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California Spotted Owl, Songbird, and Small Mammal Responses to Landscape Fuel Treatments

SCOTT L. STEPHENS, SETH W. BIGELOW, RYAN D. BURNETT, BRANDON M. COLLINS, CLAIRE V. GALLAGHER, JOHN KEANE, DOUGLAS A. KELT, MALCOLM P. NORTH, LANCE JAY ROBERTS, PETER A. STINE, AND DIRK H. VAN VUREN

A principal challenge of federal forest management has been maintaining and improving habitat for sensitive species in forests adapted to frequent, low- to moderate-intensity fire regimes that have become increasingly vulnerable to uncharacteristically severe wildfires. To enhance forest resilience, a coordinated landscape fuel network was installed in the northern Sierra Nevada, which reduced the potential for hazardous fire, despite constraints for wildlife protection that limited the extent and intensity of treatments. Small mammal and songbird communities were largely unaffected by this landscape strategy, but the number of California spotted owl territories declined. The effects on owls could have been mitigated by increasing the spatial heterogeneity of fuel treatments and by using more prescribed fire or managed wildfire to better mimic historic vegetation patterns and processes. More landscape-scale experimentation with strategies that conserve key wildlife species while also improving forest resiliency is needed, especially in response to continued warming climates.

Keywords: adaptive management, mixed conifer, restoration, Sierra Nevada, wildlife conservation

The role of wildfire in many of the world's forests that are adapted to frequent, low- to moderate-intensity fire regimes has been altered through fire exclusion, timber harvesting, livestock grazing, and urbanization (Agee and Skinner 2005, Collins et al. 2010). In the western United States, these land-use practices have affected forest structure and species composition, increasing surface fuel loads, tree density, the dominance of shade-tolerant tree species, and forest homogeneity (Hessberg et al. 2005, North et al. 2009, Chiono et al. 2012). As a consequence, many forests in the western United States are experiencing higher-severity burns—in some cases, producing large patches of tree mortality that can severely hinder the reestablishment of conifer forests (Roccaforte et al. 2012, Collins and Roller 2013). Consequently, one of the primary focuses of contemporary forest management is the treatment of fuels and vegetation to reduce fire hazards, especially as climate continues to warm (Stephens et al. 2013).

There is increased recognition that forests adapted to low- to moderate-intensity fire regimes experienced some high-severity fire (Perry et al. 2011, Marlon et al. 2012). Patchy, high-severity fire provides opportunities for early-seral habitat development and the production of large pieces of deadwood resources that are important to many wildlife species (Fontaine and Kennedy 2012). As such, forest fuel treatments should not be used to eliminate all high-severity fire. Rather, treatments should allow for patterns of fire effects that approximate those occurring under more natural forest conditions. What little information we have on fire patterns under these conditions suggests that high-severity fire constitutes fairly low proportions of the overall burned area (5%–15%) in these forest types, which is generally aggregated in relatively small patches (smaller than 4 hectares [ha]), as is the case in the upper mixed-conifer forests in Yosemite National Park (Collins and Stephens 2010, Mallek et al. 2013).

Forest management involving habitat used by wildlife species at risk has been one of the principal challenges to US federal land managers for the last 25 years. In the Sierra Nevada, an ongoing debate is focused on several species that use old-growth forest, including the California spotted owl (CSO; *Strix occidentalis occidentalis*) and the Pacific fisher (*Martes pennanti pacifica*). Forest managers need information on appropriate levels of forest manipulations to create the desired balance between habitat conservation for wildlife populations and modifications of forests to improve their resilience to large high-severity fires that could prove more expensive and detrimental than the short-term effects of restoration treatments.

Fuel-reduction treatments reduce the potential impacts of wildfire by reducing the only aspect of the fire behavior

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Figure 1. Fuel treatments implemented in the Meadow Valley project area. (a) Pretreatment mixed-conifer forest. (b) Whole-tree harvester cutting small trees (thinning from below). (c) Small trees, tree tops, and limbs being chipped and shipped by truck to a bioenergy plant to produce electricity. (c) Posttreatment defensible fuel profile zone, taken from the same perspective as in panel (a). Photographs: Keith Perchemlides.

triangle (i.e., topography, weather, fuel) that can be modified by managers: the quantity and continuity of fuel. A number of techniques are employed to reduce fire hazards, and each technique has associated effects on forest structure (Agee and Skinner 2005). Mechanical treatments can reduce stand density, basal area, and ladder and canopy fuel. To reduce accumulated surface fuel and to offset the detritus added from harvest operations, prescribed fire is sometimes used following forest thinning to reduce fire hazards, but whole-tree harvesting (i.e., complete tree removal, with the materials chipped and trucked to a processing facility; figure 1) can also effectively keep much of the harvest detritus from being added to the forest floor. Broadcast burning alone is very effective in elevating canopy base height and in reducing surface fuel (Agee and Skinner 2005).

Recent research confirms the ability of fuel treatments to alter potential fire behavior (Fulé et al. 2012) and actual wildfire effects (Safford et al. 2012). Research has also determined that fuel-reduction treatments achieve their objectives with generally positive or neutral ecological effects (Stephens et al. 2012); however, almost all research on the effects of fuel treatments has been performed at the stand scale (10–25 ha). Given the large home ranges of many key wildlife species commonly at the crux of forest management issues in the western United States (e.g., the CSO, the northern spotted owl [*Strix occidentalis caurina*], the Pacific fisher), it is important to understand fuel-treatment impacts at larger spatial scales. This is particularly relevant because many fuel-treatment projects are being proposed—and, in a few instances, implemented—at landscape scales (15,000–40,000 ha; Ager et al. 2007, Collins et al. 2010).

Fuel treatments directly alter wildlife habitat by removing both aerial (trees) and ground (coarse wood, shrubs) cover. These altered conditions can affect both habitat suitability, which influences the number of individuals that an area can support, and habitat quality, which directly affects the fitness

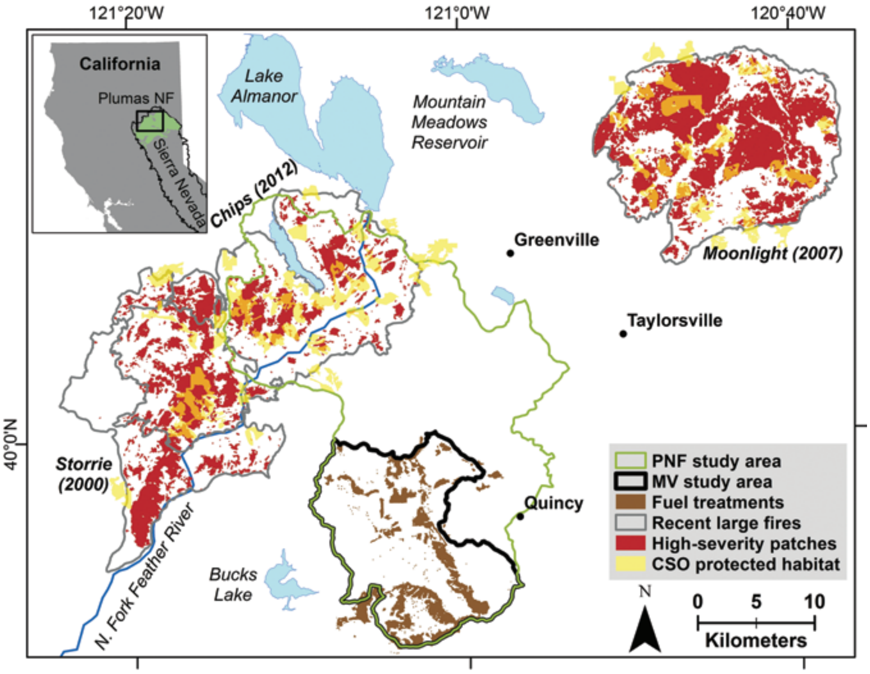

Figure 2. Meadow Valley study area with completed landscape fuel-treatment network. Recent large wildfires and the resulting patches of high-severity fire effects are also indicated. Three wildfires are shown: Storrie (2000), Moonlight (2007), and Chips (2012). These were selected on the basis of the following criteria: proximity to the study area (closer than 25 kilometers), vegetation type (conifer dominated), size (larger than 10,000 hectares), and age (since 2000). Abbreviations: CSO, California spotted owl; MV, Meadow Valley; N, north; NF, national forest; PNF, Plumas National Forest; W, west.

and productivity of individuals. Because more-suitable habitat for certain at-risk wildlife species is associated with greater aerial and ground cover, the effects of fuel treatments are generally perceived as negative. However, large patches of wildfire-caused tree mortality can also negatively affect both habitat suitability and quality (Tempel et al. in press). To the extent that fuel treatments reduce the potential for large patches of tree mortality in wildfire, there may also be an indirect benefit of fuel treatments to certain species' habitat. Finding a balance between these influences is a crucial management need.

