Is fire "for the birds"? How two rare species influence fire management across the US

Scott L Stephens[1]*, Leda N Kobziar[2], Brandon M Collins[3], Raymond Davis[4], Peter Z Fulé[5], William Gaines[6], Joseph Ganey[7], James M Guldin[8], Paul F Hessburg[9], Kevin Hiers[10], Serra Hoagland[11], John J Keane[12], Ronald E Masters[13], Ann E McKellar[14], Warren Montague[15], Malcolm North[12], and Thomas A Spies[16]

The US Endangered Species Act has enabled species conservation but has differentially impacted fire management and rare bird conservation in the southern and western US. In the South, prescribed fire and restoration-based forest thinning are commonly used to conserve the endangered red-cockaded woodpecker (*Picoides borealis*; RCW), whereas in the West, land managers continue to suppress fire across the diverse habitats of the northern, Californian, and Mexican spotted owls (*Strix occidentalis* subspecies; SO). Although the habitat needs of the RCW and SO are not identical, substantial portions of both species' ranges have historically been exposed to relatively frequent, low- to moderate-intensity fires. Active management with fire and thinning has benefited the RCW but proves challenging in the western US. We suggest the western US could benefit from the adoption of a similar innovative approach through policy, public–private partnerships, and complementarity of endangered species management with multiple objectives. These changes would likely balance long-term goals of SO conservation and enhance forest resilience.

Front Ecol Environ 2019; 17(7): 391–399, doi:10.1002/fee.2076

The US Endangered Species Act (ESA) influences forest and fire management across the US. In both the southern and the western US, several species of conservation concern exist in forests with historically frequent, low- to moderate-intensity fire regimes. In the southern US, the use of prescribed burning to restore historical fire regimes has strong institutional support; it is ubiquitously applied for a broad range of resource benefits (Kobziar *et al*. 2015; Melvin 2015), which are familiar to both the general public and land management personnel. Across the western US, however, wildfire suppression is favored over prescribed burning, which is carried out relatively infrequently due to a number of factors, including limited institutional capacity (Quinn-Davidson and Varner 2011; Schultz *et al*. 2018), air quality concerns (Schultz *et al*. 2018), and the lack of a large trained workforce.

In a nutshell:

- The US Endangered Species Act has influenced fire management differently across regions, even with species that are adapted to similar fire regimes
- Frequent prescribed fire and restoration thinning have greatly improved red-cockaded woodpecker (*Picoides borealis*) recovery in the southern US, while in the western US, large severe wildfires are a major threat to spotted owl (*Strix occidentalis*) recovery
- Complementary benefits from habitat restoration and fuels reduction using fire and thinning help explain the red-cockaded woodpecker's recovery in the South
- Integrating the beneficial roles of fire and restoration thinning into spotted owl conservation in the West may be critical for maintaining its habitat, especially with a changing climate

Given the nationwide requirements for species conservation across the US, the differences between approaches in the two regions may be linked to how the ESA differentially affects fire management. Here, we focus on two emblematic species – the red-cockaded woodpecker (*Picoides borealis*; RCW) of the southern US and the spotted owl (*Strix occidentalis*, including three subspecies; SO) of the western US (Figure 1) – to explore the relationship between the ESA and fire management. RCW habitat and population recovery programs are widely hailed as a success, whereas conservation of SO habitat has been less effective.

The ESA and fire management intersect in three important ways. First, conservation goals are driven by the ecology of the species at risk, how fire affects its preferred habitat, and the scale at which those effects are relevant. Second, even where the relationships between fire regimes and threatened species habitat factors are well understood, the ESA can be used to justify fire suppression and to limit active management. Finally, when considering practices directly aimed at species conservation, policy makers may view fire manage-

*[1]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA *(sstephens@berkeley.edu); [2]Department of Natural Resources and Society, University of Idaho, Moscow, ID; [3]Center for Fire Research and Outreach, University of California, Berkeley, Berkeley, CA; [4]US Department of Agriculture (USDA) Forest Service, Pacific Northwest Region, Corvallis, OR; [5]School of Forestry, Northern Arizona University, Flagstaff, AZ; [6]Washington Conservation Science Institute, Leavenworth, WA; [7]USDA Forest Service, Rocky Mountain Research Station, Flagstaff, AZ;* *(continued on last page)*

T Tanaka

D Walsh

Figure 1. (a) Red-cockaded woodpecker (*Picoides borealis*; RCW) in Florida; (b) California spotted owl (*Strix occidentalis occidentalis*; CSO) in the Sierra Nevada.

ment objectives as being of equal or greater importance. For this reason, fire management may be driving endangered species management decisions rather than the reverse.

We recognize that there are differences between the life histories and habitat needs of the RCW and SO (WebTable 1). However, our goal is to compare and contrast two distinct but related fire paradigms affecting these iconic birds in the US. We explore how the intersection of fire management and rare species protection differs between the two regions in order to better understand what promotes species conservation success in the context of wildland fire management.

Red-cockaded woodpecker in longleaf pine

The RCW is endemic to the pine–grasslands, woodlands, and savannas of 11 US states, and was federally designated as "Endangered" in 1968, prior to passage of the ESA. The species was once common throughout the southern US, coinciding primarily with the distribution of fire-maintained southern pines. Current RCW populations are scattered, and many are isolated, with less than 3% of the bird's pre-colonial population remaining (USFWS 2003). RCWs prefer low-density, pine-dominated habitats, which in the South were historically maintained by very frequent (1–5-year intervals), low-intensity fires. The drastic reductions in RCW abundance that have occurred over the past several decades are primarily due to habitat loss caused by land conversion, development, logging, loss of mature living pines (>75 years), and fire exclusion. Collectively, these changes have resulted in the proliferation of hardwoods and reduced herbaceous understories. The RCW was initially considered an old-growth obligate fire-dependent species because these birds created roost cavities exclusively in large, fire-maintained living pines. Today, RCWs utilize most southern pine tree species even at younger ages, partially as a result of artificial nest cavity installations (Conner *et al.* 2001).

