Forest restoration limits megafires and supports species conservation under climate change

Gavin M Jones[1,2*], Alisa R Keyser[3,4], A Leroy Westerling[3], W Jonathan Baldwin[3], John J Keane[5], Sarah C Sawyer[6], John DJ Clare[2], RJ Gutiérrez[2,7], and M Zachariah Peery[2]

Climate change and fire suppression have altered disturbance regimes in forest ecosystems globally. In the seasonally dry forests of western North America, large-scale restoration may reduce severe fire and increase forest resilience but also eliminate existing habitat for sensitive wildlife species. We modeled bioregional-scale effects of forest restoration on future severe fire activity and occupancy dynamics of an old-forest species declining in abundance, the spotted owl (*Strix occidentalis*), in the Sierra Nevada mountains of California. Our findings suggest restoring historical forest structure may mitigate severe fire activity as the climate warms, particularly when restoration occurs in owl habitat. On average, benefits provided by restoration to owls (reduced severe fire) were found to exceed potential costs (direct habitat alteration) by mid-century. However, the magnitude and direction of restoration trade-offs varied spatially, which informs restoration planning. When large, old trees are maintained, forest restoration can provide co-benefits to old-forest species and forest ecosystem resilience under climate change.

Front Ecol Environ 2022; 20(4): 210–216, doi:10.1002/fee.2450

Climate change is profoundly altering forest distribution and disturbance regimes worldwide (Seidl *et al*. 2017). Humans also continue to shape forests globally. In the seasonally dry forests of western North America, a century of fire suppression and large-tree logging has transformed forest structure away from historical conditions (Collins *et al*. 2017). Forests that were historically open with low tree densities now have high densities of small- and medium-sized trees and a deficit of large trees (Safford and Stevens 2017). These altered forest structures combined with climate change have led to larger, more severe fires (Steel *et al*. 2015; Westerling 2016) and widespread drought-related tree mortality (Fettig *et al*. 2019), with substantial impacts to humans and forests. These increasingly common "mega-disturbance" events pose a major threat to forest persistence, and to forest species and ecosystem services (Stephens *et al*. 2018; Wood and Jones 2019).

Landscape-scale forest restoration may increase seasonally dry forest ecosystem resilience (Stephens *et al*. 2020). Thinning and prescribed/managed fire can reduce accumulation and increase heterogeneity of fuels (Knapp *et al*. 2017); promote development of large, fire-resistant trees (Agee and Skinner 2005); alter fire behavior and lower severe fire likelihood (Tubbesing *et al*. 2019); and reduce risk of drought-related tree mortality (Bradford and Bell 2016). However, restoration alters forests inhabited by wildlife that depend on large, old trees, high canopy cover, and complex vertical structure (Tempel *et al*. 2014). Concern over wildlife habitat has limited the pace and scale of forest restoration efforts (North *et al*. 2015a). Thus, restoring seasonally dry forest ecosystems while safeguarding vulnerable populations of old-forest species presents a conservation conundrum: how can restoration occur without jeopardizing species that use "departed" forest conditions (Peery *et al*. 2017)?

Solving this conundrum involves understanding whether or how the potential negative short-term impacts of restoration on old-forest species can be outweighed by reducing habitat loss to future severe wildfires. To address this question, we developed a novel bioregional-scale severe fire model (hereafter, "fire model") that generates robust, fine-grain (30-m) predictions of future severe fire activity linked to climate and vegetation (eg fuels) conditions. We coupled the severe fire model with a spatial occupancy model ("occupancy model") to evaluate relative and scale-dependent effects of restoration and severe fire on a focal old-forest species, the spotted owl (*Strix occidentalis*) (Figure 1), across the Sierra Nevada mountains of California (~120,000 km^2). In doing so, we assessed two central questions about bioregional-scale forest restoration. First, can restoration effectively reduce future severe fire activity in a changing climate? Second, can restoration provide co-benefits to old-forest species?