Over the past decade, we have studied the ecological effects of one of the few completed landscape-level fuel-treatment networks in western US forests. Here, we distill the results of these efforts. We quantify change in vegetation structure and modeled fire behavior as a result of fuels treatments and assess treatment effects on the CSO, songbirds, and small mammals. Modeling studies have been published in which the trade-offs in these systems have been conceptually examined (Lee DC and Irwin 2005), but this is one of the first studies in which these questions have been empirically examined at landscape scales.

Study area and design

Our study area is located in the Meadow Valley area of the Plumas National Forest, situated in the northern Sierra Nevada, at 39 degrees (°) 56 minutes (′) north, 121°3′ west (figure 2). The climate is Mediterranean, with warm, dry summers and cool, wet winters, which is when most precipitation (1050 millimeters per year; Ansley and Battles 1998) occurs. The core study area is 19,236 ha, with elevations ranging from 850–2100 meters (m). The vegetation is primarily mixed-conifer forest, consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and other less common hardwood species. White fir is the most abundant tree, although large (e.g., larger than 1 m in diameter) stumps of pines encountered frequently in the forest attest to a change in composition and structure in recent history. Red fir (*Abies magnifica*) is common at higher elevations, where it mixes with white fir. In addition, a number of species are found occasionally in or on the edge of the mixed-conifer forest, including western white pine (*Pinus monticola*) at higher elevations, lodgepole pine (*Pinus contorta* var. *murrayana*) in cold air pockets, and western juniper (*Juniperus occidentalis*) on xeric sites. California hazelnut (*Corylus cornuta*), dogwood (*Cornus* spp.), and willow (*Salix* spp.) are found in moister riparian areas. Montane chaparral and some meadows are interspersed in the landscape. Tree density varies as a result of recent fire- and timber-management history, elevation, slope, aspect, and edaphic conditions. Historical fire occurrence, which can be inferred from fire scars recorded in tree rings, suggests that the fire regime was predominantly frequent, low- to moderate-severity fires, at intervals ranging from 7–19 years, with the last widespread fires occurring 85–125 years ago (Moody et al. 2006).

Fire activity in the last 15–20 years has been notably higher in the northern Sierra Nevada than in the rest of the range (Collins 2014). Since 2000, there have been three megafires (covering more than 10,000 ha; Stephens et al. 2014) within 25 kilometers (km) of our study area, burning a total of 73,000 ha (figure 2). These fires burned predominantly in mixed-conifer forests, encompassing approximately 60 CSO protected activity centers (figure 2). Cumulatively, 34% of the area burned in these three fires suffered high-severity fire (more than 95% dominant tree mortality; figure 3a; Miller et al. 2009). More important than the total proportion of area severely burned is the distribution of high-severity patches over the burned area, because this can limit tree seed

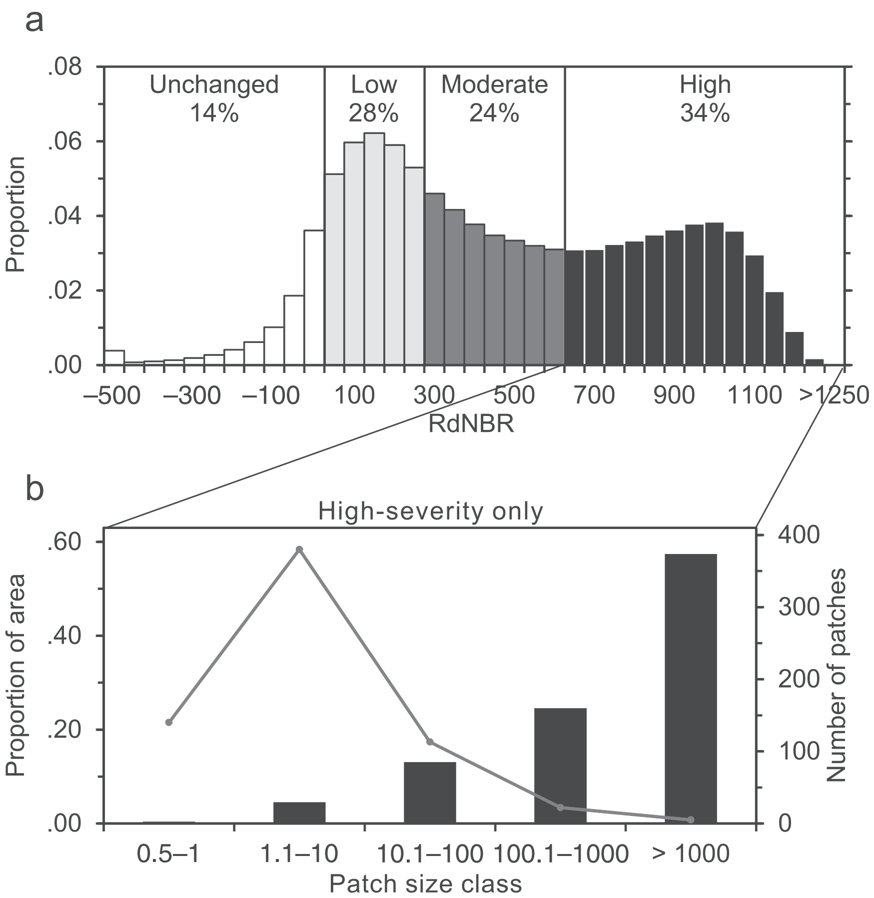

Figure 3. (a) Fire severity distribution for the three recent large fires in the Meadow Valley study area (see figure 2). The fire-severity estimates are based on the relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007). (b) The proportion of total high-severity area (bars) and the number of patches (line) as a function of patch size class.

dispersal from wind and animals (Perry et al. 2011, Collins and Roller 2013). Large patches (defined here as larger than 1000 ha) accounted for a disproportionate amount of the total high-severity-fire area in the recent wildfires near the study area (figure 3b).

The projects that contributed to the fuel-treatment network are part of the larger Herger-Feinstein Quincy Library Group Pilot Project (USHR 1998). This project was directed by the US Congress to involve local communities in forest management. The project objectives included improving forest health, reducing uncharacteristic high-severity fire, conserving wildlife habitats, and stabilizing economic conditions in local communities. The projects in Meadow Valley encompassed a range of treatment types and intensities reflecting changes in regional management directions and differing land-management constraints across a complex landscape (Collins et al. 2010, Moghaddas et al. 2010). The primary fuel treatment used in Meadow Valley was defensible fuel profile zones (DFPZs), which are areas approximately 0.4–0.8 km wide in which surface, ladder, and crown fuel loads are reduced with a combination of moderate thinning from below (Moghaddas et al. 2010) and prescribed fire treatments (figure 1).