Specific fire regime attributes are critically important for promoting and conserving longleaf pine (*Pinus palustris*) habitat for the RCW, with the most important factor being consistent application of frequent fire. Ultimately, the formula for RCW recovery in longleaf pine has been straightforward ever since the bird was listed: sustaining prescribed fire management explicitly supported by policy, strategic creation and preservation of nest cavities, RCW introduction and translocation programs, and reduced regulatory burden of recovery on private lands through "Safe Harbor" programs (Trainor *et al.* 2013). These measures have likely prevented socioeconomic obstacles from hindering RCW restoration (eg forest thinning can continue as long as RCW habitat is maintained) and have contributed to the widespread support for fire restoration across land ownerships. Also critical is the compatibility of RCW habitat restoration actions with broader forest management goals. Potential wildfire severity reduction associated with prescribed burning has been compatible with the land management needs of government agencies, especially the US Department of Defense (DoD), as well as those of private landowners. Although current RCW population numbers are well below historical estimates, results indicate a clear positive trajectory (Figure 2).

However, this trajectory has not been without costs. Although no official figures have been published regarding the cost of recovery, the DoD – which manages all or part of six of 13 core RCW populations – has provided more than $10 million annually for management for nearly 25 years, with an additional estimated $67 million spent on research and development for RCW recovery between 1991 and 2004 (K Hiers pers comm). This investment often goes toward what some see as excessive use of expensive techniques for managing overly precise habitat parameters (Hiers *et al.* 2014, 2016), which may jeopardize habitats for other rare taxa (Hiers *et al.* 2014). Recent research shows that in relatively well-restored habitat, RCWs may be more tolerant of a wider range of modest hardwood densities than was previously seen in degraded habitat, and therefore "one-size-fits-all" guidelines are not appropriate across the species' range (McKellar *et al.* 2014, 2016). A focus on narrow habitat metrics can lead to ecosystem homogenization, which can compromise long-term resilience of longleaf pine ecosystems. Such considerations are particularly critical to climate resilience strategies that call for RCW habitat expansion outside of the former range of longleaf pine.

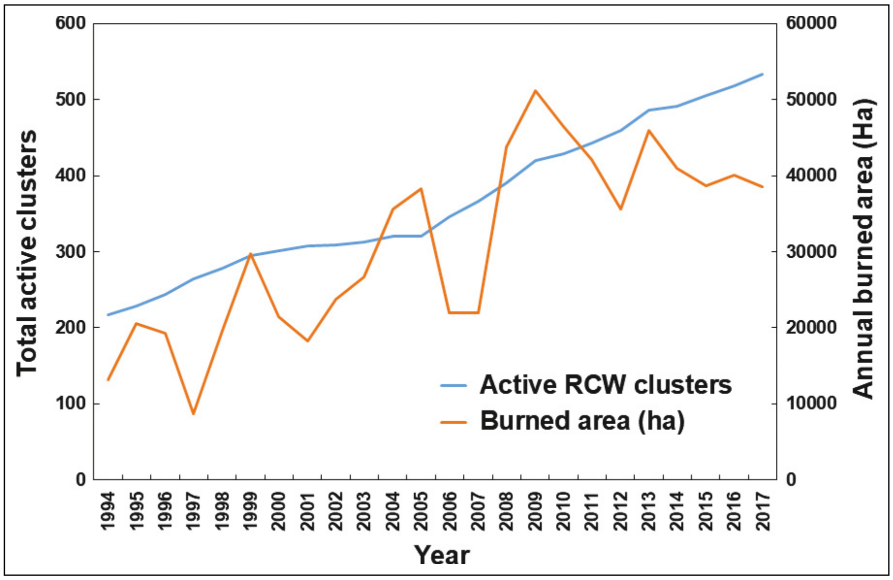


Figure 2. Red-cockaded woodpecker (*Picoides borealis*; RCW) recovery at the US Department of Defense Eglin Air Force Base in northern Florida shows population increases (as indicated by active use of cavity trees by RCW) correspond with increasing area of prescribed burning over the past 23 years.

Red-cockaded woodpecker in shortleaf pine

Farther north, the RCW was once common in fire-dependent shortleaf pine (*Pinus echinata*)–bluestem (*Andropogon* spp) ecosystems, and is at present most abundant in the Ouachita Highlands of Arkansas and Oklahoma. In these areas, prior to the mid-1920s, low tree density and pine dominance were maintained with low-intensity surface fires (every 1–12 years, mean interval = 4.6 years) that limited hardwood establishment (Masters *et al.* 1995). By 1970, this community type, along with the RCW, had all but disappeared because of logging and fire exclusion (Hedrick *et al.* 2007). Following a Forest Plan revision in 2005, the Ouachita National Forest committed to restoring this ecosystem for RCWs and associated species on over 100,000 ha in Arkansas and Oklahoma. Restoration efforts consist of thinning to modify stand density, basal area, and composition, and reintroducing frequent (3-year return interval) prescribed fire (Figure 3; Bukenhofer *et al.* 1994; Guldin 2007). Restored stands are characterized by a three- to seven-fold increase in grass and forb productivity, depending on time since fire (Sparks *et al.* 1998).