Methods

We fit the fire and occupancy empirical models independently over the period for which common historical data existed (1984–2015), then linked them together during forward simulations of restoration- and climate-induced changes in patterns of severe fire and owl occupancy dynamics (through 2064; WebFigure 1). Climate-change effects in the fire model

---

[1] *US Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station, Albuquerque, NM* *(*gavin.jones@usda.gov*);* [2] *Department of Forest & Wildlife Ecology, University of Wisconsin–Madison, Madison, WI;* [3] *Sierra Nevada Research Institute, University of California–Merced, Merced, CA;* [4] *Department of Biology, University of New Mexico, Albuquerque, NM;* [5] *USDA Forest Service, Pacific Southwest Research Station, Davis, CA;* [6] *USDA Forest Service, Pacific Southwest Region, Vallejo, CA;* [7] *Department of Fisheries, Wildlife & Conservation Biology, University of Minnesota, St Paul, MN*


D Hofstadter

Figure 1. An adult male spotted owl (*Strix occidentalis*) located in Sequoia and Kings Canyon National Parks in the southern Sierra Nevada, California.

were represented using the Representative Concentration Pathway 8.5 (RCP8.5) and the global circulation model (GCM) CNRM-CM5. We chose RCP8.5 because it reflected a "business-as-usual" emissions scenario; however, we considered only projections through mid-century, when the divergence between RCP8.5 and other more optimistic scenarios is modest compared to the final decades of the 21st century. The CNRM-CM5 model typically reflects moderate to warmer conditions than other commonly used GCMs and therefore represents a "higher end" warming scenario that produced greater future fire activity in our model. The fire model produced annual realizations of severe fire occurrence across the Sierra Nevada through mid-century (2064) that fed into the occupancy model. The behavior of both models was linked to a factorial design that varied the extent and location of restoration activities (changes to "fire regime condition class" [FRCC]; see WebPanel 1) across the landscape (Westerling 2018). By using changes in FRCC to reflect effects of restoration activities (eg fuels reduction), we assume that such activities, however implemented, can return forests to their historical range of variability.

Restoration (or "treatment") was simulated in areas without substantial mechanical operability constraints on non-subalpine federal lands (hereafter "treatable" lands; Collins *et al.* 2010; North *et al.* 2015a), with total treatment extent varying in equal intervals (20%, 30%, 40%, 50%, and 60% of the Sierra Nevada bioregion treated). Treatable lands (approximately 60,000 km^2) excluded wilderness areas, inaccessible areas, and other sensitive areas that cannot be treated under current regulatory frameworks. The highest treatment level (60%) represented ~90% of the total "treatable" area in the Sierra Nevada. A second set of treatment scenarios maintained the same total treatment extent but excluded treatment from spotted owl territories. Restoration treatments were introduced into the fire and owl occupancy models in year one of the forward projection and were implemented "instantaneously", meaning that treatment effects were immediate. Consequences of this simplifying assumption likely include an overestimation of the short-term effects of treatments (because they cannot be implemented across such large scales immediately) both in terms of their ability to reduce severe fire behavior and their effects on owl habitat. We evaluated the effect of our assumptions about how treatments would alter owl habitat by conducting a sensitivity analysis in which we varied the extent to which treatment modified habitat within the occupancy model ("no habitat alteration", "weak habitat alteration", "strong habitat alteration"; see WebPanel 1).

Fire model

We developed a novel multiscale fire model using remotely sensed burn severity data (WebFigure 1; WebPanel 1). We defined high severity as 90% basal area killed (hereafter "stand-replacing" or "severe" fire). The multiscale fire model consisted of large-scale (~6-km) and fine-scale (30-m) "submodels" that interacted to produce spatial realizations of severe fire. We developed the large-scale submodel by fitting a spatially explicit logistic regression model on a ~6-km grid to estimate the monthly probabilities of the occurrence of at least one fire >400 ha as a function of topography, human population, vegetation fraction, and climate (WebPanel 1; Westerling 2018). Then, for each fire >400 ha, the probability of a minimum threshold (>50 ha) burning in a stand-replacing fire was estimated by fitting a logistic regression with climate covariates. To estimate conditional extent of stand-replacing burned area, we fitted a generalized Pareto distribution with climate and FRCC covariates for each fire with >50 ha stand-replacing burned area (WebFigure 2). We used this model system to simulate large-scale stand-replacing burned area for each climate and treatment scenario (see WebPanel 1).