The DFPZs were excluded from portions of the landscape set aside as reserves and from designated CSO protected activity centers, which are 121-ha areas of high-suitability nesting habitat designated by forest biologists. In addition, the project predominantly excluded all riparian habitat conservation areas or stream buffers intended to protect riparian and aquatic resources (figure 4). The activities conducted in the DFPZs were chainsaw thinning and pile burning of trees up to 30 centimeters (cm) in diameter at breast height (dbh); mastication: primarily shrubs and small trees were shredded and chipped in place, with the material left on site; prescription burning: stands were burned under conditions of moderate relative humidity and fuel moisture; and a combination of mechanical thinning and prescription burning of trees up to 51 or 76 cm dbh, depending on whether the stands were in the wildland–urban interface, using a whole-tree harvest system (figure 1) to achieve a residual canopy cover of approximately 40%, and some were underburned (Moghaddas et al. 2010). In addition to the DFPZs, group-selection treatments were implemented as part of the project. The group-selection treatments included the removal of all conifers up to 76 cm dbh within an area of 0.8 ha, followed by residue piling and burning, then either natural regeneration or replanting to a density of 270 trees per ha with a mix of sugar pine, ponderosa pine, and Douglas-fir. These treatments collectively covered 3688 ha (3448 ha in the DFPZs, 240 ha in the group-selection treatment), or 19% of our study area, and were implemented between 2003 and 2008.

Forest structure and microclimate

Although they are designed to reduce fire hazards, forest treatments alter stand conditions directly by reducing tree density and canopy cover, and indirectly by altering microclimate conditions affecting the understory community. To assess these changes we measured stand structure, light, understory plant cover, micro-meteorological variables, soil moisture, and fuel moisture in replicated control, thinning, and group-selection treatments plots embedded within the landscape-level treatments (see Bigelow al. 2009, 2011, Bigelow and North 2012 for detailed methods).

The mean forest canopy cover was 69% (standard deviation [SD] = 7%) before treatment; after treatment it was 53%

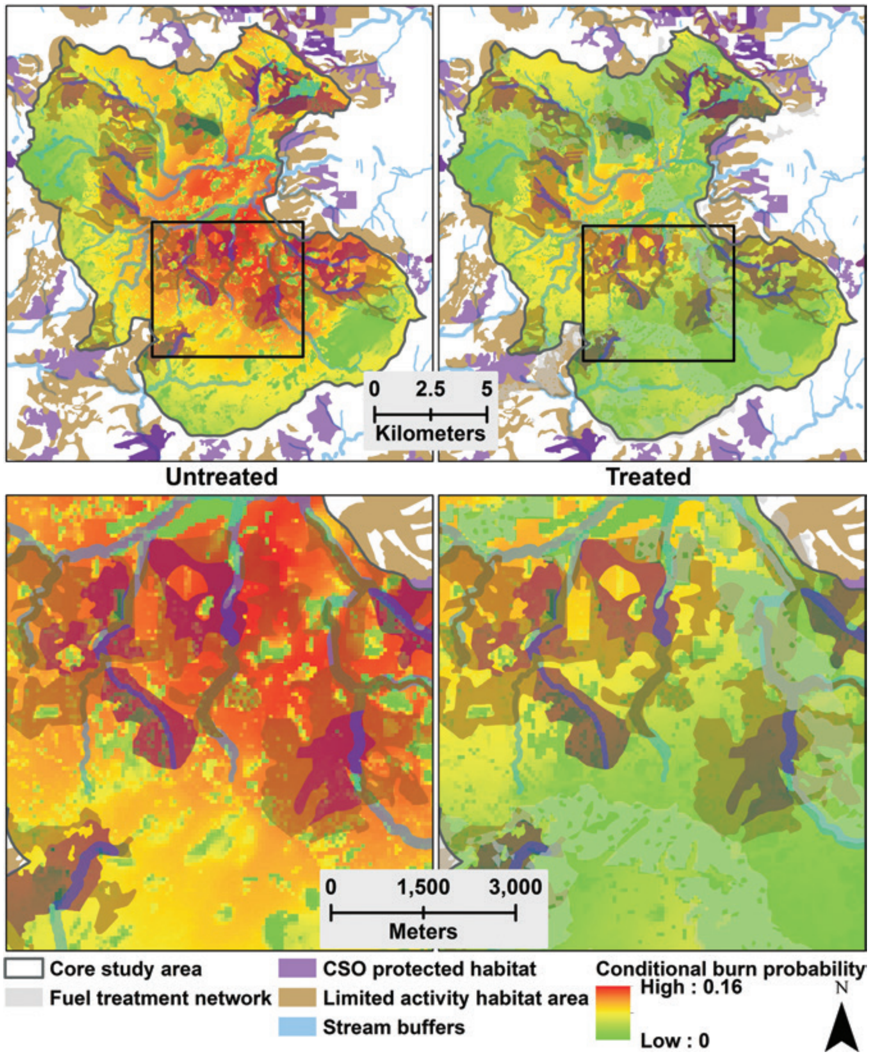

Figure 4. Hazardous fire potential across the Meadow Valley study area for the untreated and treated landscape conditions. This fire potential is based on the conditional burn probability of fire occurring with flame lengths greater than 2 meters, which is consistent with tree torching (see Collins et al. 2013 for specific details). Land designations that often limit or exclude active forest management (e.g., California spotted owl [CSO] protected habitat, stream buffers) are also shown to illustrate off-site effects of the landscape fuel-treatment network. The black square in the upper panels indicates the focal area shown in the bottom panels.

(SD = 7%) in thinned stands and 12% (SD = 6%) in the group-selection openings (Bigelow et al. 2011). These differences were reflected in growing-season understory light, which averaged 17% of full sun before treatment and increased to 26% in thinned stands and 67% in group-selection openings. Models of regenerating tree growth and light availability demonstrated that the height growth rates of shade-intolerant yellow pines (ponderosa and Jeffrey pines) and shade-tolerant white fir were equal at 41% of full sun. Light levels greater than this correlated exponentially with the height growth of the pines. The group-selection treatments provided ample light to recruit shade-intolerant species to the canopy, but only 8% of the sample locations in the thinning treatments had light levels exceeding the 41% crossover point, which suggests that these treatments would not substantially contribute to pine restoration across the landscape. An analysis of hemispherical photographs showed that the treatments decreased canopy closure following thinning. At the plot (1-ha) scale 3 years after treatment, cover of understory plant life-forms only changed under group selection ($p < .05$). Shade-tolerant conifers decreased, and graminoids, forbs, and broad-leaved trees (mainly California black oak and dogwood) increased (figure 5). There was no increase in exotic plant species cover with any of the treatments (Chiono 2012).

Changes in abiotic conditions followed differences in canopy cover for only some of the variables measured (Bigelow and North 2012). Soil moisture increased and duff moisture decreased in the group-selection treatments relative to the thinned and pretreatment conditions. Wind gust speeds (measured 2.5 m above ground) averaged 31% higher in the thinned stands than in the controls, but this was far less than the 128% increase in the group-selection openings. However, there was no difference in air temperature or relative humidity among the treatments, possibly because the increase in understory wind increased air mixing and eliminated any gradients in air temperature and humidity that might have resulted from increased irradiance.