The benefits of this ecosystem management approach extend well beyond a single species. Research has demonstrated marked increases in a suite of at least 16 woodland–grassland obligate songbirds, most of which are of special management concern in Arkansas and Oklahoma (Figure 4; Wilson *et al.* 1995). The small mammal community and game species of local interest have benefited (Masters *et al.* 1993, 1998; Cram *et al.* 2002; Masters 2007), and plant and invertebrate communities, particularly lepidopterans, have also experienced substantial population growth (Sparks *et al.* 1998; Hedrick *et al.* 2007).

Treatments are funded by commercial timber sales. Sale receipts are disbursed to the US Treasury and to local governments, with a portion of the timber sale proceeds reinvested in treatments to improve habitat under provisions of the Knutson-Vandenberg Act (Guldin 2007). As such, the presence of viable local markets for timber has been an instrumental element of the success of the RCW recovery in shortleaf pine ecosystems.

RCW population growth was further accelerated by artificial management tactics, such as translocations and augmentations, snake exclusion devices, cavity inserts and restrictor installations, and the control of southern flying squirrels (*Glaucomys volans*), which compete with the RCW for cavity occupancy.

Another unique feature of this restoration program is the introduction of prescribed fire during the tree regeneration phase (stand age 3–5 years), which is crucial for the establishment of open stand structures conducive to other flora and fauna associated with this ecosystem. Fire use in the early stages of stand development also serves to favor native shortleaf pine over loblolly pine (*Pinus taeda*) and should eliminate the need for future treatments in middle-aged stands. If sufficient landscape-scale area is to be restored and maintained, increased use of prescribed burning is imperative.

As a result of improved understanding of RCW ecology and dedicated, ecologically informed fire management, most RCW populations across the South are now either stable or increasing. Recent range-wide population assessments show that the number of RCW breeding groups has increased from an estimated 4694 in the 1990s to 7800 at present (ie >49,000 individuals; W McDearman pers comm). This trend suggests that down-listing or even delisting of the species could occur 20 years ahead of previous expectations (USFWS 2003).

Spotted owls

Northern spotted owl

The northern spotted owl (*Strix occidentalis caurina*; NSO), designated as "Federally Threatened" in 1990, is found from

Figure 3. The wildlife stand improvement (WSI) process on the Ouachita National Forest in Arkansas and Oklahoma consists of: (a) hardwoods and smaller shortleaf pine (*Pinus echinata*) trees thinned from below, (b) prescribed burning on a 3-year cycle, (c) hardwood sprouts restricted to <1-m height, and (d) the cumulative effects of 3–4 burns, which promote grass understory. The frequent burn cycle is then continued.

southwestern British Columbia, through Washington and Oregon, and into California. Although habitat loss from logging remains a concern on state and private lands, the primary threats to the NSO on federal lands are competition from the invasive barred owl (*Strix varia*; Singleton *et al*. 2010; Wiens *et al*. 2014) and loss of habitat due to large, high-severity wildfires (WebTable 1; Davis *et al*. 2016). Efforts to conserve the NSO on federal lands have included the establishment of a system of large Late-Successional Reserves, designated under the 1994 Northwest Forest Plan, and additional areas designated as Critical Habitat (Lesmeister *et al*. 2018).

In contrast to habitats for the RCW and other SO subspecies, the 23 million-ha range of the NSO encompasses a wide variety of fire regimes (WebFigure 1). In moist areas where fire occurred infrequently, the NSO's preferred habitat consists of large patches of older, structurally complex, closed canopy conifer forests. In the eastern and southern portions of the NSO's range (~40% of total range), where fire regimes promoted open canopy pine and mixed-conifer forests, nesting and roosting patches were far less common, occurring in locally moist or topographically protected areas (Hagmann *et al*. 2017). In the southern part of the NSO's range, consisting of relatively mesic sites where mixed-severity fire was once common, fires created a patchy landscape mosaic of shrubby vegetation, and open and closed canopy forests that favored the NSO and its prey (Figure 5).

In contrast to that of the RCW, portions of the NSO's range were historically supported by relatively frequent wildfires (return interval <20 years) occurring across large landscapes (10^4–10^5 ha). Spatial heterogeneity resulting from an intact fire regime allowed for the varied structures needed for viable nesting, roosting, and foraging. However, fire exclusion has resulted in fuels accumulation, greater tree density, and a higher degree of canopy layering, which have increased the abundance of NSO nesting and roosting habitat coincident with the likelihood of uncharacteristically large, high-severity fires. Fire exclusion in historically frequent-fire areas of the NSO's range allowed for widespread development of habitat in areas where it had not previously occurred (Hessburg *et al*. 2005). Now, competition from the barred owl may be displacing NSOs in these fire-excluded forests, which are on the margin of the NSO's range (Dugger *et al*. 2016).

Management actions in dry and mesic mixed-conifer forests that promote ecological resilience to fire and climate change at the landscape scale include allowing some wildfires to burn, reducing fuel continuity to enable safe reintroduction of fire, implementing restoration thinning and prescribed burning to restore the dominance of medium- and large-sized fire-resistant trees, restoring the patchwork of open and closed canopy forests and non-forest patches, and tailoring conditions to the topography (Hessburg *et al*. 2015). These actions would reduce the short-term availability of suitable NSO forest cover, but the remaining and future suitable forest cover would be more likely to persist in the face of wildfire and climate change. Meeting dual goals for conservation of fire-dependent ecosystems and NSO populations will require the development of dynamic, landscape-level habitat plans based on difficult trade-offs (Gaines *et al*. 2010; Hessburg *et al*. 2015).