We developed the fine-scale submodel (a mapping algorithm) by selecting 20 fires for model training that yielded the most complete coverage of latitude, year, ignition month, fire size, and severity in the Sierra Nevada (WebTable 1). Random Forests, a machine-learning algorithm, was used to predict occurrence of stand-replacing fire pixels (30 m) on the landscape as a function of topography, vegetation type, and fire size, and a spatial allocation algorithm was developed to link the large- and fine-scale model to assign severely burned pixels to the 30-m landscape surface using a Monte Carlo simulation. Starting with a randomly assigned ignition point (using a uniform distribution) within the large-scale modeling pixel, the algorithm assigned 30-m pixels as stand-replacing fire (true/false) in an iterative fashion based on the modeled fine-scale probability surface until the predicted fire size from the large-scale model was reached. This procedure was repeated for the entire suite of models 100 times for each unique treatment scenario, and each individual simulation was delivered to the spatial occupancy model for spotted owls (see below). Full model description, evaluation, accuracy and error assessments, and allocation examples are provided in WebPanel 1.

Occupancy model

We modeled spotted owl territory (hereafter, "site") occupancy using a Bayesian spatial occupancy model (Chandler *et al.* 2015) with detection/non-detection data from n = 275 owl survey areas collected between 1993 and 2011 (WebFigure 1; Tempel *et al.* 2016). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites representing nearly all suitable habitat in the Sierra Nevada (see Jones 2019). Site extinction probability and detection probability were modeled as a function of forest structural variables representing the proportion of each owl site containing large trees (quadratic mean stand diameter ≥61 cm) and high canopy closure (≥70% canopy cover), and large trees and medium canopy closure (40–70% canopy cover), respectively (WebFigure 1; WebPanel 1; Jones *et al.* 2018).

We combined output from the multiscale fire model with 500 multivariate posterior draws of parameter distributions to project the spotted owl population forward over the period 2012–2064 while incorporating the full parameter uncertainty (WebFigure 1; WebPanel 1). Simulated treatment effects within individual owl territories were modeled by modifying forest structure covariate values (see above) in a manner consistent with expected changes in horizontal canopy structure due to treatments (ie reducing fuel continuity by reducing canopy cover). Severe fire effects were modeled using an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a before–after control–impact natural experiment (WebFigure 1; Jones *et al.* 2016). In forward projections of the model system, we focused on reporting expected (mean) outcomes to guide discussion of management implications, but we also acknowledge and discuss the role of prediction uncertainty in interpretation of results. For full model description and reporting, see WebPanel 1.

Results

In the absence of forest restoration treatments, severe fire was predicted to burn an average of ~24,000 ha/year (maximum annual prediction 235,000 ha) in the Sierra Nevada, or a total of ~720,000 ha (range 453,585–1,068,009 ha over 100 simulations) during the years 2035–2064 (Figure 2a; WebFigure 2). Restoration changed the expected severe fire area by a minimum of −6.8% (a reduction of 45,930 ha of severe fire) to −55.8% (a reduction of 257,880 ha of severe fire) over the period 2035–2064 depending on treatment extent and location (Figure 2, b and c). However, uncertainty in annual decreases of severe fire extent across the stochastic fire replicates resulting from treatment effects was large (orders of magnitude; WebFigure 2). More extensive treatments consistently reduced expected severe fire area across the landscape, and this effect was proportionally larger when treatments were included in owl territories (Figure 2c; WebFigure 2). For example, treating 60% of the landscape but restricting treatments to occur outside of owl territories reduced severe fire area by 29%, whereas allowing treatments to occur in owl territories reduced severe fire by nearly 56%. Moreover, higher levels of treatment (eg >40% of the Sierra Nevada) appeared to reduce expected severe fire activity even in years when climate models produced extreme fire conditions, most notably when treatments were included in owl territories (WebFigure 3).

The degree to which owl territories were exposed to local extinction-inducing severe fire depended on the spatial extent of simulated restoration treatments and whether treatments were allowed within owl territories (WebFigure 3). Forest restoration has the potential to provide expected net benefits to spotted owls inhabiting the Sierra Nevada by the mid-21st century under all scenarios considered (Figure 3). When treatments were excluded from owl territories (Figure 3a), owl populations experienced expected net benefits that increased with more treatment, but the long-term benefits were lower compared to scenarios where owl territories received treatments (Figure 3, b–d). Owls were expected to benefit most when treatments occurred within territories and when treatments avoided modifying large tree/high canopy cover forest (Figure 3b). When treatments occurred inside territories and owl habitat was modified (Figure 3, c and d), a downward pressure was imposed on owl populations over initial years of the simulation but varied in degree depending on assumptions made about the extent to which treatment directly altered owl habitat. The expected net costs of treatment were offset by the cumulative benefits of reduced severe fire exposure by the 2040s and 2050s for all treatment scenarios (Figure 3, c and d). Importantly, the scenarios involving treatment in owl territories (and therefore simulated changes to forest structure in the owl model) introduced additional variability into the model system because of uncertainty associated with effects of habitat alteration, which resulted in wider prediction intervals (WebFigure 4).

