire models are needed to more reliably assess how fuels treatments modify fire behavior and effects on forest structure especially under extreme conditions. Fourth, we did not simulate post-fire salvage logging (which often occurs after fires) on the habitat suitability of burned areas, and post-fire salvage logging has been shown to negatively affect spotted owl occupancy rates (Clark et al. 2013, Lee et al. 2013). Finally, the net effect of fuels treatments on spotted owls depends upon the true, but unknown, probability that high-severity fire effects will occur within individual owl territories. If individual territories have a low probability of experiencing high-severity fire effects, a relatively small portion of the owl population would accrue the long-term benefits of fuels reductions, whereas a greater portion of the population would experience the unfavorable short-term impacts. However, it is difficult to estimate spatially explicit, future probabilities for specific fire behaviors (e.g., crown-fire initiation) on specific areas of the landscape, and it is thus difficult to quantify trade-offs associated with fuel treatments on large spatial scales and in absolute terms (Finney 2005). We note, however, that the area burned by high-severity fire in the Sierra Nevada has increased in the past 30 years (Miller et al. 2009, Miller and Safford 2012) and may increase further in upcoming years because of climate change (Westerling and Bryant 2008, Liu et al. 2013). In addition, several fires on or near our study area have burned large areas of the landscape in the last 15 years (2001 Star Fire [6,817 ha], 2013 American Fire [11,305 ha], 2014 King Fire [39,545 ha]) and provide circumstantial evidence that a significant probability of large-scale, high-severity fire effects can be expected, at least in this region of the north-central Sierra Nevada. All three of these fires were human-ignited, which further complicates the estimation of future fire probabilities. In sum, future research on the short- versus long-term benefits of fuels treatments would benefit from a greater understanding of the probability of fire under various climate change scenarios, and linking replicated fire and forest-growth simulations to spotted owl population dynamics at landscape scales using spatially explicit population models.

In conclusion, our results suggest that fuels-reduction treatments, as currently implemented by the U.S. Forest Service in the Sierra Nevada, have the potential to provide long-term (30-year) benefits to spotted owls in the event of fire under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. Furthermore, major uncertainties remain (e.g., What is the future probability that high-severity fire effects will occur within individual owl territories?). In conjunction with the observed population declines in the last 20 years (Conner et al. 2013, Tempel et al. 2014*b*), we believe these uncertainties warrant an informed approach to landscape fuels management that explicitly balances the seemingly conflicting goals of providing habitat for owls and reducing hazardous fire potential. Specifically, we recommend that the U.S. Forest Service continue its current policy that restricts timber harvest within spotted owl Protected Activity Centers (PACs), which contain ~125 ha of the best habitat that owls use for nesting and roosting over long time periods (up to 24 years; Berigan et al. 2012). Furthermore, fuels-treatment arrangements should be designed to limit the potential for high-severity fire to spread into PACs.

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Supplemental Material

Ecological Archives

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