California spotted owl

The California spotted owl (*Strix occidentalis occidentalis*; CSO) is found throughout the Sierra Nevada and the mountains of central coastal California, and in the Transverse and Peninsula ranges of southern California. A recent assessment found that CSO populations have declined in three of four long-term study areas over the past 20 years (Gutiérrez *et al*. 2017). All three areas of CSO decline are on US National Forest lands interspersed with private industrial timberland, whereas the study area in which there is a stable to increasing population is entirely on US National Park Service land. The amount of forest composed of large trees (>60 cm diameter at breast height [DBH]) and high canopy cover (>70%) within an owl territory was determined to be the best predictor of territory extinction rates (Jones *et al*. 2018). The invasive barred owl is also a serious threat to the CSO (Keane *et al*. 2017).

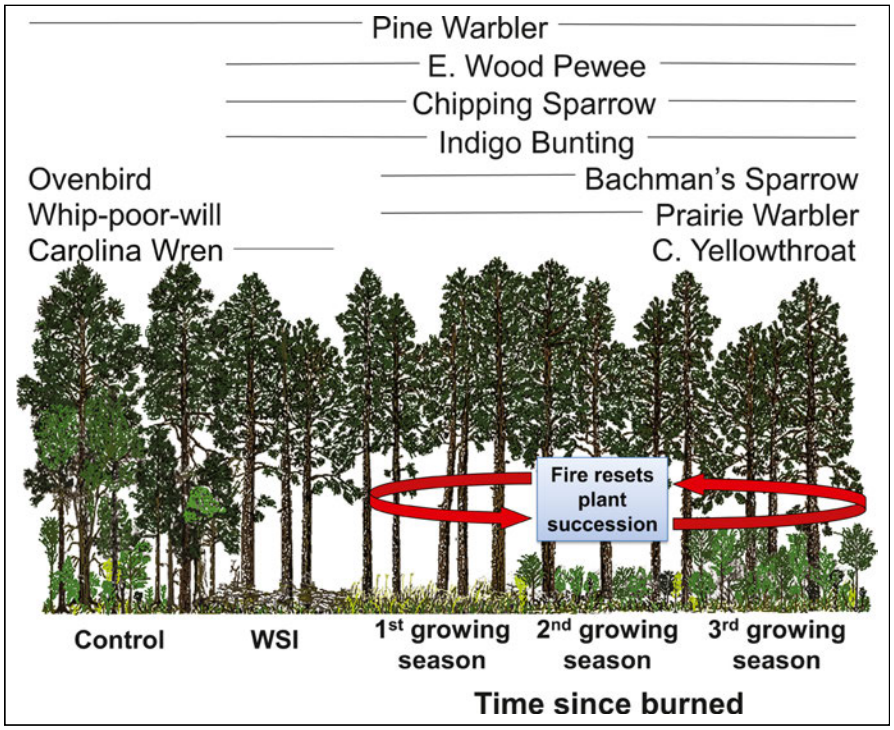


Figure 4. Community response of important bird species to a gradient of forest structures created in shortleaf pine–RCW restoration process that includes wildlife stand improvement (WSI) (thinning from below) and 1-, 2-, and 3-year post-burn conditions in contrast to controls. Bird names along with adjacent lines indicate species presence in the below structural stage. Bird occurrence in diagram is based on study data (1992–1993 and 1999–2000) from the Ouachita National Forest, Arkansas, in Wilson *et al.* (1995) and Masters *et al.* (2002). RCW habitat preferences consist of fire-maintained, thinned forests, which also promote increased songbird, amphibian, and small mammal diversity.

Most CSO habitat is mid-elevation (600–2200 m) mixed-conifer forest that historically experienced frequent (5–25 years) low- to moderate-intensity fires. Historical data and stand reconstruction studies suggest that prior to fire exclusion and large-tree logging, mixed-conifer forests averaged about 160 stems ha^{-1} and ~32% canopy cover, and included areas of denser forest (Safford and Stevens 2017). Since fire exclusion and large-tree logging became commonplace in the early 1900s, many Sierra Nevada mixed-conifer forests now have high surface and ladder fuel loads, with canopy cover exceeding 65% (Safford and Stevens 2017). Most modern-era burns result from wildfires escaping suppression (Miller *et al.* 2009). These wildfires commonly burn large areas with 25–35% stand-replacing effects and, perhaps more importantly, include large and homogenous areas characterized by stand-replacing severity (Stevens *et al*. 2017).

In response to the loss of large trees from past timber harvesting, mechanical fuel reduction treatments are now limited to trees <75 cm DBH on US Forest Service lands. Current CSO management maintains high canopy cover (>70%) within 120-ha protected activity centers (PACs) surrounding nest locations. As a result, PACs are often untreated and vulnerable to stand-replacing fire. For example, the 2014 King Fire severely burned one of the CSO long-term study areas, resulting in the largest owl population reduction over the study's 24-year history (Jones *et al*. 2016). On the basis of observed trends over the past several decades, Stephens *et al*. (2016a) projected that severe wildfire will reduce all potential CSO nesting habitat to <25% canopy cover within 75 years.

Given wildfire and drought trends, a new approach to managing CSO habitat is warranted. Conventional methods focus on maintaining relatively static "reserves" with high canopy cover. Much of the CSO's association with high canopy cover, however, comes from rough model estimates and limited sampling with imprecise field measurements. A study using LiDAR and a complete landscape census found total canopy cover was not as important to the CSO as tall (>32-m) tree cover (Figure 6; North *et al*. 2017). Furthermore, owls avoided cover in the 2–16-m height strata, suggesting that ladder fuel reduction may not be detrimental to CSOs. This more detailed understanding of canopy structure could be used to promote highly heterogeneous forest conditions, providing foraging habitat for prey species while maintaining dense local patches of tall tree cover in moister areas (Gutiérrez *et al*. 2017). Ecologically beneficial fire could also help sustain forests critical to CSO populations (Roberts *et al*. 2011), although such management has attendant risks and less precision than resto-