When averaged across the entire Sierra Nevada, expected treatment effects on population occupancy were apparent but modest in magnitude (eg –0.01 to +0.04; Figure 3). However, larger expected effects that varied considerably in space were apparent at the territory scale (eg ±0.30; Figure 4; WebFigure 4). When treatments were excluded from owl territories, there

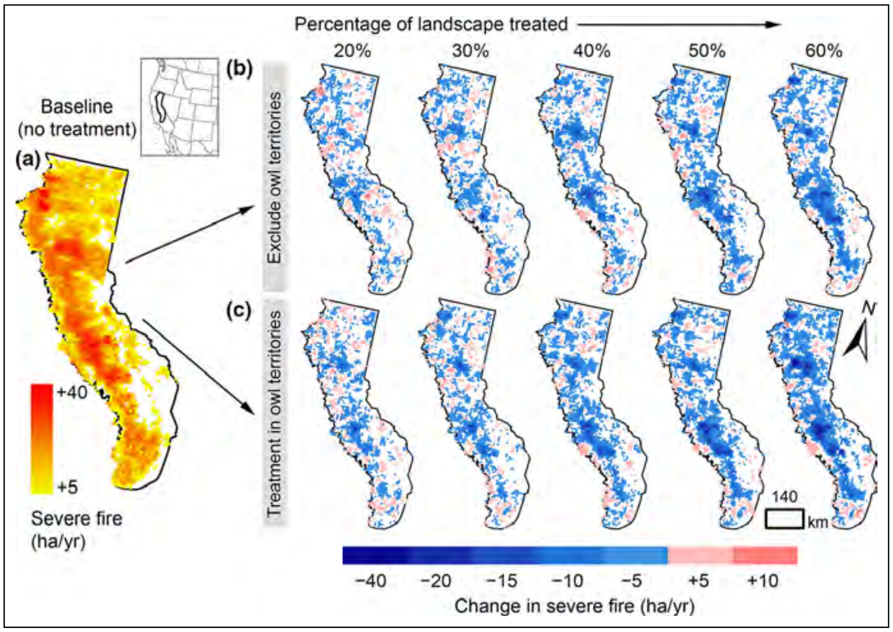

Figure 2. Severe fire activity in the Sierra Nevada is expected to increase by mid-century but was altered by treatment location and extent. (a) Mean annual increase in severe fire (90% basal area killed) over a mid-century climate period (2035–2064) under the baseline no-treatment (0%) scenario; (b) expected effects of treatment on severe fire activity when treatments excluded from spotted owl (*Strix occidentalis*) territories at varying levels of treatment extent (increasing from left to right); (c) expected effects of treatment on severe fire activity when treatments are included in owl territories. The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in severe fire are not all equal.

were relatively uniform expected benefits to mid-century territory occupancy compared to a no-treatment scenario (eg –0.06 to +0.11; range of 99th percentile of values; Figure 4b). These benefits grew (eg –0.07 to +0.20) when treatments were simulated to occur within owl territories but were assumed to avoid modifying large tree/high canopy cover forest (Figure 4c). When simulated treatments were applied in owl territories and treatment was assumed to modify owl habitat, strong regional-scale patterns in trade-offs emerged (eg –0.11 to +0.22; Figure 4d). Broad-scale patterns in trade-offs were driven by regionally varying treatment effects to owl habitat estimated from occupancy data (WebTable 2) and spatial variation in future severe fire exposure (Figure 2).

Discussion

Our analysis indicates that climate change will result in increased severe fire extent in the Sierra Nevada through mid-century, but that bioregional-scale restoration has the potential to offset this increase. Restoration also appears to support spotted owl conservation, suggesting co-benefits between forest resilience and old-forest species conservation objectives. Owls experienced relatively large expected benefits from treatment in areas where treatments considerably reduced future severe fire (Figures 2 and 4). Conversely, areas where owls experienced net negative treatment effects (eg southern Sierra Nevada) were characterized by lower future exposure to severe fire, more pronounced direct treatment impacts on predicted territory extinction rates, or both (Figures 2 and 4; WebTable 2). When treatments occurred in owl territories but were assumed not to alter key owl habitat, benefits were nearly universal and larger than other scenarios (Figures 3b and 4b) with less prediction uncertainty (WebFigure 4). Optimal management strategies might therefore entail a mixed approach where treatments are excluded from owl territories or designed to avoid high-quality owl habitat in certain regions where expected negative impacts of treatment are greatest, and included elsewhere where expected direct effects

