

Appendix 1. Background Information

California Spotted Owl Ecology and Threats

Geographic Range

The CSO occur in forests of the western Sierra Nevada, with few locations documented east of the Sierran Crest (Verner et al. 1992). They also occur in southern California and central coastal California, though those populations are not the focus of this Strategy. Within the Sierra-Cascade Region, CSO inhabit largely mixed conifer and yellow pine forests (~80-90% of known sites), with some presence in red fir forests (~10%) and riparian/ hardwood forests (~3%; Verner 1992). Thus, the specific habitat recommendations in this Strategy focus largely on the Mixed-Conifer and Yellow Pine habitats within the CSO range. The Sierran population occurs from roughly 1,000 to 7,740 feet in elevation, with 86% occurring between 3,000 and 7,000 feet (Verner 1992). In southern California they are known to occur at even higher elevation (up to 8,400 ft; Verner 1992).

Population Trends

California spotted owl populations appear to have declined over the past approximately 20 years in the three demographic study areas occurring primarily on national forest lands in the Sierra Nevada. Estimates of the total percentage declines in abundance range from 11% on the Sierra to 22% on the Plumas-Lassen to 50% on the Eldorado (Tempel et al. 2014b, Connor et al. 2014). The cause of these observed declines has not been established conclusively. All three declining populations are located on national forests, with the only stationary population occurring within Sequoia-Kings Canyon National Park (SEKI), the only national park included in these studies. Disparity in population trends between national forests and national parks may be related to differences in past or current forest management strategies (Blakesley et al. 2005, Seamans and Gutierrez 2007, Tempel et al. 2014a) and/or different levels of restoration of natural disturbance regimes, specifically through restoration of important ecological processes such as fire (Kilgore and Taylor 1979, van Wagtenonk 2007). Additionally, several ecological factors differ between landownerships, including the presence of giant sequoia groves on SEKI (relative to the other three study areas) and the prevalence of oaks that could also be contributing to differences in population trends (Blakesley et al. 2010). The declining populations have likely not been exposed to significant impacts by barred owls (*Strix varia*) or high severity fire (Tempel et al. 2014b).

CA Spotted Owl Ecological Areas of Significance

Core nesting/roosting (activity center).

In response to conservation concerns regarding the California spotted owl, the US Forest Service (USFS) developed Protected Activity Centers (PACs) which contain 121 ha (300 ac) of the best available, contiguous habitat around a nest or roost. These PACs encompass habitat that is most likely essential for nesting and roosting, but not for foraging or territorial defense; habitat that has closed-canopy ($\geq 60\%$ canopy cover) forest with \geq two layers of tree canopy and many large trees and snags (Verner et al. 1992b). PACs were intended to protect critical habitats at and around nest and roost sites (Verner et al. 1992b), and have been found to generally accommodate spotted owl nesting and roosting activities over the long term (25 years; Berigan et al. 2012).

Territory

A 'territory' represents the area within a home range that is defended by the resident pair of owls from conspecifics (Tempel 2016, Assessment). An owl pair's territory is smaller than their home range, as not all areas within home ranges are defended against other owls. To date, the precise size and location of spotted owl territories has been estimated in various ways. 'Core areas' are geographic areas in which a pair of territorial owls concentrates its nesting, roosting, and foraging activities, and they contain critical habitat components (Swindle et al. 1999). Core area size in the Sierra Nevada likely varies geographically and by ecotype (as is the case with home range size; *see below*), but geographic variation in core area size has not yet been characterized. Based on radio-marked owls, Bingham and Noon (1997) suggested that core area size for California spotted owls was ~813 ha (2000 ac) in the northern Sierra Nevada. However, Blakesley et al. (2005) noted that core areas of this size overlap considerably among adjacent owl sites and therefore considered circular analysis areas of 203 ha (~ 520 ac), a size that was based on half the "minimum-nearest-neighbor distance" between adjacent owl sites. Studies in the central Sierra Nevada have used a radius equal to half "mean-nearest-neighbor distance" between the centers of adjacent owl sites (1.1 km) which yielded core areas of 400 ha (1000 ac) in size (Seamans et al. 2007, Tempel et al. 2014a, Jones et al., In Review).

Home range

A home range is defined as the area used by an individual to meet its life-history requirements and typically includes all nesting, roosting, foraging, and territorial activities within a period of interest (e.g., breeding season). Home range size estimates vary among studies (634 – 2,195 ha; 1500 – 5400 ac), study area (latitude), and individuals. Generally, California spotted owl home ranges are the largest in the northern Sierra Nevada and smallest in the southern Sierra Nevada, particularly where oaks (*Quercus* spp.) are the dominant tree type (Zabel et al. 1992).

Habitat Selection

California spotted owls nest in the oldest and largest live and dead trees, especially those having structural defects like cavities, broken tops, and platforms ((Verner et al. 1992a, Gutiérrez et al. 1992, North et al. 2000), and those that are removed from high-contrast edges (Phillips et al. 2010). Nest stands are characterized by high canopy closure and cover ($\geq 75\%$ for both), an abundance of large (>61 cm dbh; 24 in) trees, higher than average basal area, an abundance of coarse woody debris, and multiple canopy layers comprised of trees of different sizes, but numerically dominated by medium-sized trees (30 to 61 cm; 12-24 in) (Bias and Gutiérrez 1992, Blakesley et al. 2005, Moen and Gutiérrez 1997, North et al. 2000).

California spotted owls seem to prefer mature forests with moderate to high canopy cover ($\geq 40\%$) for foraging (Williams et al. 2011), but also tend to select edge habitat for foraging, perhaps using the complex structure within mature patches to access abundant prey in early seral stage patches (Williams et al. 2011, Eyes 2014). Thus, owls may benefit from the juxtaposition of mature forests with a mosaic of vegetation types and seral stages, which may promote higher prey diversity and abundance by increasing habitat diversity within foraging areas (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000, Williams 2001, Tempel et al. 2014a).

Dietary Habits

In the Sierra Nevada, woodrats (*Neotoma* spp.) and northern flying squirrels (*Glaucomys sabrinus*) comprise the majority of the diet of California spotted owl by biomass, although a wide array of other small mammals, as well as a smaller amount of birds, lizards, and insects are also consumed (Gutiérrez et al. 1995, Munton et al. 1997). In the southern Sierra Nevada, woodrats tend to dominate (74% by biomass) spotted owl diets within oak woodlands and riparian-deciduous forests (i.e., low elevation), and mid elevation habitats (Laymon 1988, Thraillkill and Bias 1989), whereas northern flying squirrels are more important in conifer forests at higher elevations during the breeding season and comprise 46% of owls diets (Munton et al. 2002). Pocket gophers comprise the second most important food by biomass at both low and higher elevations (Munton et al. 2002). Flying squirrels often occur in closed-canopy forests (Pyare and Longland 2002, Meyer et al. 2005, Roberts et al. 2015), whereas woodrats often occur in more open habitats, oak woodlands, and early seral-stage forests (Innes et al. 2007). Thus, at high elevations, mature forests may be the most critical for the California spotted owl prey base, whereas heterogeneous forest conditions are likely to enhance prey habitat at both upper and lower elevations (Sollmann et al. 2016, Jones et al. *In Review*).