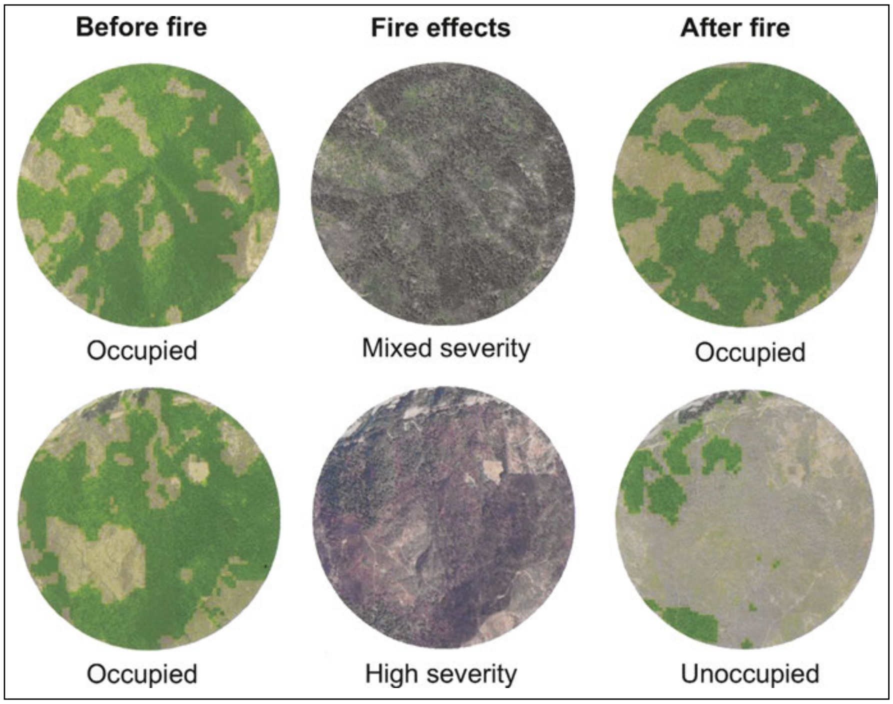


Figure 5. Aerial images of nesting and roosting (NR) forest cover (green shading) before and one year after wildfire in northwest California. The top row shows northern spotted owl (*Strix occidentalis caurina*) response to a mixed-severity fire that did not appreciably alter the pattern of NR forest cover; the territory was not abandoned. In contrast, the bottom row shows high-severity fire, which removed enough NR cover to cause territory abandonment. Occupancy data from Rockweit *et al.* (2017).

ration thinning. Without change, current policies will leave CSO habitat susceptible to severe wildfire, drought, and bark beetle mortality.

Mexican spotted owl

The Mexican spotted owl (*Strix occidentalis lucida*; MSO) inhabits forests and canyonlands in the southwestern US and the highlands of Mexico. Its distribution is driven largely by availability of suitable nesting habitat, which includes mixed-conifer or pine–oak forests with large trees and high canopy cover, and rocky canyons with shaded caves and cliff ledges (USFWS 2012). With recent reductions in timber harvests, high-severity wildfire is now considered by many researchers to be the primary threat to MSO nesting habitat. However, proposed restoration thinning treatments to alleviate risks of high-severity fire can also modify nesting habitat, and the effects of such modifications on MSOs remain largely unknown.

Some habitats used by MSOs in the southwestern US were historically among the most frequently burned forests in western North America (Swetnam and Baisan 2003). Repeated fires maintained relatively open canopy forests with thick-barked, dominant overstory species and rich understory diversity. A century of fire exclusion has led to substantial forest alteration, including increased tree density, canopy cover, and ladder fuels, and a shift in composition to shade-tolerant species in mixed-conifer forests (Margolis and Balmat 2009). A warming climate interacts with heavy fuels in modern forests to shift the fire regime toward infrequent, large, high-severity fires. Because trees in these forests lack adaptations that facilitate regeneration after large, severe fires, such as fire-induced sprouting and cone serotiny (which are also uncommon features in other SO habitats), recovery of MSO habitat can be slow or absent in some areas (Roccaforte *et al.* 2012). Management aimed at restoration of historical ecosystem attributes, including frequent low- to moderate-intensity fire regimes, has proven successful on some Native American lands (Stan *et al.* 2014), and tribal mandates of sustained-yield timber harvesting practices may be consistent with managing for the MSO (Hoagland *et al.* 2017). However, future warming increases uncertainty about maintaining these habitats even if uncharacteristically severe fires can be curtailed (Loehman *et al.* 2018).

Since 1989, management recommendations for MSOs on federal lands have emphasized protection of "Management Territories" or, more recently, PACs (USFWS 2012). Each of these PACs protects a minimum of 243 ha surrounding occupied nests. Secondary recommendations focus on protecting and developing "Recovery Habitat" to provide additional areas similar to nesting habitats, to facilitate population expansion. Desired forest habitat characteristics include large old trees and high canopy cover (USFWS 2012). These areas often also feature high fuel loads, and are therefore susceptible to high-severity wildfire. Thinning and burning is allowed in both PACs and Recovery Habitats, but requires considerable additional justification, analysis, and monitoring (USFWS 2012). Consequently, many managers focus fire-risk reduction activities outside of these areas, leaving occupied nesting sites vulnerable to high-severity fires. As with the CSO, integrating nesting habitat retention with plans to reduce landscape-scale fire risk and restore resilient forests remains one of the greatest challenges facing land managers in the southwestern US (Ganey *et al.* 2017; Wan *et al.* 2018).