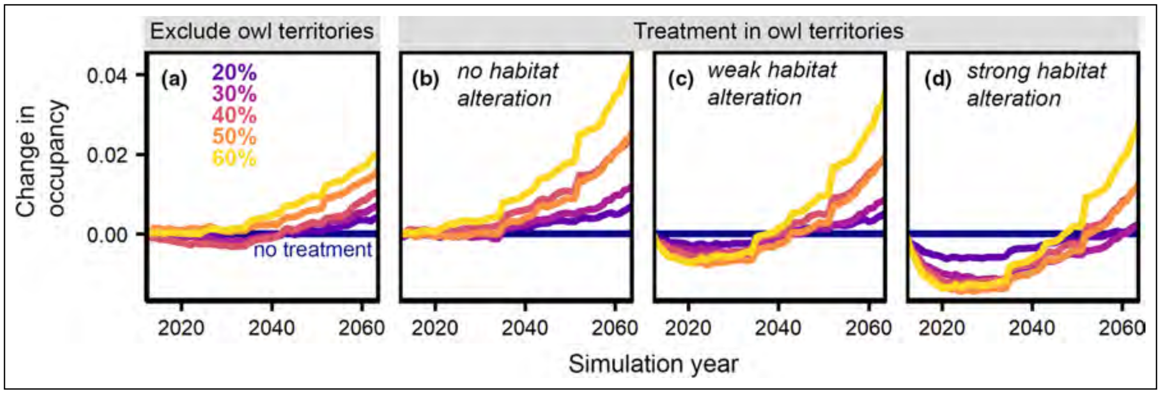

Figure 3. Sierra Nevada-wide site occupancy trajectories for each treatment scenario relative to the baseline no-treatment scenario (dark blue line). (a) Occupancy when treatments are excluded from owl territories; (b–d) occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (no habitat alteration, weak habitat alteration, strong habitat alteration; see WebPanel 1). Trajectories represent means across 50,000 simulations. For full uncertainty across stochastic replicates, see WebFigure 4.

of treatment are less negative or are positive (Figure 4).

Landscape fuel treatments will never stop a fire but they can change how fires burn, thereby mediating fire-related tree mortality and resulting effects to species and ecosystems. Both model simulations (eg Collins *et al.* 2011; Tempel *et al.* 2015) and empirical studies (eg Safford *et al.* 2012; Tubbesing *et al.* 2019) have suggested landscape fuel treatments are effective in altering fire behavior and can greatly reduce severe fire activity in seasonally dry forests. In accordance with these findings, our results suggest that returning forest conditions to within the historical range of variability reduces expected high-severity burned area at a bioregional scale (Figure 2; WebFigure 2). Although this was an expectation for fuel-limited seasonally dry forest ecosystems, concern exists that fuels management may be inadequate to modify severe wildfire in a changing climate when extreme fire conditions become more common on an annual basis (Schoennagel *et al.* 2017). Indeed, we observed some degree of increase in severe fire activity under all treatment scenarios with climate warming (eg WebFigure 3). However, as more of the landscape was treated, expected future severe fire extent was reduced (Figure 2) even in years with extreme fire weather, an effect that was particularly notable when larger proportions of landscapes were treated (eg >40%; WebFigure 3). At high levels of treatment extent, expected increases in severe fire activity were completely offset by expected reductions in severe fire due to treatment in some areas (Figures 2 and 4), although real changes could be much larger or smaller because of prediction uncertainty (WebFigure 2). These results suggested that large-scale forest restoration efforts have the potential to meaningfully alter severe fire activity and reduce fire-related risk to spotted owls in a changing climate.

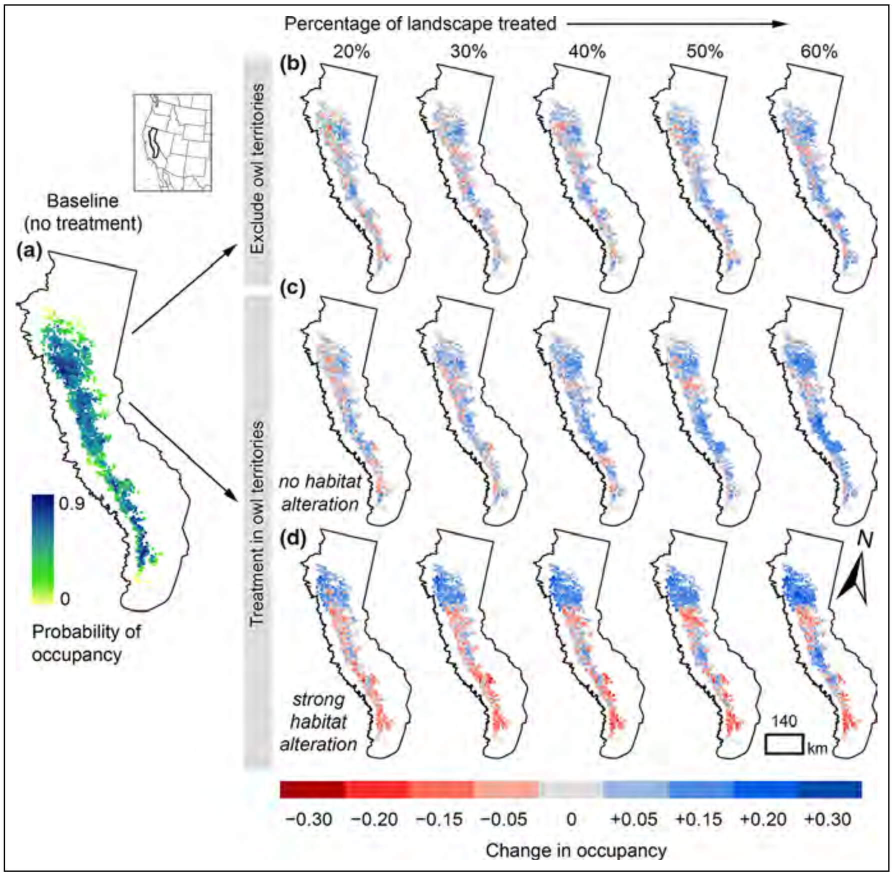

Figure 4. Spatial variation in effects of the location and extent of fuel treatments on spotted owl site occupancy by mid-century (2064). (a) Expected mid-century site occupancy under a no-treatment scenario; (b) difference in occupancy when treatments are implemented but are excluded from owl territories at varying levels of treatment extent (increasing from left to right); (c, d) difference in occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (see WebFigure 4 for "weak habitat alteration"). Values represent the average across 50,000 simulations (WebPanel 1). The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in occupancy are not all equal.

Although our model offers a robust starting point for forecasting wildfire and population dynamics across this large bioregion, we made simplifying assumptions to make our model tractable. We assumed stationarity in fire–climate relationships over the forward simulation period, which may become less likely further into the future (Parks *et al.* 2016; Littell *et al.* 2018). Vegetation (ie fuels) within our models were static, and treatments were introduced once at the beginning of forward simulations and assumed to be maintained when in reality treatments would take decades to implement and maintenance would be variable. As such, effects of treatments to owls via direct habitat alteration only occurred once, whereas maintenance of treated areas could result in recurring effects. We also assumed that treatment applications varying in their direct effects to owl habitat (eg Figure 3, b–d) would all be equally effective at altering fire behavior, which is unlikely; in addition, we only considered how the expected changes in forest structure resulting from treatment interacted with our models, not potential effects of the treatment method itself (eg prescribed burning, hand-removal of small trees, thinning and/or logging of medium-sized trees). Finally, treatments were simulated randomly across the landscape because the fine-scale spatial patterning would not influence our statistical fire model, but strategic placement in areas with high baseline fire risk can make treatments more effective at lower treatment extents in the real world (McGarigal *et al.* 2018; Tubbesing *et al.* 2019).

Forest restoration currently occurs below desired levels because of legal, administrative, and financial constraints (Collins *et al.* 2010; North *et al.* 2015a). Increasing the pace and scale of restoration to levels that will alter fire activity at the bioregional scale (Figure 2) will require greater funding, more effective integration of silvicultural approaches with prescribed and managed fire to increase treatment extent at the landscape scale (North *et al.* 2012, 2021; York *et al.* 2021), and a recognition that while short-term costs may be high, they will be eclipsed by future costs under the status quo (North *et al.* 2015b). Over the past several decades, treatments have sometimes been implemented within portions of owl territories (~300–600 ha), but generally not within the "core" areas of the territory corresponding to management units called "protected activity centers" (PACs; ~121 ha). Our study treated the entire territory as the management unit (including the smaller PAC) and therefore we did not estimate potential effects of treatments at the PAC scale alone. Previous syntheses have recommended lower-intensity fuel treatments at the scale of the activity center (nest, roost) to reduce potential habitat-related negative effects to owls (Peery *et al.* 2017). Our results suggest that implementing treatments within owl territories could have an outsized effect on reducing future severe fire activity in the Sierra Nevada compared to treating the same area outside of owl territories (Figure 2).

Dry forest ecosystems, like those in the Sierra Nevada, face an increased probability of disturbance-initiated transition to non-forest landscapes without active management to restore ecologically appropriate forest conditions and reduce accumulated fuels (Stephens *et al.* 2020). Broadening forest restoration efforts in dry forests has the potential to enhance forest resilience and reduce risk of severe fire that negatively impacts forests, carbon storage, water supply, air quality, and local communities as the climate changes (Wood and Jones 2019; Stephens *et al.* 2020). As a complement to previous mechanistic work that examined forest restoration trade-offs at smaller spatial scales (Scheller *et al.* 2011; Tempel *et al.* 2015), our work suggests bioregional-scale forest restoration appears to be largely compatible with conservation of old-forest-dependent wildlife species.

Fire-suppressed forests that are well outside their historical range of variability are prone to severe fire and are also preferred by many forest-dependent wildlife species. Treatments within these forests are likely to reduce severe fire extent and therefore provide greater long-term benefits to species like the spotted owl. Treatments that increase landscape-scale heterogeneity are likely to provide shorter-term benefits as well by promoting habitat for key prey species (Hobart *et al.* 2019; Kramer *et al.* 2021). Additional targeted research that narrows uncertainties about the effects of different types of treatments (eg hand removal, pre-commercial thinning, prescribed fire) on species habitat will be needed to better inform planning. However, to minimize the effects of fuel reduction and forest restoration on spotted owls and other old-forest species, including the fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*), it is essential that large, old trees and core nesting/roosting areas within territories be maintained (Jones *et al.* 2018). When large, old trees are maintained and recruited, fuel reduction and forest restoration in the Sierra Nevada can benefit both old-forest species, forest ecosystem resilience, and people in a changing climate.

Acknowledgements

We thank MG Turner, B Zuckerberg, VC Radeloff, and SL Stephens for insightful comments on an earlier draft that improved the paper. R Chandler and P Howell provided helpful discussion about spatial occupancy models; M Meyer provided advice on how forest restoration treatments affect forest structure; and JA Fites-Kaufmann helped us think about how fire creates ecological change. ARK and ALW thank W Sinclair for assistance developing the first version of the fine-scale allocation algorithm. The authors gratefully acknowledge the Multi-Environment Computer for Exploration and Discovery (MERCED) cluster at the University of California–Merced, which was funded by US National Science Foundation grant #ACI-1429783. GMJ thanks L Michael and C Koch from the University of Wisconsin–Madison Center for High-Throughput Computing (CHTC) for providing logistical support to complete owl population projections. JDJC was supported by National Aeronautics and Space Administration #NNX16A061H. This work was funded by the US Department of Agriculture (USDA) Forest Service Region 5, USDA Forest Service Pacific Southwest Research Station, the US Fish and Wildlife Service, and the California Energy Commission. The findings and conclusions in this article are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Government of any product or service.

References

Agee JK and Skinner CN. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecol Manag* **211**: 83–96.

Bradford JB and Bell DM. 2016. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. *Front Ecol Environ* **15**: 11–17.

Chandler RB, Muths E, Sigafus BH, *et al.* 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *J Appl Ecol* **52**: 1325–33.

Collins BM, Fry DL, Lydersen JM, *et al.* 2017. Impacts of different land management histories on forest change. *Ecol Appl* **27**: 2475–86.

Collins BM, Stephens SL, Moghaddas JJ, and Battles JJ. 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. *J Forest* **108**: 24–31.

Collins BM, Stephens SL, Roller GB, and Battles JJ. 2011. Simulating fire and forest dynamics for a landscape fuel treatment project in the Sierra Nevada. *Forest Sci* **57**: 77–88.

Fettig CJ, Mortenson LA, Bulaon BM, and Foulk PB. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. *Forest Ecol Manag* **432**: 164–78.

Hobart BK, Jones GM, Roberts KN, *et al*. 2019. Trophic interactions mediate the response of predator populations to habitat change. *Biol Conserv* **238**: 108217.

Jones GM. 2019. Fire, forest restoration, and spotted owl conservation in the Sierra Nevada, CA. Madison, WI: University of Wisconsin-Madison.

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.

Knapp EE, Lydersen JM, North MP, and Collins BM. 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *Forest Ecol Manag* **406**: 228–41.

Kramer A, Jones GM, Whitmore SA, *et al*. 2021. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. *Forest Ecol Manag* **479**: 118576.

Littell JS, McKenzie D, Wan HY, and Cushman SA. 2018. Climate change and future wildfire in the western United States: an ecological approach to nonstationarity. *Earths Future* **6**: 1097–11.

McGarigal K, Mallek M, Estes B, *et al*. 2018. Modeling historical range of variability and alternative management scenarios in the upper Yuba River watershed, Tahoe National Forest, California. Fort Collins, CO: US Department of Agriculture Forest Service.

North MP, Collins BM, and Stephens S. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *J Forest* **110**: 392–401.

North MP, Brough A, Long J, *et al*. 2015a. Constraints on mechanized treatment significantly limit mechanical fuels reduction extent in the Sierra Nevada. *J Forest* **113**: 40–48.

North MP, Stephens SL, Collins BM, *et al*. 2015b. Reform forest fire management: agency incentives undermine policy effectiveness. *Science* **349**: 1280–81.

North MP, York RA, Collins BM, *et al*. 2021. Pyrosilviculture needed for landscape resilience of dry western United States forests. *J Forest* **119**: 520–44.

Parks SA, Miller C, Abatzoglou JT, *et al*. 2016. How will climate change affect wildland fire severity in the western US? *Environ Res Lett* **11**: 035002.

Peery MZ, Manley PN, Stine PA, *et al*. 2017. Synthesis and interpretation of California spotted owl research within the context of public forest management. 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.

Safford HD and Stevens JT. 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.

Safford HD, Stevens JT, Merriam K, *et al*. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *Forest Ecol Manag* **274**: 17–28.

Scheller RM, Spencer WD, Rustigian-Romsos H, *et al*. 2011. Using stochastic simulation to evaluate competing risks of wildfires and fuels management on an isolated forest carnivore. *Landscape Ecol* **26**: 1491–504.

Schoennagel T, Balch JK, Brenkert-Smith H, *et al*. 2017. Adapt to more wildfire in western North American forests as climate changes. *P Natl Acad Sci USA* **114**: 4582–90.

Seidl R, Thom D, Kautz M, *et al*. 2017. Forest disturbances under climate change. *Nat Clim Change* **7**: 395–402.

Steel ZL, Safford HD, and Viers JH. 2015. The fire frequency–severity relationship and the legacy of fire suppression in California forests. *Ecosphere* **6**: 8.

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, Westerling ALR, Hurteau MD, *et al*. 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Front Ecol Environ* **18**: 354–60.

Tempel DJ, Gutiérrez RJ, Battles JJ, *et al*. 2015. Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. *Ecosphere* **6**: 261.

Tempel DJ, Gutiérrez RJ, Whitmore SA, *et al*. 2014. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. *Ecol Appl* **24**: 2089–106.

Tempel DJ, Keane JJ, Gutiérrez RJ, *et al*. 2016. Meta-analysis of California spotted owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: habitat associations and their implications for forest management. *Condor* **118**: 747–65.

Tubbesing CL, Fry DL, Roller GB, *et al*. 2019. Strategically placed landscape fuel treatments decrease fire severity and promote recovery in the northern Sierra Nevada. *Forest Ecol Manag* **436**: 45–55.

Westerling AL. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philos T Roy Soc B* **371**: 20150178.

Westerling AL. 2018. Wildfire simulations for California's Fourth Climate Change Assessment: projecting changes in extreme wildfire events with a warming climate. Sacramento, CA: California Energy Commission.

Wood CM and Jones GM. 2019. Framing management of social–ecological systems in terms of the cost of failure: the Sierra Nevada, USA as a case study. *Environ Res Lett* **14**: 105004.

York RA, Noble H, Quinn-Davidson LN, and Battles JJ. 2021. Pyrosilviculture: combining prescribed fire with gap-based silviculture in mixed-conifer forests of the Sierra Nevada. *Can J Forest Res* **51**: 781–91.

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.2450/suppinfo