Threats

Altered Disturbance Regimes:

Prior to Euro-American settlement, fires in the Sierra Nevada occurred frequently (5-15 year), generally burned at low- to moderate-severity (Van de Water and Safford 2011, Mallek et al. 2013, North et al., *In Review*), and maintained low-density stands across much of the landscape, composed of primarily large, fire-resistant trees (Taylor 2004, Scholl and Taylor 2010, Collins et al. 2011). A century of fire suppression, however, has led to an ingrowth of shade-tolerant trees and an accumulation of surface fuels that have increased the frequency and burn patch size of high-severity fires in the Sierra Nevada (Miller et al. 2009, Mallek et al. 2013, Steel et al. 2015). High-severity fires now pose a significant threat to California spotted owls and their habitat, a threat that is expected to increase under most climate change scenarios (*see below*).

In some recent studies, California spotted owls continue to occupy sites that experience low, moderate, and a mixture of fire severities (Roberts et al. 2011; Lee et al. 2012, 2013), suggesting the value of restoring natural levels of disturbance. However, there is likely an upper threshold to the amount of high-severity fire that owls can tolerate within their territory (Lee et al. 2012; but see Lee and Bond 2015), and trends in fire size and severity suggest that without active restoration this threshold is likely to be surpassed more and more often in the future (Stephens et al. *in review*). A recent study shows that occupancy of severely burned territories declined substantially and that severely burned areas were avoided by owls, even when foraging (Jones et al. *in Press*).

One particularly salient concern involves the susceptibility of spotted owl habitat to high-severity fire given it is typically characterized by forest conditions that are prone to severe fire (e.g., high vertical and horizontal fuel continuity). Indeed, approximately 88,000 acres of owl PACs, representing about 15% of the total PACs acres, burned from 1993 to 2013 (Keane, *In Review*). However, approximately 28% of burned PAC area experienced high-severity, which was similar to the overall landscape (26%) during this period (Keane, *In Review*). While the proportion of burned area in PACs that burned at high severity aligns with the larger landscape, it is far greater than would be expected under a more natural fire regime (< 5-15%; Mallek et al. 2013) and historic stand conditions. Unnaturally high proportions of high

severity fire are also associated with large high severity patches that are linked to decreases in spotted owl occupancy, colonization, and habitat use (Eyes 2014, Roberts et al. 2011, Tempel et al. 2014) and increases in owl extinction probability (Lee et al. 2013).

Over a century of fire suppression in the Sierra Nevada has resulted in denser, more contiguous and homogenous forests (Hessburg et al. 2005). While these denser forests may be conducive to spotted owl reproductive success in the near term, landscapes with restored fire regimes (e.g., Yosemite National Park) show greater small mammal species evenness, which could promote increased stability and resilience in spotted owl prey populations (Roberts et al. 2015). Contiguous homogenous forests are not sustainable over the long-term (Stephens et al. In Review), and reduce the habitat diversity that can promote long term resilience of owl populations and their prey (Kelt et al. 2013).

Climate Change.

Projected changes in climate constitute an emerging threat to California spotted owls and their forest habitat, and may have significant impacts to owl populations in the Sierra Nevada over the coming decades. General climate change model projections for the Sierra Nevada indicate that temperatures will increase by 3-6 °C during the 21st century and, while projections of changes to precipitation patterns are less certain, decreased winter snowpack and increased ecosystem moisture stress are expected (Cayan et al. 2013). Increases in temperature and changes in precipitation patterns associated with climate change may impact spotted owls via (i) direct, physiological effects on individuals; (ii) alterations to prey communities, interactions with predators and competitors, and disease dynamics; and (iii) changes in habitat quantity, quality and distribution. In some parts of the spotted owl's range, drought and high temperatures during the previous summer have been linked to lower survival and recruitment of spotted owls (Franklin et al. 2000, Glenn et al. 2011, Jones et al. *in Review*), and decreases in precipitation (and associated moisture stress) may reduce plant production, seeds and fungi that are important food for spotted owl prey (Seamans et al. 2002; Olson et al. 2004; Glenn et al. 2010; 2011). Impacts to owl populations, however, are likely to be complex as warm, dry springs tend to increase reproductive success and spotted owls exhibit population-specific demographic responses to regional climate and weather patterns (Glenn et al. 2010, Glenn et al. 2011, Peery et al. 2012, Jones et al. *In Review*).

Climate change projections of future vegetation distribution in the Sierra Nevada suggest that much of the low and mid-elevation forests that currently comprise owl habitat are vulnerable to conversion to woodlands, shrublands, and grasslands. Recent drought has led to extensive mortality of trees in CSO habitat, with the full extent of impacts still as yet largely unknown (Asner et al. 2015; FHP 2015). Moreover, projected increases in temperature and decreases in snow pack for the Sierra Nevada (Safford et al. 2012) are likely to continue the increasing trend in the size of stand-replacing fires and proportion of landscape impacted by stand-replacing fire (Stephens et al. 2013). These threats may be somewhat mitigated by the upslope advancement of mixed-conifer forests and the development of habitat for owls where none now exists (Peery et al. 2012). However, to the extent that it occurs, development of suitable forest structure at higher elevations will likely take many decades and may not keep pace with the loss of habitat at lower elevations due to the aforementioned processes (Stephens et al. in review).

Forest Management

The effects of specific forest management activities on spotted owls is not well understood (USFWS 2011). Moreover, the specific vegetation conditions (e.g., density of large trees, canopy cover levels) and the area of suitable habitat required to maintain viable populations remain a source of uncertainty. However, all three correlative studies addressing the effects of post-CASPO habitat change on the demography of California spotted owls have detected negative impacts (Seamans and Gutiérrez 2007, Tempel et al. 2014a, Stephens et al. 2014). Seamans and Gutiérrez (2007) found that California spotted owl territories in which > 20 ha (50 ac) of mature forest was altered experienced a 2.5% decline in territory occupancy probability. Stephens et al. (2014) showed that the number of occupied owl territories declined from 7 to 9 territories before and during implementation of landscape-scale treatments (2002-2007) to four territories 3-4 years after treatments were completed, though longer term impacts are unknown.

Timber harvesting on a large portion private of lands within the CSO range uses even-aged silvicultural approaches, which may reduce spotted owl habitat quality by reducing or eliminating critical habitat elements (old, large-diameter trees and associated large downed logs (McKelvey and Weatherspoon 1992, Keane Assessment). However, a recent study suggests that California spotted owls may occur on private timberlands at greater density than expected, despite having higher harvest rates (Roberts et al. 2015), but additional work is required to determine the quality of habitats on private lands, their contribution the viability of the regional spotted owl population, and the long-term effects of even-aged systems. Spotted owls have also been observed avoiding private lands, presumably because of a dearth of key habitat elements (Bias et al. 1989).