Management implications

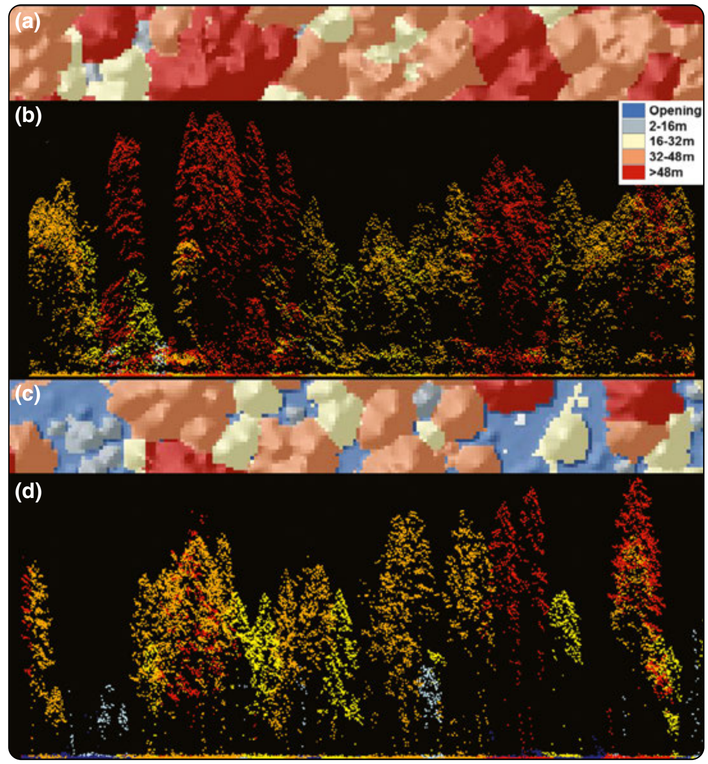
Although US federal law applies to both the southern and western US, the ability to implement effective, large-scale fire management and fuel treatment options varies greatly between the two regions, with differing consequences for the conservation of the RCW and SO. The considerable uncertainty regarding how the SO responds to fire (Ganey *et al.* 2017) likely contributes to a precautionary principle–driven management response (ie limited active fuels management and fire exclusion). There is ample evidence that this approach is likely to be counterproductive over the long term (Stephens *et al.* 2016a). It may be that fire suppression is exerting an equal or greater influence on SO habitat planning with regard to the ESA, rather than the reverse.

In the southern US, managing RCW habitat is a major driving force for fire use, in part because it complements conservation of other important species and improves long-term forest resilience. This is likely because the scale of treatments applied is consistent with RCW nesting and foraging needs. Moreover, despite substantial costs and a risk of homogeneous conditions resulting from overly precise management, prescribed fire, restoration thinning, cavity creation, and translocations have successfully expanded habitat for the RCW. This approach has profited economies and associated species while reducing fire severity, representing critical complementary benefits. Without such complementary benefits, it is unlikely that this management program would be exceeding projected recovery rates.

In the southern US, institutionally prioritized prescribed burning programs and state laws have facilitated the use of fire. RCW populations began to increase soon after the passage of the 1990 Florida Prescribed Fire Act and similar legislation across many southern states. In shortleaf pine forests, restoration thinning is also supported and, when combined with prescribed burning, provides timber resources for local governments and produces positive results for the RCW and associated species.

History and cultural context greatly influence fire management paradigms in each region: the complexity and nuance of ecological fire knowledge integration with Anglo-American forest management took four centuries to evolve in the South (Ryan *et al.* 2013). The integration in the West is comparatively new and is impeded by groups with polarizing views. There are several reasons for this, but the two key issues are lack of trust in agency motives for restoration and lack of willingness on the part of the interested public to prioritize large-scale forest resilience over potential impacts to local SO populations (Stephens *et al.* 2016b). Proactive fire use (prescribed and wildfire) and restoration thinning may be key to the long-term conservation of SO habitat; not only are these treatments appropriate for the majority of SO habitat types, they could improve resilience in forests adapted to frequent fire (Hessburg *et al.* 2015; Stephens *et al.* 2018). SO management could be shifted from a focus on habitat preservation to the dynamism associated with more intact fire regimes, as has occurred in the southern US. Such a shift may result in short- and long-term reductions in total amounts of SO nesting and roosting habitat but will accrue longer term benefits to the remaining habitat in the face of severe wildfires and climate change.

Fire management and ESA habitat requirements are powerful drivers of forest management. We recognize that the habitat needs of the RCW and SO are not strictly analogous (WebTable 1), but in a large portion of the range of both birds, their habitats are adapted to relatively frequent, low- to moderate-intensity fire regimes. A policy of active management with fire and restoration-based thinning has benefited the RCW and overall ecosystem resilience in the southern US; management of the SO in the western US could also benefit from adopting those actions. By providing late-seral habitats in patch sizes and locations where they would historically occur, and by actively restoring fire regimes over large landscapes with successional conditions to support them, it is likely that more SOs, and more of their habitat, would be conserved over the long term. Importantly, the ESA requires that conservation planning be based on the best available scientific data, but in the case of the SO, recent science on SO vulnerability to wildfire has not translated to management. Implementing conservation plans informed by science would entail revising policies, establishing public–private partnerships, and designing endangered species management plans that complement other forest objectives that have enabled RCW recovery. The co-benefits of improved conservation habitat for multiple species, reduced fire severity, and timber revenues have resulted from decades of experience and an active management culture to include more, not less, fire and restoration thinning. Finding ways to



J Kane, U Washington

Figure 6. LiDAR (light detection and ranging) transect images in two CSO nesting areas, showing (a and c) top-down and (b and d) profile views. LiDAR returns are classified into tree approximate objects (TAOs) and in all four images are color-coded by height strata (ranges in meters). The top pair of images from Eldorado National Forest (a and b) show a common nesting condition of fire-suppressed, dense forest with 75% canopy cover. The bottom pair of images (c and d), from a fire-restored location in Sequoia and Kings Canyon National Parks, show that an owl nesting area can have more open forest conditions with 40% canopy cover, if large trees are present.

accelerate these efforts while ensuring SO conservation is a complex task, but such integration would likely improve long-term conservation of the SO and ultimately improve western US forest resilience.