Treatment increased within-stand variability for some vegetation and microclimate conditions but, in general, did not create the landscape-level heterogeneity characteristic of historic forest conditions in the Sierra Nevada (North et al. 2009). Mixed-conifer forests support the highest vertebrate diversity of California forests (Verner and Boss 1980), and studies suggest that this may result from habitat variability associated with the observed range of tree species diversity, canopy cover, microclimate, and deadwood conditions (Rambo and North 2009, Ma et al. 2010, White et al. 2013). This historic forest heterogeneity appears to reflect differences in fire intensity and site productivity associated with local and large-scale changes in slope, aspect, soil, and slope position (North et al. 2009, Lydersen and North 2012). On average, more mesic sites (e.g., drainage bottoms and north-facing slopes) historically supported greater stem density, canopy cover, and tree basal area, whereas drier and

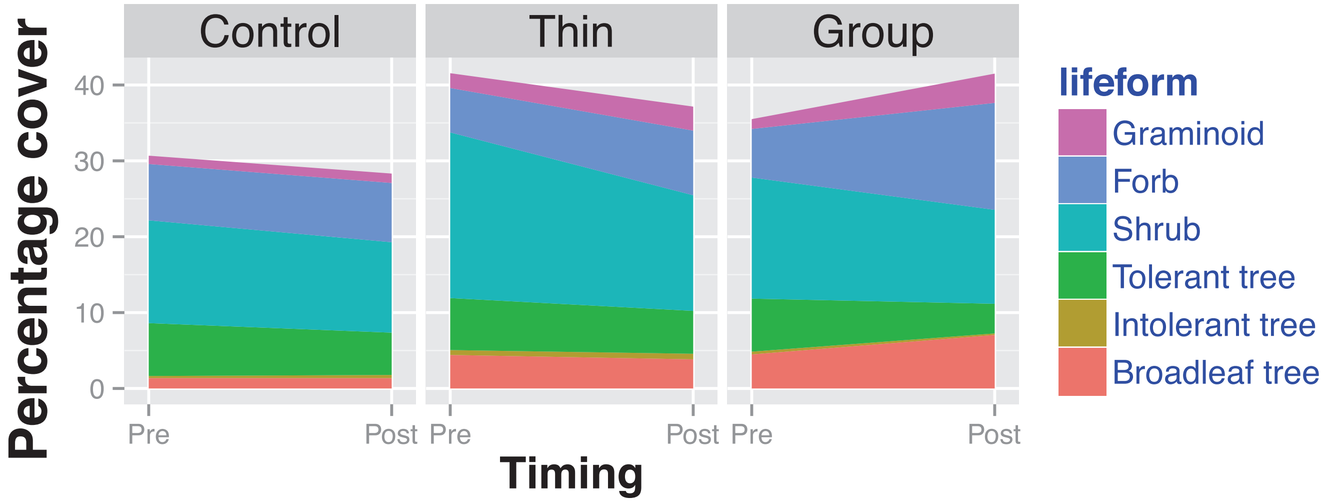

Figure 5. The percentage cover of plant life forms before (pre) *and 3 years after* (post) *fuel-reduction thinning and group-selection treatments* (n = 300 *subplots per treatment) that were implemented in 2007 in Meadow Valley. Changes in understory cover in thinned stands were not significant* ($p > .16$)*. Graminoids, forbs, and broadleaf trees increased and shade-tolerant conifers decreased* ($p < .05$) *in group selection openings.*

steeper areas burned more frequently and intensely, creating more-open, pine-dominated forests (North et al. 2009). Although the Meadow Valley treatments did increase within-stand heterogeneity, they were not explicitly designed to vary with site topography or local productivity to produce this historic landscape variability.

Potential fire behavior

We employed a spatially explicit fire behavior model (Finney et al. 2007) to simulate fire spread across the Meadow Valley area. We simulated 10,000 individual fire events, with random ignition locations, and compared patterns of burn probability based on the number of times a particular area burned with the given ignition locations and simulated flame lengths for the study area prior to and following the implementation of landscape fuel treatments. Each fire event simulated burning for 240 minutes (one 4-hour burn period) under 97th percentile fuel moisture and wind conditions. These are the conditions associated with large-fire growth in this region (Collins et al. 2013). The burn period duration was selected such that the simulated fire sizes (for one burn period) approximated large-spread events observed (daily) in nearby recent wildfires (Collins et al. 2013). One of the primary assumptions with this approach is that, during these large-spread events (burn periods), fire suppression operations have limited impact, which is consistent with observed large-fire occurrence throughout the western United States (Finney et al. 2007). We summarized the burn probabilities across the Meadow Valley area into land allocations determined by the US Forest Service (USFS; Moghaddas et al. 2010).

The simulated fire behavior indicated that the landscape-scale network of DFPZs and prior fuel treatments were effective at reducing conditional burn probabilities across all land-allocation types, except the small area of off-base lands (figure 4; Moghaddas et al. 2010). Because burn probabilities are correlated directly and positively to fire size (Finney et al. 2007), it is clear that the pretreatment landscape was more conducive to large-fire growth than the posttreatment landscape was (Moghaddas et al. 2010, Collins et al. 2013). Although the influence of the treatments on the modeled burn probabilities of each land allocation varied, the untreated stands (e.g., those designated for protected CSO habitat, riparian and aquatic resources, and reserve lands) and the remaining private and unclassified lands all experienced reduced burn probabilities from the application of fuel treatments at the landscape scale (figure 4; Moghaddas et al. 2010). A similar reduced burn severity immediately adjacent to treated areas has been reported for actual fires across the western United States (Finney et al. 2005).

The substantial reduction in both the total area and the area burned at higher flame lengths under a posttreatment wildfire scenario was notable, given that only 19% of the study area had been treated (Moghaddas et al. 2010, Collins et al. 2013). Both the orientation of the treatments (approximately orthogonal to the predominant wind direction throughout the duration of the simulated fire), and the long, continuous shape of the DFPZs resulted in potential wildfires' intersecting fuel treatments in multiple places. In addition, the treatments were somewhat concentrated in the southwestern portion of the study area (figure 2), which is the dominant direction of strong winds during the fire season (Collins et al. 2013). In combination, these factors limited the ability of the simulated fire to both circumvent the treated areas and to regain spread and intensity after encountering the treatments. These results are important to managers, because similar installations of fuel and restoration treatments are needed in many Sierra Nevada

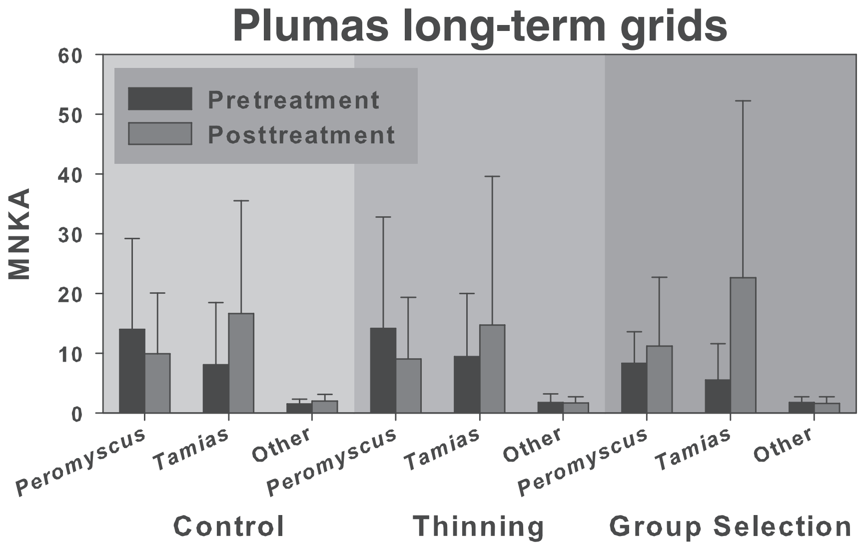

Figure 6. The mean minimum number of small animals known alive (MNKA), recorded before and after fuel treatments in the Plumas National Forest study area. For ease of presentation, we present three species groups (**Peromyscus boylii** ***and*** **Peromyscus maniculatus; Tamias quadrimaculatus** ***and*** **Tamias senex*****; all other species; see Kelt et al. 2013 for details). The bars represent the means of the replicate sampling grids. The error bars represent the positive standard deviation.***

mixed-conifer forests, where the present treatment rates are very low (North et al. 2012).