Update with any new information from the Conservation Assessment regarding the importance of very big trees, as well as uncertainties and tradeoffs

Barred Owls.

Barred owls have invaded western North America over the past century (Livezy 2009) and threaten northern spotted owl population viability in many parts of this subspecies' range (USFWS 2011, Wiens et al. 2014). While they presently occur in relatively low densities in the Sierra Nevada, they are expanding their range (Dark et al. 1998, Keane 2014), may soon colonize large parts of the Sierra Nevada and become a primary threat to the California spotted owl (Gutierrez et al. 2007, USFWS 2011, Wiens et al. 2014). Barred owls are competitively dominant to spotted owls, and interspecific interactions lead to negative impacts on spotted owl population (Dugger et al. 2011; Yackulic et al. 2012, 2014; Wiens et al. 2014). Northern spotted owls have greater territory extinction probabilities, lower colonization probabilities (Olson et al. 2005, Dugger et al. 2011, Yackulic et al. 2014), lower nest success (Wiens et al. 2014), and lower probability of habitat use (Van Lanan et al. 2011) when barred owls are present. Similar studies have not been conducted on California spotted owls but little reason exists to suspect interspecific interactions will be different in the Sierra Nevada. Barred owl removal experiments indicate that spotted owls re-occupy sites within one year but that barred owls again displace spotted owls at some sites within 1-4 years after initial removal.

Disturbance.

Disturbance resulting from human recreation and management activities (e.g., noise from chainsaws or motorized vehicles) has the potential to impact California spotted owls, although considerable uncertainty remains in how much and what types of disturbance are detrimental. One study found that

nesting Mexican spotted owls exhibited behavioral responses when exposed to helicopter and chainsaw noise, although no differences in reproductive success were detected (Delaney et al. 1999). Mexican spotted owls exhibited little behavioral response to hikers within ≥ 55 m distance, and juveniles and adults were unlikely to flush from hikers at distances >12 or >24 m, respectively (Swarthout and Steidl 2001), although cumulative effects of high levels of recreational hiking near nests may be detrimental (Swarthout and Steidl 2003). Wasser et al. (1997) reported higher stress levels (as indicated by fecal corticosterone) in male northern spotted owls within 0.41 km of roads in Washington, suggesting higher stress levels were correlated with proximity to roads, although Tempel and Gutierrez (2004) did not detect elevated stress hormones in California spotted owls exposed to disturbance from chainsaws or motorized vehicles. Hayward et al. (2011) also did not detect an association between hormone levels and distance to road, but did find that owls had higher corticosterone levels and lower reproductive success when exposed to continuous traffic and that response varied by age and body condition. Thus, while owls likely tolerate various levels and types of disturbance, some disturbance may affect behavior and reproduction.

Other

Update with any new information from Assessment – e.g. rodenticides, etc.

Past, Current, and Future Conditions

Environmental Context

Mid-Elevation Sierra Nevada forests are highly productive and have some of the highest biomass values for temperate forests worldwide. Their component tree species are long-lived, achieving a size that produces tall, complex canopy structures that significantly influence site microclimate and habitat conditions. Additionally, Sierra Nevada forests are fire-dependent ecosystems. Historically, frequent (generally < 20 years), low-moderate severity (generally surface fire with localized high-severity patches) fire reduced stem density and moisture stress in these drier environments while increasing spatial, habitat and microclimate heterogeneity. Early surveys noted that fire produced variable but generally low-density forest conditions with one source (Lieberg 1902) noting Sierra Nevada forests were at only 30% of their carrying capacity for timber production. Over the last few decades, research has demonstrated that more resilient forests have lower density more open conditions than the traditional concept of full stocking for maximum timber production (Collins et al. 2011, 2015, Stephens et al. 2015).

Unique to their closest neighbors (the moist forests of the Pacific Northwest and the drier forests of the interior Southwest), Sierra Nevada forests combine these drier and moister conditions into one, highly variable ecosystem. Like the Pacific Northwest, overstory forest conditions are shaped by the number, size, and composition of large, long-lived trees. These conditions are influenced by local levels of productivity. In particular, areas with higher soil moisture availability support more large structures (live and dead), denser canopy cover and greater biomass. Understory conditions, however, like the Southwest, are strongly influenced by the local fire regime, with tree regeneration dynamics, stand density, shrub cover and microclimate conditions affected by the frequency, intensity and spatial extent of burn patterns (Knapp et al. 2013, Collins et al. 2015). Because fire is a frequent and keystone process shaping the system in the Sierra Nevada, old forests there generally exhibit spatial segregation of different canopy strata (Stephens and Gill 2005), which reduces crown fire potential. This is very different from the stand structural measures many consider indicative of old-growth forests elsewhere (like the Pacific Northwest), such as densely overlapping multi-layer canopies. The Sierra Nevada ecosystem condition cannot be assessed by the abundance and size of forest structures alone, but needs to strongly consider fire history including severity, frequency and patch structure (Collins and Stephens 2010).

Stand and landscape patterns of forest conditions appear to be generally influenced by local rates of actual evapotranspiration (AET) and climatic water deficit (CWD). AET is a measure of how much water actually transpired and consequently potential tree growth and size. CWD is a measure of the difference between potential and actual evapotranspiration and consequently an indirect measure of a site's moisture stress on vegetation (i.e., how 'dried out'). AET has been significantly correlated with the abundance of large forest structures (live trees, snags, and large logs), canopy cover, and biomass. CWD has been generally correlated with fuel moisture conditions and in some instances susceptibility to bark beetle attack, therefore, indirectly with local fire regimes, although the association is not as strong as AET's correlation with large tree biomass. Local fire regimes most directly influence understory conditions such as shrub cover and composition, small tree density, and surface soil substrates (i.e., litter and bare ground conditions that influence germination success of different species). In general, AET and CWD may be an improvement over topographic categories in predicting historic forest condition associated with large trees because it is one step closer to a more mechanistic understanding

of ecosystem processes (Stephenson 1998). Areas of low productivity can be generally identified through their association with low AET. Locations of frequent fires may be roughly associated with high CWD, but physiographic characteristics (slope position, aspect, steepness, etc.) may be a more direct measure of factors that affect fire occurrence and intensity. However, historic forest conditions were also influenced by other factors such as tree-killing insects (e.g., bark beetles; Fettig 2015), disease, and wind-throw, as well as the spatial and temporal variability inherent in disturbance events.

Current Conditions Relative to Historic Conditions

Driving Forces

In general, the two strongest management influences on current forest conditions in the Sierra Nevada are logging and fire suppression over the last 100 or more years. Logging often removed the largest trees and preferentially selected pines over fir and cedar (Laudenslayer and Darr 1990, Stephens 2000). Forest management also removed 'defect' trees (i.e., broken tops, multiple leaders, mistletoe-infested, etc.), which had characteristics associated with preferred habitat for some sensitive species such as the California spotted owl. In general, historic logging and forest management practices reduced spatial heterogeneity and stand structures (large trees, snags and logs, and defects) associated with old-forest conditions.