Acknowledgements

We thank J Kane (University of Washington) for providing the LiDAR images in Figure 6, and M Slifko (University of Idaho) for conducting an initial literature review.

References

Bukenhofer GA, Neal JC, and Montague WG. 1994. Renewal and recovery: shortleaf pine/bluestem grass ecosystem and red-cockaded woodpeckers. *J Arkansas Acad Sci* **48**: 243–45.

Conner RN, Rudolph DC, and Walters JR. 2001. The red-cockaded woodpecker: surviving in a fire-maintained ecosystem. Austin, TX: University of Texas Press.

Cram DS, Masters RE, Guthery FS, *et al*. 2002. Northern bobwhite population and habitat response to pine–grassland restoration. *J Wildlife Manage* **66**: 1031–39.

Davis RJ, Hollen B, Hobson J, *et al*. 2016. Northwest Forest Plan – the first 20 years (1994–2013): status and trends of northern spotted owl habitats. Portland, OR: US Department of Agriculture Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-929.

Dugger KM, Forsman ED, Franklin AB, *et al*. 2016. The effects of habitat, climate, and barred owls on long-term demography of northern spotted owls. *Condor* **118**: 57–116.

Gaines WL, Harrod RJ, Dickinson J, *et al*. 2010. Integration of northern spotted owl habitat and fuels treatments in the eastern Cascades, Washington, USA. *Forest Ecol Manag* **260**: 2045–52.

Ganey JL, Wan HY, Cushman SA, and Vojta CD. 2017. Conflicting perspectives on spotted owls, wildfire, and forest restoration. *Fire Ecol* **13**: 146–65.

Guldin JM. 2007. Restoration and management of shortleaf pine in pure and mixed stands – science, empirical observation, and the wishful application of generalities. In: Kabrick JM, Dey DC, and Gwaze D (Eds). Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium. Newtown Square, PA: US Department of Agriculture Forest Service, Northern Research Station. General Technical Report NRS-P-15.

Gutiérrez RJ, Manley PN, and Stine PA (Eds). 2017. The California spotted owl: current state of knowledge. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-254.

Hagmann K, Johnson DL, and Johnson KN. 2017. Historical and current forest conditions in the range of the northern spotted owl in south central Oregon, USA. *Forest Ecol Manag* **389**: 374–85.

Hedrick LD, Bukenhofer GA, Montague WG, *et al*. 2007. Shortleaf-pine restoration in the Ouachita National Forest. In: Kabrick JM, Dey DC, and Gwaze D (Eds). Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium. Newtown Square, PA: US Department of Agriculture Forest Service, Northern Research Station. General Technical Report NRS-P-15.

Hessburg PF, Agee JK, and Franklin JF. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecol Manag* **211**: 117–39.

Hessburg PF, Churchill DJ, Larson AJ, *et al*. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. *Landscape Ecol* **30**: 1805–35.

Hiers JK, Jackson ST, Hobbs RJ, *et al*. 2016. The precision problem in conservation and restoration. *Trends Ecol Evol* **31**: 820–30.

Hiers JK, Walters JR, Mitchell RJ, *et al*. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. *J Wildlife Manage* **78**: 383–93.

Hoagland SJ, Beier P, and Lee D. 2018. Using MODIS NDVI phenoclasses and phenoclusters to characterize wildlife habitat: Mexican spotted owl as a case study. *Forest Ecol Manag* **412**: 80–93.

Jones GM, Gutiérrez RJ, Tempel DJ, *et al*. 2016. Megafires: an emerging threat to old-forest species. *Front Ecol Environ* **14**: 300–06.

Jones GM, Keane JJ, Gutiérrez RJ, and Peery MZ. 2018. Declining old forest species as a legacy of large trees lost. *Divers Distrib* **24**: 341–51.

Keane JJ. 2017. Threats to the viability of California spotted owls. In: Gutiérrez RJ, Manley PN, and Stine PA (Eds). The California spotted owl: current state of knowledge. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-254.

Kobziar LN, Godwin D, Taylor L, and Watts AC. 2015. Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern US. *Forests* **6**: 561–80.

Lesmeister DB, Davis RJ, Singletown PH, and Wiens JD. 2018. Northern spotted owl habitat and populations. In: Spies TA, Stine PA, Gravenmier R, *et al.* (Eds). Science synthesis to inform land management within the Northwest Forest Plan Area, vol 1. Portland, OR: US Department of Agriculture Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-966.

Loehman R, Flatley W, Holsinger L, and Thode A. 2018. Can land management buffer impacts of climate changes and altered fire regimes on ecosystems of the southwestern United States? *Forests* **9**: 192.

Margolis EQ and Balmat J. 2009. Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *Forest Ecol Manag* **258**: 2416–30.

Masters RE. 2007. The importance of shortleaf pine for wildlife and diversity in mixed oak–pine forests and in pine–grassland woodlands. In: Kabrick JM, Dey DC, and Gwaze D (Eds). Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium. Newtown Square, PA: US Department of Agriculture Forest Service, Northern Research Station. General Technical Report NRS-P-15.

Masters RE, Lochmiller RL, and Engle DM. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. *Wildlife Soc B* **21**: 401–11.

Masters RE, Skeen JE, and Whitehead J. 1995. Preliminary fire history of McCurtain County Wilderness Area and implications for red-cockaded woodpecker management. In: Kulhavy DL, Hooper RG, and Costa R (Eds). Red-cockaded woodpecker: species recovery, ecology and management. Nacogdoches, TX: Stephen F Austin University.