Small mammals

The northern Sierra Nevada supports a diverse fauna of small mammals that play key ecological roles as consumers, seed and fungal dispersers, and prey for both terrestrial and aerial predators (Hallett et al. 2003, Kelt et al. 2013). We studied small mammals in the Meadow Valley study area and the greater Plumas National Forest study area (PNFSA; figure 2), with a particular focus on two species that are key prey of the CSO (Gutiérrez et al. 1995): the dusky-footed woodrat (*Neotoma fuscipes*) and the northern flying squirrel (*Glaucomys sabrinus*). Results on focal species efforts have been reported elsewhere (Innes et al. 2007, Smith et al. 2011), but one finding merits emphasis here. California black oak, the primary hardwood in mixed-conifer forests, is an important habitat element for both the woodrat and the flying squirrel. Woodrat density was positively correlated with black oak density (Innes et al. 2007), and both species strongly preferred black oaks for nest sites (Innes et al. 2008, Smith et al. 2011). California black oak may be important for other wildlife species as well (Zielinski et al. 2004), but its persistence in our study landscape is in doubt. California black oak is shade intolerant, and across our study area, there were few thriving seedlings and many mature trees in decline as adjacent conifers overtopped them. California black oak trees were present in only 133 of 602 plots placed randomly in the PNFSA and were in a codominant canopy position in less than 10% of the plots in which it was present (see supplement S1).

Our broader studies on the management needs of entire small mammal assemblages included two complementary efforts. We sampled small mammals annually for 8 years on replicate trapping grids in treated and untreated mixed-conifer forests dominated by white fir in order to evaluate the responses of the small mammal community to canopy thinning (Kelt et al. 2013). To determine whether the habitat associations of the mammals in these forests were similar to those of mammals in other forest types, we expanded our efforts to include stratified random sampling of the PNFSA that encompassed the Meadow Valley study area (figure 2).

Whereas canopy thinning in white-fir-dominated mixed-conifer forests caused some significant changes in forest structure, small mammal assemblages were similar before and after canopy thinning and group selection (Kelt et al. 2013), which suggests a minimal response in the short-term to these treatments (*contra* Suzuki and Hayes 2003, Gitzen et al. 2007, but see Carey and Wilson 2001). Although each treatment may have elicited somewhat different responses (figure 6), the variance across replicate plots eroded any such differences even in the face of the substantial variation in canopy cover. The lack of a short-term response may not be surprising in a system characterized by high interannual variation in weather and in a system dominated by generalist species; we look forward to resampling these sites after 10–15 years to assess potential longer-term responses. Because our manipulative experiment was focused on white-fir-dominated mixed-conifer forests, we pursued a more general assessment of mammalian responses to habitat and environmental variation across the entire PNFSA, capitalizing on a series of point-count transects established throughout the forest in a stratified (by forest type) random manner (see the “Songbirds” section below). We sampled eight randomly selected points on each of 74 transects to characterize how small mammals respond to broader variation in forest structure.

We assessed assemblage-wide responses to this variation with ordination (canonical correspondence and canonical correlation) and species-specific responses with multiple stepwise regression. All data were standardized (both rows and columns) by centering and normalizing, and the mammal data were log-transformed to prevent domination of the axes by common species. The results from all of the analyses were qualitatively identical to those of the Meadow Valley experimental grids, which indicates minimal responses of small mammal assemblages to variation in forest structure or composition. Although the spatial arrangement of the

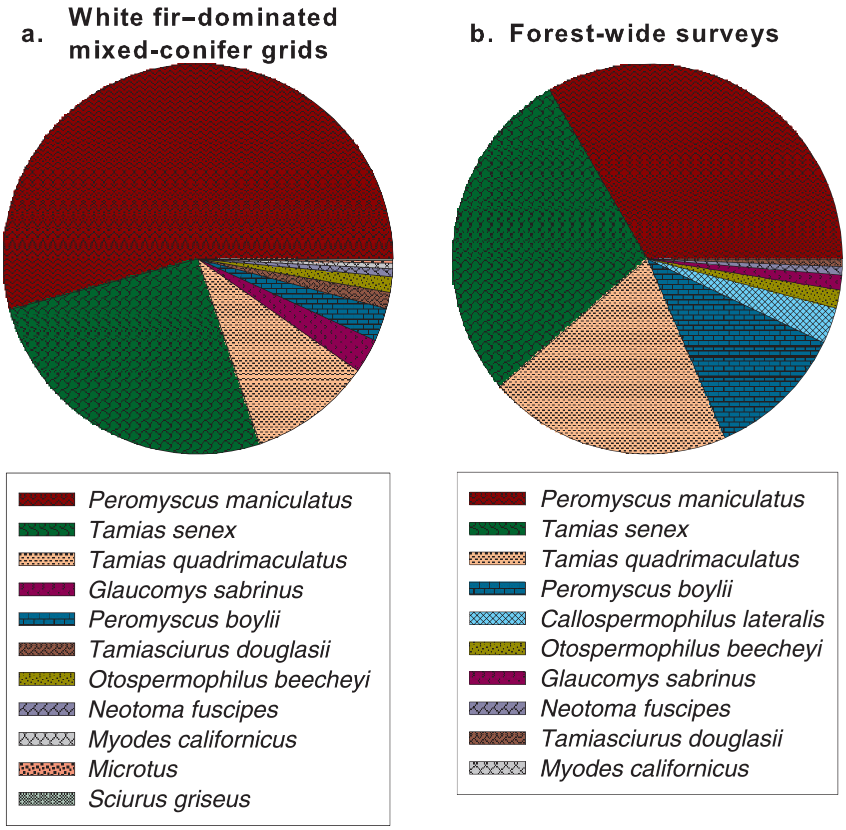

Figure 7. Small mammal composition at two spatial scales in the Plumas National Forest study area. At both scales, captures were dominated by three species. At the forest scale, only one other species was highly represented. All other species at both scales were only minor elements.

small mammal species in the ordination space was ecologically reasonable (e.g., woodrats and brush mice [*Peromyscus boylii*] associated with oaks, and chipmunks [*Tamias*] and Douglas squirrels [*Tamiasciurus douglasii*] associated with conifers and with a high basal area of trees and snags), ordination explained only a small proportion of variance in the distribution of small mammals. Similarly, regression failed to produce compelling associations for any species (or for community metrics such as species richness or diversity). The coefficients for both sets of analyses were universally low (Kelt et al. 2013).

In trapping efforts on the Meadow Valley experimental grids and in the larger PNFSA (figure 2), our captures were overwhelmingly dominated by 3–5 species (figure 7). Deer mice (*Peromyscus maniculatus*) dominated the captures at both spatial scales, comprising a full 55% of the captures on the Meadow Valley experimental grids and just over one-third of the captures in the PNFSA. Two species of chipmunk (*Tamias quadrimaculatus*, *Tamias senex*) represented an additional 40%–44%, and brush mice were an additional 8% in the PNFSA. Therefore, our samples were dominated by ecological generalists known to be tolerant of diverse habitats. What appears to be missing is a reasonable representation of species with more restricted niche requirements. Our sampling was not designed to sample shrews (*Sorex*), but California red-backed voles (*Myodes* [formerly *Clethrionomys*] *californicus*) may have been more common in this region in the 1940s and 1950s (Kelt et al. 2013) and should have been present in our study. This species forages on fungi, however, and requires large downed woody debris and a closed-canopy forest to allow sufficient moisture retention to promote fungal growth (Alexander and Verts 1992). In 177,216 trap nights of effort, we captured only 11 *Myodes* (all but one on Meadow Valley experimental grids). Other species that are mesic habitat specialists were not sampled (e.g., *Zapus trinotatus, Sorex palustris*).

It is not clear whether the taxonomically depauperate assemblage structure documented in our study represents a relatively recent reduction or is more historic for this region. No data on mammal assemblages exist prior to European settlement and the beginning of widespread changes to the Sierra Nevada forest ecosystems (Merchant 2012). However, one implication of this research is that, in spite of nearly a kilometer of vertical elevation relief and diverse forest types from ponderosa pine to red fir, the current forest conditions support a relatively homogeneous small mammal community dominated by ruderal species. It is unclear whether this reflects a legacy of fire exclusion and the resulting accumulation of fine woody debris or, perhaps, a response to a history of logging and fire suppression in this region. In contrast, other recent work in Yosemite (Roberts et al. 2008) confirms that small mammals respond strongly to variation in burn history. Taken together, these results support the fundamental ecological role of fire and broadscale forest heterogeneity in managing mixed-conifer forests in the Sierra Nevada (North et al. 2009).

Songbirds

To evaluate the effects of the Meadow Valley fuel-treatment network on songbirds, we compared avian community diversity before and after treatment. From 2004 to 2011, we surveyed the breeding community in and adjacent to Meadow Valley, using standardized point-count surveys with a 50-m radius (Ralph et al. 1995). Surveys were conducted at 51 stations where DFPZs were implemented (treated) and 201 stations where no treatments were implemented (untreated), proportional to the 19% of the study area treated. An additional 180 stations were surveyed in adjacent untreated PNFSA (figure 2) watersheds (the reference group). We used geographic information systems to establish locations

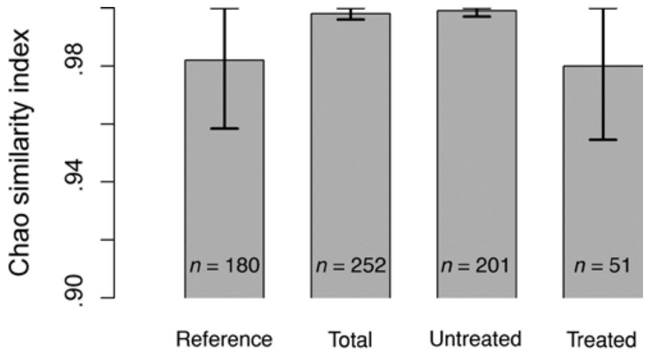

Figure 8. Chao similarity index for the avian community (60 species) before and after treatment at treated and untreated locations in the Meadow Valley study area and reference locations in the adjacent Plumas National Forest study area that also received no treatment. This metric ranges from 0–1, with 1 representing perfect similarity (all species and relative abundances shared among both samples). The error bars are 95% confidence intervals.

for the untreated and reference stations from a randomly selected origin (constrained by slopes lower than 35% and on USFS land) along a random compass bearing in a linear array of 4–12 points. The treated stations were placed within proposed DFPZ treatments across the breadth of treatment types and geography described above. All of the stations were a minimum of 250 m apart.

We surveyed all of the stations in both 2004 and 2005, prior to treatment, and for 2 years after all treatments were implemented (2010–2011). In each year, we surveyed every station twice during the peak of the breeding season (15 May–10 July), with a minimum of 10 days between visits. We limited our analyses to the 60 species breeding in upland habitats that were reliably recorded with point counts (Hutto et al. 1986). The results were summarized at the level of the three treatment groups described above (treated, untreated, reference) and for treated and untreated locations in Meadow Valley combined. For all of the analyses, we summed detections across four surveys (two visits per year over 2 years) for the pre- and posttreatment periods. We compared avian assemblages before and after the treatment with Chao–Jaccard's similarity index (Chao et al. 2005), calculated using EstimateS (version 9.1, University of Connecticut, Storrs). Chao–Jaccard similarity is sensitive to changes in species composition and abundance. Differences in avian diversity were evaluated using the exponent of the Shannon index (Nur et al. 1999). For both analyses, 95% confidence intervals were derived from estimated standard errors from 1000 bootstrap samples.

Our results indicate little change in the Meadow Valley avian communities in response to treatment. The communities were similar across the treated, untreated, and reference samples (figure 8). There was some evidence that the treated areas were less similar to each other than were the untreated areas, but this was not statistically significant ($p > .05$). Avian diversity (the Shannon index) was lowest for the treated sample prior to treatment but increased more in the posttreatment period, such that the Shannon index after treatment was equivalent in the treated and untreated samples (figure 9).

Evaluating the effects of fuel treatments with coarse metrics such as similarity and diversity can cause one to overlook large effects on select species (Hurteau et al. 2008). Numerous studies in seasonally dry fire-prone US forests have shown that fuel treatments can result in at least modest changes in the abundance of a broad range of avian species (Fontaine and Kennedy 2012). We recently reported that mechanical fuel-reduction treatments in the northern Sierra Nevada (including Meadow Valley) resulted in modest decreases in the abundance of a few closed-canopy associates and increases in some edge and open forest associates (Burnett et al. 2013). None of the 15 species evaluated in that study showed a significant decline following the construction of shaded fuel break DFPZ treatments—the primary treatment used in the Meadow Valley study area. With the moderate portion of the landscape treated, small differences in avian community similarity and diversity resulting from treatment, and the results from our previous evaluation of individual species response, we conclude that the effects of the Meadow Valley fuel-treatment network on the songbird community were minimal.

The fuel treatments implemented in Meadow Valley were typically less intense than those shown to result in large changes in avian communities (for a review, see Vanderwel et al. 2007). The treatments were applied to 19% of the landscape, and the prescriptions left relatively high canopy cover. Fire suppression and silvicultural practices over the last century have reduced forest heterogeneity and increased stand density (Scholl and Taylor 2010, Collins et al. 2011). In the Sierra Nevada, most fuel treatments changed the forest structure moderately from historic forest conditions (North et al. 2007). The Meadow Valley mechanical treatments primarily removed ladder fuels, which reduced crown fire potential but did not substantially alter the existing habitat features associated with songbirds, such as shrub cover or large overstory trees.

Our results should be considered in the context of the conditions that existed in the study area prior to the implementation of the landscape treatments. If an objective of these treatments was to maintain the existing avian assemblage and diversity, they appear to have been successful. However, a frequently stated objective for fuel reduction is to act as a surrogate for the natural fire regime (Stephens et al. 2012). Therefore, the maintenance of the pretreatment wildlife community may not always be the most desirable outcome in landscapes such as Meadow Valley and the larger PNFSA, where fire has been excluded for 85–125 years (Moody et al. 2006). Creating or enhancing

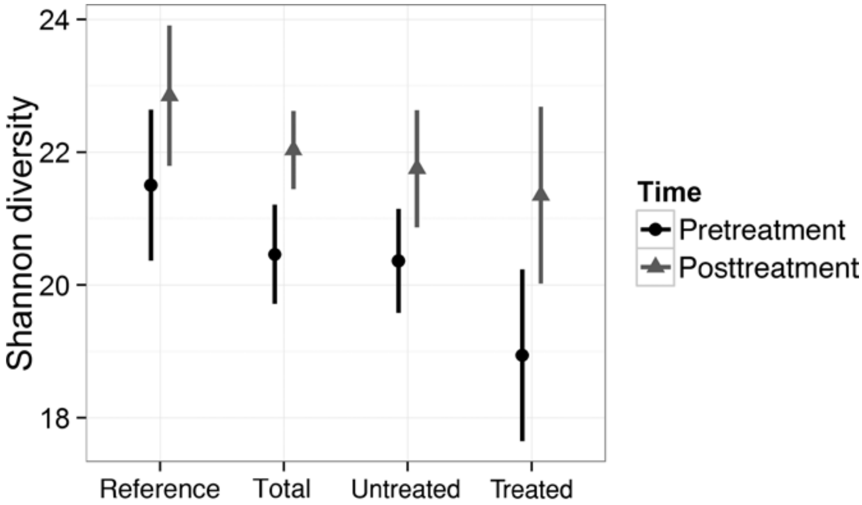

*Figure 9. Shannon diversity index of avian diversity before (*pretreatment*) and after (*posttreatment*) fuel treatments were implemented at treated (*n = 51*) and untreated (*n = 201*) locations and the first two combined (*Total; n = 252*) in the Meadow Valley study area and in reference locations in the adjacent Plumas National Forest study area, which received no treatment (*n = 181*). The error bars are 95% confidence intervals.*

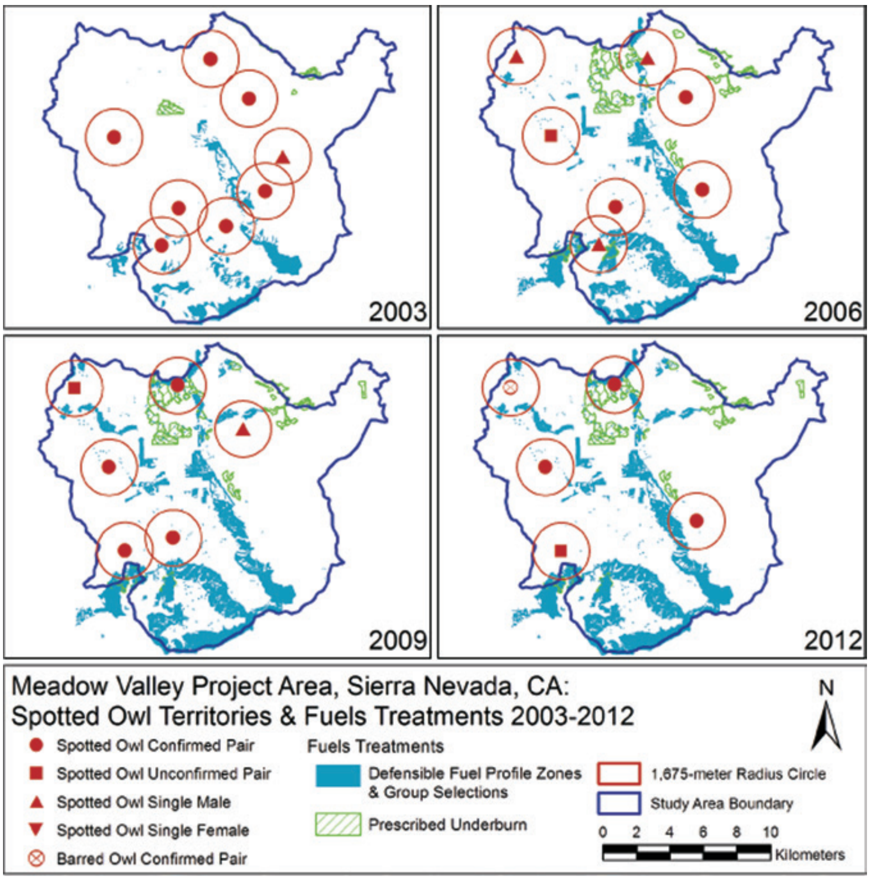

Figure 10. Distribution of territorial California spotted owl sites and landscape forest fuel treatments within the Meadow Valley study area from 2003 to 2012.

conditions for species associated with postdisturbance habitat, some of which have experienced recent declines, may be a prudent approach for achieving some biological diversity objectives (Fontaine and Kennedy 2012). If fuel-reduction treatments are to be a complementary tool to fire in achieving biological objectives, we suggest that they be designed to further increase landscape heterogeneity in fire-excluded forests.

California spotted owls

Modeling studies have projected that fuel treatments on a portion of the landscape (20%–35%) may have minimal effects on owl habitat and that the longer-term benefits of reduced wildfire risk may outweigh the short-term treatment effects on owl habitat (Ager et al. 2007, Roloff et al. 2012). However, no empirical data are available to assess the effects of landscape fuel treatments on the CSO and its habitat.

We used standardized surveys and color banding of individual owls to monitor the distribution, occupancy, survival, and reproduction of CSO sites annually across 1889 square kilometers between 2003 and 2012 in the Plumas and Lassen National Forests. Within this area, four areas were identified for implementation of landscape-scale fuel and restoration treatments. Our initial objectives were to establish baseline values for CSO distribution and abundance and to monitor the owl's response in the treated and untreated landscapes in posttreatment years. However, complete implementation of the fuel-treatment network only occurred on one (Meadow Valley; figure 10) of the four landscapes because of legal challenges to the proposed US Forest Service management strategy.

In the Meadow Valley study area, the number of territorial owl sites declined after treatment. Prior to and throughout the implementation of the treatment, the number of owl sites ranged from seven to nine. Between the final year of the DFPZ and group-selection installations (2008) and 2 years after treatment (2009–2010), the number of owl sites declined by one (six territorial sites), and by 3–4 years after treatment (2011–2012), the number of sites had declined to four—a decline of 43% from the pretreatment numbers (figure 11). These results mirror similar declines of the CSO in the larger Plumas-Lassen CSO study area over the past 20 years (Conner et al. 2013) but suggest a greater magnitude of decline within Meadow Valley (figure 11).

The CSO nests and roosts in dense, multilayered, mature forest patches, and the adult survival and territory occupancy of these owls is positively correlated to the amounts of mature forest in core areas around CSO sites (Dugger et al. 2011). For foraging, however, the CSO uses a broader range of vegetative conditions. Radio-telemetry conducted in Meadow Valley indicates that the CSO avoids foraging in DFPZs in the first 1–2 years after fuel treatments and that the owl's home range size was positively correlated with the amount of treatment within the home range (Gallagher 2010). Barred owls (*Strix varia*) began to colonize the Meadow Valley study area in 2012 and are likely to become a threat to the CSO and a confounding factor to be accounted for in assessments of forest management effects (Keane 2014).

Although inference must be tempered from a single study, the Meadow Valley area is the first large area to receive full the implementation of landscape-scale DFPZ and group-selection treatments in which CSOs were monitored annually both before and after treatment. CSOs are long-lived (up to 20 years) and exhibit high site fidelity as adults, although there is high annual variation in reproduction associated with weather and food (Gutierrez et al. 1995). Given these traits, individual CSOs may exhibit both short- and long-term responses to fuel treatments or wildfire, and understanding both is important to land-use managers. Our results documented a decline in CSO territories as a result of landscape fuel treatments, but the factors driving the decline remain unknown.

Conclusions

This study has shown that coordinated landscape-scale fuel treatments can substantially reduce the potential for hazardous fire across a large montane region, even when a moderate proportion of the area that could not be treated because of management constraints. In many cases, lands with designated management emphasis, such as wildlife habitat reserves and stream buffers, are distributed throughout the landscape. Creating fuel treatments that exclude these lands can result in a patchwork of treated areas heavily dissected by, for example, untreated stream buffers. Hazardous fire potential decreased in untreated areas, but that effect is not stable over time. Even if the existing network was maintained in a "treated" condition (i.e., periodic prescribed fire to keep surface and ladder fuels low) hazards will continue to increase in untreated areas because of stand development (Collins et al. 2013).

Our results indicate negative CSO responses to treatments, supported by the avoidance of DFPZs by foraging owls, larger owl home ranges associated with increasing amounts of treatment within the home ranges, and a 43% decline in the number of territorial CSO sites across the Meadow Valley study area within 3–4 years of the implementation of landscape treatments. In addition to changes in the number of owls, we also observed spatial redistribution of owl sites over time across the landscape (figure 10). The specific mechanisms driving these observations are unclear, but given the region-wide decline in the CSO population (Conner et al. 2013) and the increasing barred owl populations, it is difficult to disentangle fuel treatment effects from background or external pressures. Despite the challenges of working at landscape scales, studies such as this provide opportunities for addressing scale-dependent ecological phenomena, such as population-level species responses and responses to management strategies that cannot be addressed at smaller spatial scales.

To date, little discussion has been focused on what may constitute sustainable, viable CSO populations under various landscape conditions designed to address projected fire and climate scenarios. Furthermore, there is not a clear understanding of the balance between the potential short-term impacts from treatments and the longer-term benefits provided by introducing landscape heterogeneity (North et al. 2009), reducing potential for severe fire (Ager et al. 2007, Collins et al. 2013), increasing the potential for more desirable fire effects (North et al. 2012), and increasing resilience to climate change (Stephens et al. 2010). The Meadow Valley study is an important step in learning about the responses of wildlife species to fuel-reduction treatments.

Recent research in Yosemite National Park suggests that CSOs are not adversely affected by low- to moderate-severity fire (Roberts et al. 2011, Lee et al. 2013). Studies of the CSO both in Yosemite and in Sequoia and Kings Canyon National Parks have not shown population declines that have been found in several national forests in California. There are many differences between the two ownerships: National forest lands generally contain younger forests and lack the large tree structures associated with preferred owl habitat. With continued fire suppression, national forest lands continue to develop dense, small-tree stand conditions, reducing the habitat heterogeneity associated with a variety of small mammals that constitute the CSO's prey base. Because of these differences, it is difficult to determine whether more recent mechanical treatments or existing fire-suppressed conditions might be associated with declining CSO populations. Uncertainty also persists regarding the potential thresholds at which the amounts and patch sizes of high-severity fire reduce the postfire probabilities of CSO occupancy, survival, and reproduction. This is a significant information gap, given the trend for increasing amounts and patch sizes of high-severity fire in many Sierra Nevada forests (Miller et al. 2009). Unfortunately, only one CSO pair in Meadow Valley used an area that received prescribed burn treatments, but unlike those in some of the mechanically treated areas, these owls continued to occupy the burned area through the duration of the study and foraged within the burn-treatment areas (Gallagher 2010). The introduction of barred owls to Meadow Valley adds another important factor that may

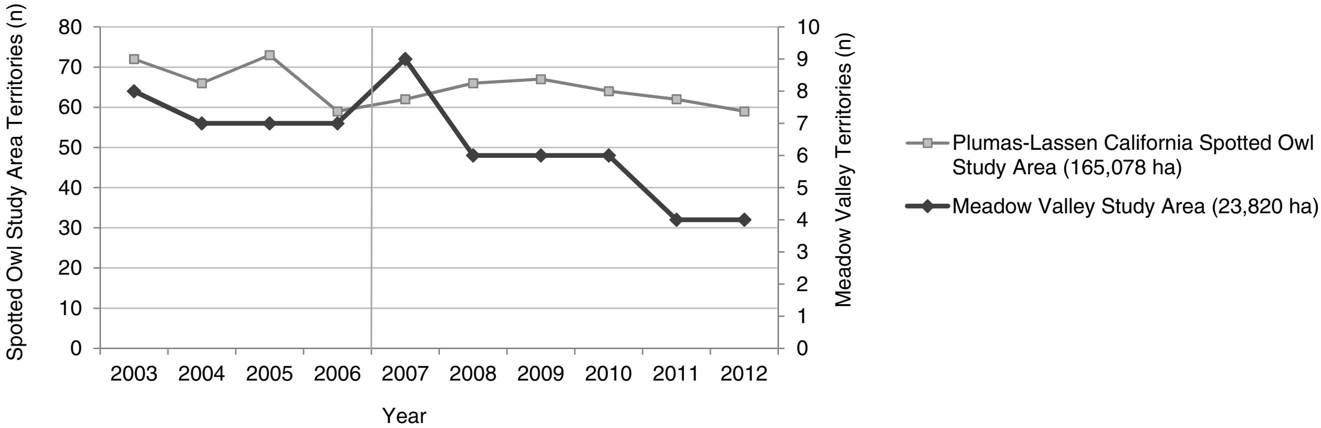

Figure 11. The annual number of territorial California spotted owl sites from 2003 to 2012 within the Meadow Valley study compared with the rest of the Plumas-Lassen study area (in the Plumas and Lassen National Forests). Vertical line represents completion of >80% of treatments.

reduce the population and viability of the CSO, possibly independent of forest structure.

Mechanical treatments can reduce fuels, but, in this study, they also left the largest trees and retained more than 40% canopy cover, two structural characteristics associated with CSO habitat use (Verner et al. 1992). However, although mechanical treatments retain these live features, they often remove snags for operator safety and fuel objectives; reduce tree density and canopy layering; reduce canopy cover to the minimum level (around 40%) considered to function as owl foraging habitat; and simplify the ground structure through a reduction of logs and small trees. Furthermore, DFPZ treatments are often uniformly implemented over large areas along roads, which results in extensive patches of simplified stand structure with regularly spaced trees. Another concern is that treatment size and placement are determined by land-use constraints (gentle slopes, access to roads) and opportunities to affect fire behavior. We have little information about how the location of treatments may affect CSOs' use of areas outside their core nesting locations. Several small mammals appeared to favor sites with steeper slopes (Kelt et al. 2013), possibly reflecting the spatial allocation of treatments in this landscape.

The importance of increasing heterogeneity within stands and across the landscape in mixed-conifer forests is well documented to meet restoration objectives (North et al. 2009, Stephens et al. 2010). Our ability to optimize heterogeneity at large scales may be more effectively achieved with prescribed and managed fires that are allowed to burn under moderate weather conditions. This type of burn often produces variable forest conditions that mimic historic patterns (Collins et al. 2011) to which this fauna, including the CSO, has adapted. Alternatively, mechanical treatments that produce the complex forest structure and composition that more closely mimic the patterns generated under a more active fire regime (North et al. 2009) may provide habitat conditions to support CSOs and a diverse fauna superior to those of the DFPZ and group-selection treatments implemented in Meadow Valley. Although mean stand conditions (e.g., canopy cover) have often been used to infer management impacts on preferred habitat (Tempel et al. in press), the historic heterogeneity of frequent-fire forests suggests we have yet to identify the optimal scales at which to create variable forest conditions.

We encourage further work to examine landscape-level treatments that are intended to emulate the influence of fire in creating spatial heterogeneity in vegetation and fuel conditions. A working hypothesis is that increased habitat heterogeneity, including the retention and development of currently limited but ecologically important forest conditions (areas of large, old trees) and more-open, patchy, early-seral stage conditions, would promote a diverse wildlife community while providing a more fire-resilient landscape. The results from the Meadow Valley study area illustrate the benefits and challenges of working at the landscape scale. Rigorous and controlled experiments are difficult because of the inherent variability across landscapes, sociopolitical constraints, and competing management objectives that can influence planned treatments. However, inferences from these studies can be strengthened by careful replication of management strategies across multiple landscapes.

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Supplemental material

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*Scott L. Stephens (*sstephens@berkeley.edu*) is affiliated with the Division of Ecosystem Science at the University of California, Berkeley. Seth W. Bigelow, Brandon M. Collins, Claire V. Gallagher, John Keane, Malcolm P. North, and Peter A. Stine are affiliated with the US Department of Agriculture, Forest Service, Pacific Southwest Research Station, in Davis, California. BMC is also affiliated with the University of California Center for Fire Research and Outreach, in the College of Natural Resources at the University of California, Berkeley. Ryan D. Burnett and Lance Jay Roberts are affiliated with Point Blue Conservation Science, in Petaluma, California. Douglas A. Kelt and Dirk H. Van Vuren are affiliated with the Department of Wildlife, Fish, and Conservation Biology at the University of California, Davis.*