The effects of fire suppression are influenced by the highly productive conditions of the Sierra Nevada. Small trees rapidly in-filled the understory and with enough time (> 40 years) grew to intermediate and then co-dominant size in many stands (Parsons and DeBenedetti 1979). This often eliminated the spatial heterogeneity [i.e., individual trees, clumps of trees and openings (ICO) pattern], reduced species diversity (as the number of fire-sensitive, shade-tolerant stems increased), structural diversity (variability in tree size and canopy position) and understory variability in microclimate and habitat conditions.

McKelvey and Johnston (1992) highlight four key changes in forests since 1850: 1) loss of old, large-diameter trees and associated large downed logs; 2) shift in species composition towards shade-tolerant; 3) increase in fuel associated with mortality of smaller trees; and 4) presence of ladder fuels that facilitate crown fire. Similarly, Franklin and Johnson (2012) outline four significant changes seen in fire-prone or dry mixed-conifer forests over the last century: (1) many fewer old trees of fire-resistant species, (2) denser forests with multiple canopy layers, (3) more densely forested landscapes with continuous high fuel levels, and, consequently, (4) more stands and landscapes highly susceptible to stand-replacement wildfire and insect epidemics.

These changes generally make current forests less resilient to two of the most common disturbances in the Sierra Nevada, fire and drought. High fuel loads and connectivity of ladder fuels and tree crowns increase the likelihood of high-intensity crown fire occurrence and extent (Agee and Skinner 2005, Stephens et al. 2009). Stands with uniformly distributed high tree density (i.e., without gaps), particularly in areas with low soil moisture holding capacity (e.g. shallow soils), are highly susceptible to drought stress. This stress, in turn, increases the likelihood of tree mortality attributed to forest insects and disease, particularly from bark beetles (Kolb et al. 2015). This decrease in resilience is likely most significant in locations where low productivity and/or frequent fire historically kept forests generally at a low density and with a higher percentage of drought and fire-resistant pines. Below, changes in forest structure and composition, and essential disturbance processes are described. A summary of information on California Spotted Owl populations relative to past conditions is also included.

Climate

Over the last 7000 to 8000 years, dry climate periods have occurred on average every 80 to 260 years, with durations of droughts lasting 20 to 100 years on many occasions (Safford and Stevens in review). While the 19th and 20th centuries have been anomalously wet, and the 19th century anomalously cool, in the Sierra Nevada (Haston and Michaelsen 1997, Hughes and Brown 1992, Safford and Stevens 2015), several recent assessments report the world's forests are increasingly vulnerable to ongoing warming and drying attributed to climate change (Allen et al. 2010, Martinez-Vilalta et al. 2012, Fettig et al. 2013, Vose et al. 2016). They suggested that the effects of a warming, drying climate on tree mortality range from modest and short-lived local increases to acute, regional-scale episodes often involving large-scale insect outbreaks. While these episodes are well-documented, the underlying causes of tree mortality are complex, and likely involve numerous predisposing, inciting and contributing factors. Nevertheless, recent and future increases in tree mortality in the Sierra Nevada and elsewhere in the western United States have been closely linked with increased moisture stress associated with warming climate (van Mantgem et al. 2009, van Mantgem and Stephenson 2007), which exacerbate the impacts of interactive stressors on forest ecosystems (Millar and Stephenson 2015). Changes to forest structure, composition, and function over the last century have placed these forests, and particularly larger and older trees on which many wildlife depend, at high risk for drought stress and mortality (McDowell and Allen 2015, van Mantgem et al. 2013).

Forest Conditions

Heterogeneity

A defining characteristic of historic Sierra Nevada forests was heterogeneity in tree spatial distribution, density and species composition (North et al. 2009, Collins et al. 2015). Recent studies have quantified the distributional heterogeneity of frequent-fire forests as characterized by a pattern of individual trees, clumps of trees and openings (ICO) (Larson and Churchill 2012, Fry et al. 2014). The proportion of area in each of these conditions, the tree density and basal area, and opening size and location, likely varied with local differences in productivity, topography, localized fire behavior, as well as the overall fire regime. Drier conditions associated with upper slope, ridge top and southwest aspects likely had smaller tree-clumps, larger openings, lower basal area and density, and a higher percentage of pine species. In contrast, more mesic locations such as lower slope and valley bottom sites more often supported large tree clumps, higher canopy closure, smaller openings and a higher percentage of fire-sensitive, shade-tolerant species such as fir and cedar.

With this heterogeneous ICO pattern occurring across the landscape, it was likely linked to forest resistance and resilience to disturbance. For example, gaps in ICO dominated forests under moderate fire weather may limit the spatial extent of high-intensity crown fires and high severity patches (e.g., Kennedy and Johnson 2014). Spatial variability in forest structure may also have made forests more drought resilient because clumped trees had adjacent openings and areas of low tree density that reduced moisture competition, thereby potentially reducing tree susceptibility to bark beetles (Fettig 2012). Likewise the extent and severity of some pathogen and pest damage can be limited by variability in tree species and spatial composition because some pests and pathogens are host-specific and influenced by overall stand density.

Forest stands at fine (stand and sub-stand) scales are more homogeneous today than historically, with less patchy patterns of tree size and density (Agee 1993, Barbour et al. 1993, 2007; SNEP 1996, Sugihara

et al. 2006), increased tree clump size (e.g. more trees per clump; Lydersen et al. 2013), and decreased proportion in canopy gaps (Lydersen et al. 2013). The density of gaps has decreased from an average around 5-6 gaps/ha (~2 – 2.5 gaps/ac) to less than 0.1 gap/ac on average (Lydersen et al. 2013), and the average gap size has decreased dramatically. Forest structure has also been ‘simplified’, including declines in large trees, snags, woody debris of large diameter, canopies of multiple heights and closures, and complex spatial mosaics of vegetation (SNEP 1996, Safford and Stevens in review). These stand and landscape-level reductions in structural and patch heterogeneity have likely dramatically decreased forest resistance and resilience to disturbance.

Tree Densities and Sizes

Reconstructed tree densities from pre-settlement conditions range from 60 to 328 trees/ha (24 – 132 trees/ac; trees > 4 in dbh), with an average of 159 trees/ha (64 trees/ac; Safford and Stevens in review, Taylor 2004, Scholl and Taylor 2010, Collins et al. 2011, 2015, Stephens et al. 2015). Contemporary mean tree density is 397 trees/ha (160 trees/ac), with densities ranging from 238 to 755 trees/ha in the same stands for which presettlement reconstructions exist. Increases in forest density range from 80% to 600% with most of this increase in trees <60 cm dbh (Safford and Stevens in review). Historically, the yellow pine and mixed-conifer forest types were characterized by higher densities of large trees and lower densities of small trees, with about the same overall basal area that occurs today (Dolanc et al. 2014). However, some studies report lower basal areas in historical periods in ponderosa pine forests (Stephens et al. 2015). Trees >36 in dbh, have declined in abundance, trees 24-36 in dbh have decreased in some places and increased in others, and trees <24 in dbh have increased (Verner et al. 1992, North et al. 2007, Fellows and Goulden 2008, Lutz et al. 2009, Scholl and Taylor 2011, Dolanc et al. 2014, McIntyre et al. 2015, Stephens et al. 2015).

Average and maximum tree sizes have declined relative to historic conditions. The lack of fire and a moderated microclimate due to forest densification have decoupled the mortality and regeneration processes from fire and climatic conditions, changing the age and size structure from one with a more even distribution to one weighted toward young, smaller trees. In terms of diameter, this changes the distribution (size [x axis] plotted against frequency) from a fairly flat slope to one more closely approximating a reverse-J. This change broadly indicates a forest shift from a diversified structure largely controlled by disturbance (fire) to a forest approaching maximum carrying capacity and controlled by resource limitation (competition for water and/or light and bark beetle-caused mortality). Compared to historic forests, the average tree size has declined 60% and 26% in the Tahoe Basin and Stanislaus National Forests, respectively (Taylor et al. 2014, Lydersen et al. 2013). In pine and mixed conifer forests, FIA data indicate that contemporary forests have an average tree diameter of 26 cm, and a quadratic mean diameter of 32 cm. Historic pine/mixed conifer forests likely contained an average of about 4-16 trees > 24 inches dbh/acre, and an average of 1.5 – 8 trees > 36 inches dbh/acre (averaged at the landscape scale; Collins et al. 2015; Stephens et al. 2015). Although the exact size threshold above which larger trees are in deficit varies among locations, trees >36 in dbh are in deficit throughout the Sierra Nevada-Cascade Region (Dolanc et al. 2014) and trees between 24 and 36 inches dbh are more common today than historically in some areas (Stephens et al. 2015). While timber harvest and tree planting explain some of these declines, similar patterns also occur in unlogged forests, suggesting that other factors are at play. These might include insects, pathogens, and drought stress, which are likely exacerbated by the much higher stand densities in modern forests (Safford and Stevens in review).

Basal area estimates for historical conditions generally ranged from 21 m²/ha to 54 m²/ha (91-235 ft²/ac) depending on site productivity, with a mean of 35 m²/ha (~150 ft²/ac; Safford and Stevens in review). Current FIA data suggest that mean basal area has not changed significantly over the last century (Safford and Stevens in review) which is a result of the two countervailing trends discussed above, increasing tree density and decreasing average tree size.

Sierra-Cascade Forests have seen increases in snag density (Safford and Stevens in review). Current trends in snag dynamics suggest that snags are more abundant but significantly smaller than historical conditions (Knapp 2015). Current snag densities (>15 cm [6 in] dbh) average about 20 – 50 snags/ha (~8- 20 snags/ac) (Safford and Stevens in review, Stephens et al. 2007, Younglood et al. 2004, Dunbar-Irwin and Safford in Review), while historic average densities likely ranged from 4 to 12 snags/ha (~1.6 – 5 snags/ac) (Stephens 2004, Stephens et al. 2007, Dunbar-Irwin and Safford in review). Agee (2002) suggested that forest types with frequent fire regimes should support around 5 snags/ha (~2 snags/ac), with the average snag size about 75 cm dbh (30 in).

Tree Mortality

Recent studies have documented high mortality rates of trees throughout the Sierra Nevada (van Mantgem et al. 2009), including higher than expected and accelerating rates of loss of the largest size classes (e.g., >36 in dbh, Smith et al. 2005, Lutz et al. 2009, Fellows and Goulден 2012, McIntyre et al. 2015). Historically, mortality was primarily driven by fire, which selects for smaller tree sizes and fire-sensitive species. With fire as a recurring event historically, small trees only survived and grew large enough to escape this mortality cycle through the stochastic nature of fire frequency and extent (Stephens et al. 2008). Some areas were randomly missed by fire and other microsites were less likely to burn due to mesic conditions or fuel barriers (i.e., streams and rocks). In general, this produced forests characterized by a low-density of large trees because, while few individuals escaped the cycle of fire-driven mortality, those that did may have thrived in conditions with reduced water and light competition, producing large, long-lived, more fire-resilient trees. The increasing mortality of large trees today is suspected to reflect effects of climate change, drought, and water stress (Fellows and Goulден 2008, Lutz et al. 2009, McIntyre et al. 2015) in interaction with multiple other factors, including pathogens, insects, and air pollution (Guarin and Taylor 2005, Smith et al. 2005, Das et al. 2011, McIntyre et al. 2015). The few data available on tree mortality rates suggest that background rates today are higher than historically. Background mortality rates (averaged over multiple years) in the Sierra-Cascade forests are between about 0.25% and 1.4% for fire-excluded forests but less than 0.5% for contemporary reference forests with a largely intact fire regime (In Safford and Stevens in review: Ansley and Battles 1998, Maloney and Rizzo 2002, Stephens and Gill 2005).

In particular, there has been a recent dramatic increase in loss of large trees due to bark beetles, which are currently considered one of the principal agents of tree mortality in the Sierra Nevada (Fettig 2012, 2015). Most notable within the range of the California spotted owl are the western pine beetle, mountain pine beetle, Jeffrey pine beetle, pine engraver, and fir engraver. Depending on the bark beetle species and numerous other factors (Fettig et al. 2007), the extent of tree mortality may be limited to small spatial scales (e.g., small groups of trees) or impact extensive areas. Outbreaks occur when favorable forest and climatic conditions coincide and climate change is likely exacerbating bark beetle impacts (Bentz et al. 2010). Warming temperatures have triggered population increases in many insect species which have served as catalysts for widespread outbreaks (Millar and Stephenson 2015).

Current examples of these widespread outbreaks and associated tree mortality are clearly evident in the low to mid-elevation coniferous forests of the southern Sierra Nevada, where western pine beetle has had an especially widespread impact on ponderosa and sugar pines (FHP 2015). The combination of unprecedented forest canopy water loss associated with drought and dense forest conditions has caused rapid (1-2 years) and extensive tree mortality (Asner et al. 2015), affecting most dominant conifer species in low- to mid-elevation forests of the southern Sierra Nevada.

Factors such as overall stand density, tree diameter, and host species density have been identified as primary attributes associated with bark beetle infestations and currently slower growing ponderosa pines are more susceptible to attacks (Craighead 1925, Miller 1926). Various measures of stand density, including stand density index (SDI) or the total basal area of all trees in a stand, are positively correlated with levels of tree mortality attributed to bark beetles (Hayes et al. 2009). Host density had less predictive power than other measures of stand density, suggesting that tree density and, indirectly, competition is more important than host tree availability (Hayes et al. 2009). It is well documented that higher density stands suffer increased competition for resources (especially water and light) and reduced tree vigor, which makes individual trees less resistant to bark beetle attack (Fettig et al. 2007, Safford and Stevens in review). For example, when soil moisture is limited trees close their stomata to avoid excessive water loss, which inherently leads to reduced productivity as stomatal closure also prohibits uptake of carbon dioxide and, ultimately, photosynthesis. Reduced productivity directly compromises a tree's pest resistance mechanisms. Conversely, reducing competition through reductions in tree density decreases the susceptibility of individual trees, stands, and forests by helping trees to maintain productivity and thereby increasing insect and disease resistance mechanisms (Fettig et al. 2007). A SDI value of 230 is the threshold for imminent bark beetle-caused tree mortality in ponderosa pine stands in northern California, with a maximum SDI of 365 (Oliver 1995, Hayes et al. 2009). Hayes et al. (2009) suggests that it might be appropriate to consider lower SDI thresholds under some conditions (e.g., during elevated bark beetle populations as associated with extended droughts in California).

Canopy Cover

Average canopy cover for historical pine and mixed conifer forests has been estimated between 17% and 49%, with many studies reporting canopy cover below 35% (Safford and Stevens in review, Collins et al. 2011, Lydersen and North 2012, Collins et al. 2015, Stephens et al. 2015). Models predict that most of the landscape was historically in open conditions of less than 50% canopy cover (<40% in yellow pine), especially in the yellow pine and dry mixed conifer types (Safford and Stevens in review). These models also predict that dense, older stands occupied around 5% of the landscape in the yellow pine and dry mixed conifer types, and around 20% of the moist mixed conifer type (Safford and Stevens in review). FIA data suggest a current average canopy cover around 46%, although this is likely an underestimation (Fiala et al. 2006). Current conditions represent an increase in average canopy cover of around 25% (Safford and Stevens in review) to an average of about 46% to 50% (Safford and Stevens in review; Stephens et al. 2015).

Tree species composition

Forest composition has shifted from historic conditions, with declines in abundance of shade-intolerant pines and increases in shade-tolerant species like firs and cedars (Barbour et al. 2002, Guarin and Taylor 2005, Dolanc et al. 2014, McIntyre et al. 2015, Stephens et al. 2015). Reduced understory light and thick

litter layers favor regeneration of fire-sensitive, shade-tolerant species. Relative proportions of shade intolerant to shade tolerant species changed from 60:40 to 35:55 between 1930s and 2000s, with the stand-component of shade intolerant species like yellow pines dropping from about 2/3 to about 1/3 of the mature forests (*define mature*) over the last century (Safford and Stevens in review). In some areas, pine forests have been replaced by mixed-conifer forests. Dolanc et al. (2014), found that 19.7% of 1930s plots were classified as ponderosa pine, versus just 8.9% of the plots from the 2000s, and 27.4% of plots were classified as mixed conifer in the 1930s dataset, versus 37.1% in the 2000s, with similar reductions in Jeffrey pine. Current Forest Service vegetation maps show 17% of the region in yellow pine and 30% in mixed conifer forests, compared to 33.7% in yellow pine and 19.8% in mixed conifer in Show and Kotok's (1929) summary of 1920s conditions (Safford and Stevens in review). The broad "mixed conifer" category represents a diverse array of habitat, including pine dominated mixed conifer (Collins et al. 2011, 2015, Stephens et al. 2015) and fir dominated mixed conifer forests (Stephens and Collins unpublished data from the El Dorado National Forest). The pine dominated mixed conifer forests had lower tree densities and canopy cover, and were dominated by shade intolerant species versus the fir dominated areas that had higher tree densities and tree basal area, and were dominated by fir.

Fire and Ecological Function

Fire Regime

Fire, a key ecological process in the Sierra-Cascade region, has changed significantly over the last century due to fire suppression becoming the pervasive forest management policy and to changing climatic conditions. Yellow Pine/Mixed Conifer forests historically supported fire regimes characterized by frequent, low to moderate severity fires (from Safford and Stevens in review: Agee 1993, Arno 2000, Barbour et al. 2007, Barbour et al. 1993, Skinner and Taylor 2006, van Wagtenonk and Fites-Kaufman 2006). Before extensive fire suppression, mean Fire Return Intervals (FRIs), the average number of years between two successive fires (Agee 1993), for yellow pine and mixed conifer forests across California ranged from 11 to 16 years (Stephens et al. 2007, Van de Water and Safford 2011, Safford and Stevens in review). Fire frequencies were highest in the drier, lower elevation forest types (yellow pine and dry mixed conifer) and lower in moister and higher elevation stands (In Safford and Stevens in review: Caprio and Swetnam 1995, Fites-Kaufman et al. 2007, Gill and Taylor 2009, Sugihara et al. 2006, Taylor 2000). The historic fire rotation, the length of time necessary for an equal-sized area to reburn (Agee 1993), for the pine/conifer forests ranged from 22 to 31 years (Mallek et al. 2013). Today, most pine/conifer forests in the central and northern portions of Sierra-Cascade range are more than 85% departed from historic fire return intervals (i.e. have seen zero to one fire in the last century; Safford and Van de Water 2014) and most in the eastern and southern portion of the region are at least 67% departed from historic FRI (ie three or fewer fires over the last century; Safford and Van de Water 2014). Current fire rotation on USFS managed pine/conifer forests averages 258 to 280 years (range 95 – 516; Miller et al. 2012b), and about 55 years in Yosemite National Park. In other words, fire rotations are about 10 times longer than historically on Forest Service lands, and about twice as long in Yosemite National Park (Miller et al. 2012b, Safford and Stevens in review).

North et al. (2012) estimated that under a historic fire regime 183,778 to 487,846 acres would have burned annually, on average, on Forest Service land in the Sierra Nevada region. The authors also estimated that the current rate of burning (including both prescribed and wildfire) on Forest Service lands is only about 59,325 acres annually (North et al. 2012). When the area of mechanical treatment is added, the total acres of fire or fire-mimicking activity, only sums to an average of 87,923 acres per year

(North et al. 2012). These annual fire/treatment rates are far below even the lowest of possible historical figures, and have led to an estimated 2.9 million acres of 'backlogged' forest in need of fire/treatment. These acres have seen increases in snag density, coarse woody debris, litter and duff depth, and surface fuel volume and continuity (Safford and Stevens in review).

Fire Severity

Historically, the amount of forest burned at high severity likely represented a very small proportion of the total area burned. Mallek et al. (2013) indicate that historically only 5-10% of any burn at any given time would have been high severity. Stephens et al. (2015) suggest an even lower proportion of high severity fire in the southern Sierra Nevada (1-3% in mixed conifer and 4-6% in Ponderosa Pine forest). These high severity areas were likely aggregated in small patches (usually <5 acres) distributed across the landscape (Show and Kotok 1924, Collins and Stephens 2010; North et al Assessment).

Recent decades have seen increases in both overall proportion and patch size of high severity (Miller et al. 2009, Miller and Safford 2012, Steel et al. 2015), which are well above historical conditions (Mallek et al. 2013, Stephens et al. 2013, Stephens et al. 2014, North et al. Assessment), with the average fire in modern mixed-conifer and yellow pine forests on USFS lands supporting 5 to 7 times more area of stand-replacing fire than fires before Euro-American settlement (29-35% high severity; Miller et al. 2009; Miller and Safford 2012; Mallek et al. 2013; Safford 2013). Recent fires in the Sierra Nevada have included some exceedingly large patches of stand-replacing fire, extending for thousands or even tens-of-thousands of acres. This is in direct contrast to the size of stand-replacing patches from active fire regime forests in reference landscapes (areas where the fire regime is intact or has been restored) of the Sierra Nevada, where mean stand-replacing patch size is <4 ha (10 ac) and maximum patch size generally is ≤100 ha (250 ac) (Collins and Stephens 2010; Miller et al. 2012; Safford 2013). Large, contiguous areas of severe fire can result in the long-term replacement of conifer forest by shrubs, which are then perpetuated by subsequent fires (Willken 1967; Biswell 1974; Bock and Bock 1977; Collins and Roller 2013). Recent studies also suggest that high severity re-burns are likely in these areas of initial high severity fire (Thompson et al. 2007; van Wagtenonk et al. 2012). In the northern Sierra/southern Cascades, under specific fire weather conditions, the high densities of snags, down woody debris, and shrubs that result from initial high severity burns are driving factors in high severity re-burns (Coppoletta et al. 2016).

Fire Size

In comparison to early 20th century fires current maximum fire sizes are much larger, but small fires (<4 ha; 10 ac) are now much more common because of the success of modern fire suppression methods. Thus, average fire size in contemporary California yellow pine/mixed conifer forests is likely much smaller than in pre-settlement forests. For example, fires <4 ha (10 ac) accounted for 96% of all fires that occurred in the Sierra Nevada Forest Plan Area during 1992-2011, but only 76% of all fires that burned during 1911-1920 in yellow pine/mixed conifer forests. As a result, mean fire size for the SNEP area during 1992-2011 was 24 ha (60 ac) compared with 51 ha (126 ac) from 1911-1920 (Show and Kotok 1923; Short 2013; J. Miller, USDA Forest Service, unpublished data). Excluding those fires that are immediately suppressed, average fire size has likely increased. Average fire size in California mixed-conifer forests before Euro-American settlement has been estimated at <300 ha (750 ac), while the average of fires greater than 4 ha over the last 25 years is closer to 1,500 ha (3,750 ac); and recent fires on USFS lands in California are much larger than that (Show and Kotok 1923; Taylor and Skinner 1998;

Minnich et al. 2000; Taylor 2000; Beaty and Taylor 2001; Taylor and Solem 2001; Collins and Stephens 2007; Miller et al. 2012; Safford and Stevens in review; A. Taylor, Pennsylvania State University, unpublished data).

California Spotted Owl Populations

Existing genetic data do not allow for strong inference about the demographic history (or historic abundance) of California spotted owls and additional analyses would be required to infer how current population numbers relate to historic ones. However, an analysis of the genetic variation across the range of the spotted owl showed that microsatellite variation in California spotted owls occurring in the Sierra Nevada does not seem atypical for wild populations (Funk et al. 2008). These results suggest there has been neither a severe and recent population bottleneck nor a recent population expansion from a small number of founders.

Shorter-term population trends are less equivocal. CSO populations remain reasonably well distributed in the Sierra Nevada, but populations within three demographic study areas located on National Forest System lands are showing declines over the last two decades (Tempel et al. 2013, 2014; Conner 2014, Assessment). On one demographic study area, declines have exceeded 50% since the early 1990s, with smaller declines detected on the two other National Forest demographic study areas (Tempel et al. 2014b, Connor et al. 2014).

To add rough overall estimated range/size of the total CSO population here (scientists may be able to extrapolate from demography studies to provide broad, very rough estimate of overall population)

Currently, designated PACs cover 5-9% of productive¹ USFS forest lands in each National Forest within the Strategy area (North et al. 2015; unpublished data). Territories currently encompass roughly 14% - 28% of productive lands in each National Forest within the Strategy area (unpublished data – note this uses 1000 ac for all forests, so underestimates some and slightly over estimates other, also some overlap). Occupied PACs and territories are well distributed across the owl's range. Trends in the number of PAC is generally increasing over time, due, in part, to the ambiguity in direction regarding retiring PACs and the lack of resources to survey PAC occupancy through time. Generally, the amount of land allocated to reserves (PACs) would not likely pose a significant impediment to large-scale landscape realignment with historic and/or more resilient conditions, especially as PACs and territories align with biophysical conditions that will support suitable habitat in the long-run. However, if the proportion of the landscape in PACs increases and unoccupied PACs continue to be managed as reserves indefinitely, that may pose real barriers to restoring landscape and habitat resilience in the long term.

Barred owl Populations

Historically, the geographic range of barred owls (*Strix varia*) was confined to eastern North America, from southeastern Canada south to western Mexico, but this species has been expanding its range westward in North America for more than 80 years. While it is not clear whether the range expansion occurred naturally or was human influenced, one hypothesis holds that the disruption of fire regimes and irrigation in the Great Plains promoted vegetation growth has facilitated westward movements (Dark et al. 1998, Gutierrez et al. 2007). Barred owls are now effectively sympatric with northern

¹ Definition of productive: Forested lands (excluding shrubs, barren, and water) with > 10% canopy cover

spotted owls in southern British Columbia, Washington, Oregon, and northern California (Anthony et al. 2006, Gutierrez et al. 2007).

Barred owls interact with spotted owls via predation, hybridization, and interspecific competition for resources, although competitive interactions appear to have the greatest impacts to spotted owls in the Pacific Northwest (Wiens et al. 2014). Significant dietary overlap exists as both species prey primarily on small mammals, although barred owls consume on a wider variety of terrestrial, aquatic prey, and diurnally active prey (Hamer et al. 2001, Wiens et al. 2014). Barred owls also use a broader array of habitat types, but habitat overlap is considerable given similar use of younger, mature, and riparian-forest types. Primary differences in foraging habitat selection include the preferential use of older forests on steep slopes by spotted owls and the selection of flat areas near streams by barred owls (Wiens et al. 2014). Nevertheless, adjacent spotted and barred owls generally occupy distinct core areas, presumably because of competitive interactions (Wiens 2014).

The apparent competitive dominance of barred owl results in reduced spotted owl territory occupancy probabilities in the presence of barred owls (Olson et al. 2005, Crozier et al. 2006, Kroll et al. 2010, Yackulic et al. 2012, 2014). Some spotted owls may become non-territorial, yet still breed, as a result of interactions with barred owls, although the extent to which this occurs is not well understood. Nevertheless, reproductive success, survival and population growth rates in territorial spotted owls tends to be reduced in the presence of barred owls (Diller et al 2016). More broadly, barred owls have had profound impacts on northern spotted owl populations across large portions of the Pacific Northwest and pose one of the most significant threats to this subspecies (USFWS 2012). Lethal removal is the primary barred owl control strategy being considered within the range of the northern spotted owl (USFWS 2011, Diller et al. 2014, 2016; Wiens et al. 2016). Indeed, recent work indicates that the removal of barred owls can increase spotted owl vital rates, population growth, and territory occupancy (Diller et al. 2016, Dugger et al. 2015).

Barred owls have recently expanded their range into the northern Sierra Nevada with a small, but increasing, number of individuals detected in the central and southern Sierra. The first barred owl detecting in the Sierra Nevada occurred in Lassen County in 1989 (J. Keane, Conservation Assessment). Detections of barred and sparrowed owl increased from 2002 to 2013, largely because of increased spotted owl survey effort on demographic study areas in the northern Sierra. Barred owls were first detected in the central and southern Sierra Nevada in 2004 (Seamans et al. 2004, Steger et al. 2006) and six barred owls were detected in the southern Sierra Nevada during 2011-2012 (J. Keane Conservation Assessment). The number of barred and sparrowed owls on the four long-term demographic study areas has remained low, although they may be increasing gradually in the northern Sierra Nevada, with eight barred and two sparrowed owls present on the Lassen demographic study area in 2013. As is the case generally for invasive species, the momentum of range expansion will be far more difficult to curtail once barred owls have reached a critical, yet unknown, density. If barred owls reach such a threshold, as they have elsewhere, we can expect a rapid increase in their numbers and significant impacts to California spotted owl populations in the Sierra Nevada.

Future Conditions

Climate Drivers

Climate models project increasing temperatures in California, ranging from increases of 2 to 9 °F by the end of century, with the greatest increases during summer (Hayhoe et al. 2005; Dettinger 2005; Haupfeld

et al. 2014). Models also suggest that a larger percentage of precipitation will occur as rain rather than snow, including a 64 to 87% decline in snowpack, and that year-to-year variability will increase (Hauptfeld et al. 2014). Predictions about changes in precipitation distribution and amount are highly variable, ranging from minor increases to major decreases. Because of these trends, models consistently suggest the frequency and strength of drought events will increase, likely making them a stronger influence on forest dynamics. Up to 44% increases in climate water deficit are predicted, especially in the Northern Sierra-Cascade region (Hauptfeld et al. 2014). This change in precipitation variability and form, coupled with increasing temperatures, is why all models also suggest an increase in fire frequency, size and severity. Predictions of future forest conditions should always be viewed with caution because of large uncertainties in how complex ecosystems may respond to potentially novel climatic and disturbance conditions and their interaction.

Projected Effects on CSO Habitat and Forest Characteristics

Predictions suggest that tall trees typical of old-growth forests are at greatest risk of loss under conditions of increasing periods of drought (Williams et al. 2013; Allen et al. 2015; McDowell and Allen 2015). Recent evidence shows that significant drought related mortality is already occurring in southern Sierra Nevada and that high levels of mortality are occurring in the larger tree size classes (FHP 2015), which has implications for owl nesting habitat. Increasing temperatures and drought stress, exacerbated by high densities of suitable and susceptible hosts, are thought to create a positive feedback loop expanding the range and epidemic populations of bark beetles (Raffa et al. 2008; Fettig et al. 2007, Vose et al. 2016). Forests that are homogeneous are more likely to experience a broad-scale mortality event in the future (Bentz et al. 2010). In addition, while the science continues to show discord about short term effects of extensive drought or beetle related tree mortality on fire behavior, it is clear that there is increasing long-term risk of extreme fire behavior due to increases in surface and ladder fuels which accumulate after each outbreak (Hicke et al. 2012). Climate change will likely affect the predictive capacities of the relationships between stand density and insect driven mortality (e.g., Hayes et al. 2009) as these relationships change due to both drought-induced host stress (Fettig et al. 2013) and changes to temperature-dependent beetle life history traits (Bentz et al. 2010). Some experts suggest that reductions in existing tree density thresholds associated with highly-susceptible stands will be required (Fettig et al. 2014).

Climate projections suggest that the southern Sierra Nevada in particular may begin to see conditions similar to areas in southern California in the coming century. Thus, lessons can be gleaned from southern California mixed conifer forests in looking towards the future. Between 2002 and 2004, a historic drought in southern California caused the widespread die-off of large-diameter conifers throughout the region (Minnich 2007). At the landscape scale, conifer mortality was especially highest on well-drained convex surfaces and south-facing slopes, which experience greater moisture stress, as well as in dense stands and/or areas that had not experienced recent fire (Minnich 2007). We are seeing, and can expect to see similar patterns in the Sierra Nevada in the future, where larger trees, critical for owls, have been shown to be particularly at risk (Smith et al. 2005).

If current forest conditions (i.e., often high density, fuel-loaded stands) continue into the future, coupled with increasing disturbance frequency and severity, some general patterns in future forest conditions are predicted. One study simulated these changes in disturbance and compared historic (low density, pine dominated) and current (high density, fir dominated) forest response. As disturbance frequency

and severity increased current forest conditions became unstable and in a large portion of the simulations shifted toward a high density, small tree size condition. Historic forest conditions were much more stable, generally perpetuating a low-density, large-tree, pine dominated condition in most scenarios unless severe disturbances occurred consecutively (Earles et al. 2014). The way forest growth models (in this case the Forest Vegetation Simulator [FVS]) simulate tree regeneration and mortality dynamics influences these predictions. High density, fuel loaded conditions tend to increase mortality and eventually reduce abundances of large trees and their associated structures (large snags and logs). Regeneration dynamics are harder to predict because disturbance timing, severity, climate and seed dynamics all interact (Collins and Roller 2013). Generally, however, under more unstable conditions, species with the largest, most consistent seed production (i.e., white fir and incense cedar) tend to be favored. Millar and Stephenson (2015) found that interactions from increasing temperature, drought, native insects and pathogens, and uncharacteristically severe wildfires are resulting in forest mortality beyond the levels of 20th-century experience. Large areas of the southern Cascades and Sierra Nevada forests are likely to experience uncharacteristic stand-replacement fires without active fuel treatments and prescribed burn programs, with the resulting loss of critical watersheds and habitat for California spotted owl and other endangered wildlife. Substantial and repeated restoration efforts will be needed to protect them (Agee and Franklin 2003, North et al. 2012).

Elevated surface fuels and a type change in vegetation (i.e., fire-resistant trees to more flammable shrubs) created by high severity burned areas can constitute a significant risk to the succeeding stand (Agee and Skinner, 2005), and van Wagtenonk et al (2012) found that high severity burn patches were perpetuated by subsequent fires. At the landscape scale, this may drive an increase in chaparral as high severity patches are converted from their initial vegetation type providing few opportunities to recreate late seral forest habitat for core nesting and roosting area due to lost habitat.

California Spotted Owl Populations

While spotted owls are not considered highly vulnerable to direct impacts of climate change, the projected future conditions described above are likely to negatively impact CSO populations by decreasing the amount of suitable habitat available. Additionally, barred owl populations have been growing in recent years in the Sierra Nevada, and are projected to increase in the future. Without intervention, a growing barred owl population is likely to cause a significant decline in the spotted owl population size in the future. Thus, projections for future CSO populations are fairly speculative, but recent trends would suggest a declining population without active management and intervention.