Masters RE, Lochmiller RL, McMurry ST, and Bukenhofer GA. 1998. Small mammal response to pine–grassland restoration for red-cockaded woodpeckers. *Wildlife Soc B* **26**: 148–58.

Masters RE, Wilson CW, Cram DS, *et al*. 2002. Influence of ecosystem restoration for red-cockaded woodpeckers on breeding bird and small mammal communities. In: Ford WM, Russell KR, and Moorman CE (Eds). The role of fire in non-game wildlife management and community restoration: traditional uses and new directions. Proceedings of a special workshop. Annual Meeting of the Wildlife Society, Nashville, TN: US Department of Agriculture Forest Service, Northeast Research Station. General Technical Report NE-288.

McKellar AE, Kesler DC, and Walters JR. 2016. Resource selection reflects fitness associations for an endangered bird in restored habitat. *Anim Conserv* **19**: 131–38.

McKellar AE, Kesler DC, Mitchell RJ, *et al*. 2014. Geographic variation in fitness and foraging habitat quality in an endangered bird. *Biol Conserv* **175**: 52–64.

Melvin M. 2015. 2015 National prescribed fire use survey report. Washington, DC: Coalition of Prescribed Fire Councils Inc. Technical Report 02-15.

Miller JD, Safford HD, Crimmins M, and Thode AE. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* **12**: 16–32.

North MP, Kane JT, Kane VR, *et al*. 2017. Cover of tall trees best predicts California spotted owl habitat. *Forest Ecol Manag* **405**: 166–78.

Quinn-Davidson LN and Varner JM. 2011. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. *Int J Wildland Fire* **21**: 210–18.

Roberts SL, van Wagtendonk JW, Miles AK, and Kelt DA. 2011. Effects of fire on spotted owl site occupancy in a late-successional forest. *Biol Conserv* **144**: 610–19.

Roccaforte JP, Fulé PZ, Chancellor WW, and Laughlin DC. 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. *Can J Forest Res* **42**: 593–604.

Rockweit JT, Franklin AB, and Carlson PC. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. *Ecology* **98**: 1574–82.

Ryan KC, Knapp EE, and Varner JM. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Front Ecol Environ* **11**: e15–24.

Safford H and Stevens J. 2017. Natural range of variation for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. Albany, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-256.

Schultz C, Huber-Stearns H, McCaffrey S, *et al*. 2018. Prescribed fire policy barriers and opportunities: a diversity of challenges and strategies across the West. Fort Collins, CO: Colorado State University. Public Lands Policy Group Practitioner Paper 2.

Singleton PH, Lehmkuhl JF, Gaines WL, and Graham SA. 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. *J Wildlife Manage* **74**: 285–94.

Sparks JC, Masters RE, Engle DM, *et al*. 1998. Effects of late growing-season and late dormant season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *J Veg Sci* **9**: 133–42.

Stan AB, Fulé PZ, Ireland K, *et al*. 2014. Modern fire regime resembles historical fire regime in a ponderosa pine forest on Native American lands. *Int J Wildland Fire* **23**: 686–97.

Stephens SL, Collins BM, Biber E, and Fulé PZ. 2016b. US federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* **7**: e01584.

Stephens SL, Collins BM, Fettig CJ, *et al*. 2018. Drought, tree mortality and wildfire in forests adapted to frequent fire. *BioScience* **68**: 77–88.

Stephens SL, Miller JD, Collins BM, *et al*. 2016a. Wildfire impacts on California spotted owl nesting habitat in the Sierra Nevada. *Ecosphere* **7**: e01478.

Stevens JT, Collins BM, Miller JD, *et al*. 2017. Changing spatial patterns of stand-replacing fire in California mixed-conifer forests. *Forest Ecol Manag* **406**: 28–36.

Swetnam TW and Baisan CH. 2003. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and southwestern United States. In: Veblen TT, Baker WL, Montenegro G, *et al*. (Eds). Fire and climate change in temperate ecosystems of the western Americas. New York, NY: Springer Books.

Trainor AM, Walters JR, Urban DL, *et al*. 2013. Evaluating the effectiveness of a Safe Harbor Program for connecting wildlife populations. *Anim Conserv* **16**: 610–20.

USFWS (US Fish and Wildlife Service). 2003. Recovery plan for the red-cockaded woodpecker (*Picoides borealis*). Atlanta, GA: USFWS.

USFWS (US Fish and Wildlife Service). 2012. Mexican spotted owl recovery plan, first revision (*Strix occidentalis lucida*). Albuquerque, NM: USFWS.

Wan HY, Cushman SA, Ganey JL, *et al*. 2018. Managing for emerging threats to spotted owls. *J Wildlife Manage* **82**: 682–97.

Wiens JD, Anthony RG, and Forsman ED. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monogr* **185**: 1–50.

Wilson CW, Masters RE, and Bukenhofer GE. 1995. Breeding bird response to pine–grassland community restoration for red-cockaded woodpeckers. *J Wildlife Manage* **59**: 56–67.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2076/suppinfo

[8]*USDA Forest Service, Southern Research Station, Hot Springs, AR;* [9]*USDA Forest Service, Pacific Northwest Research Station, Wenatchee, WA;* [10]*Tall Timbers Research Station, Tallahassee, FL;* [11]*USDA Forest Service, Rocky Mountain Research Station, Missoula, MT;* [12]*USDA Forest Service, Pacific Southwest Research Station, Davis, CA;* [13]*College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, WI;* [14]*Environment and Climate Change Canada, Saskatoon, Canada;* [15]*USDA Forest Service, Poteau Ranger District, Waldron, AR;* [16]*Emeritus Scientist, USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR*