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Accelerated forest restoration may benefit spotted owls through landscape complementation

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Abstract

Animals often rely on the presence of multiple, spatially segregated cover types to satisfy their ecological needs; the juxtaposition of these cover types is called landscape complementation. In ecosystems that have been homogenized because of human land use, such as fire-suppressed forests, management activities have the potential to increase the heterogeneity of cover types and, therefore, landscape complementation. We modeled changes to California spotted owl (*Strix occidentalis occidentalis*) nesting/roosting habitat, foraging habitat and habitat co-occurrence (i.e. landscape complementation) within a 971 245-ha forest landscape restoration project area, the Tahoe-Central Sierra Initiative (TCSI) landscape, through mid-century as a function of fuels reduction, fire and climate change. Compared to a minimal management scenario, accelerated management within the TCSI landscape was predicted to increase the number of potential 400-ha spotted owl territories containing a high degree of landscape complementation (defined as containing >20% nest/roost habitat and >20% foraging habitat) at lower elevations (<5000 ft.) by an average of 90 to 118 territories by 2050, depending on the climate scenario examined. At higher elevations (>5000 ft.), potential benefits of treatments to spotted owl nesting/roosting and foraging habitat were less evident, but accelerated management did not result in habitat loss. Our results suggest that accelerated fuels reduction and forest restoration treatments within this large landscape are expected to benefit spotted owls by improving the spatial juxtaposition of nesting/roosting and foraging cover types by 2050 compared to a minimal management scenario. Fuels reduction and forest restoration in this landscape thus can both increase the resilience of forest ecosystems to disturbances as well as benefit the habitat of a sensitive old-forest species.

Introduction

Species often require multiple non-substitutable, spatially segregated resources to satisfy their ecological needs. The linking of these resources through animal movement is called landscape complementation (Dunning et al., 1992). For example, Florida manatees (*Trichechus manatus latirostris*) use offshore seagrass beds for feeding but require inland warm-water thermal refugia for overwintering; the spatial juxtaposition of these habitats drives manatee movement ecology (Haase *et al*., 2017). Landscape complementation has important implications for understanding population ecology as well. In northern leopard frogs (*Rana pipens*), when models excluded the role of upland summer habitat (in addition to breeding season pond habitat), the true presence of a metapopulation structure was masked (Pope, Fahrig, & Merriam, 2000). Thus, considering the role of landscape complementation is critically important for understanding the nature of population processes.

At the core of the concept of landscape complementation is the concept of landscape heterogeneity. Past and ongoing human land use has substantially reduced landscape heterogeneity in some systems (Schulte *et al*., 2007; Collins, Everett, & Stephens, 2011), with consequences for biological communities. Fire suppression in the Ozark Mountains, USA produced dense forest thickets between glades used by eastern collared lizards (*Crotaphytus collaris*), resulting in substantially reduced inter-glade movement and widespread local population extinctions (Templeton, Brazeal, & Neuwald, 2011). Landscape heterogeneity also has important implications for ecological stability and resilience (Holling, 1973). Structurally simplified forests resulting from timber harvest and fire suppression can result in lower resilience and persistent ecological type conversion following wildfire (Hessburg *et al*., 2019). In contrast, greater local forest structural variability leads to greater resilience to wildfire (Koontz *et al*., 2020) and drought (Restaino *et al*., 2019). Landscape heterogeneity, therefore, has important consequences for generating complementary resources for individual species as well as ensuring ecosystem resilience.

In western North America, past logging, fire suppression and other human activities have led to forest structural homogenization and reduced forest ecosystem resilience to disturbances (Coop *et al*., 2020). Increasingly frequent megafires and drought-related tree mortality events have resulted in pervasive and rapid degradation and loss of conifer forests (Stephens *et al*., 2020) and sensitive forest species habitat (Steel *et al*., 2022). While fuels reduction and forest restoration activities at large scales could reduce fire-driven forest loss and increase whole system resilience (North *et al*., 2021; Jones *et al*., 2022), considerable apprehension exists among various stakeholders that forest restoration activities themselves could eliminate important habitat elements for species of conservation concern (e.g. spotted owls, *Strix occidentalis*; Jones *et al*., 2016, 2021). Restoration activities that include removal of live trees through harvesting as well as prescribed and managed fire tend to create more abundant 'open' forest conditions not typically associated with high-quality habitat for old-forest dependent species. However, concerns over potential negative effects of forest restoration to old-forest species rarely recognize the importance of landscape complementarity for species persistence, and the degree to which forest restoration activities could generate heterogeneity and complementarity. More broadly, changes in landscape complementarity are rarely considered in habitat-based projections of how management might impact the future viability of species under changing climate.

Here, we used a forest simulation study to understand the potential effects of landscape-scale fuels reduction and forest restoration activities on promoting landscape complementarity for California spotted owls (*S. o. occidentalis*; hereafter 'spotted owls') in a changing climate (Fig. 1). Spotted owls are known for their dependence on old-growth forest conditions for nesting and roosting (Gutiérrez, Franklin, & Lahaye, 1995). However, spotted owls rely on early-seral and more open forest conditions, particularly at lower elevations, for hunting their preferred prey, dusky-footed woodrats (*Neotoma fuscipes*). When spotted owl home ranges contain sufficient juxtaposition of nest/roost habitat with hunting habitat, individual fitness and other vital rates have been shown to increase (Franklin *et al*., 2000; Kuntze *et al*., 2023; Zulla *et al*., 2023), suggesting the importance of landscape complementation for spotted owl population persistence. Using LANDIS-II, a forest vegetation simulator, we evaluated the influence of fire, forest treatments and climate change from 2020 to 2050 on nesting/roosting habitat, foraging habitat and landscape complementation of these two habitat types in a 971 245-ha landscape restoration project area in the central Sierra Nevada, California, USA.

Figure 1 An adult California spotted owl (*Strix occidentalis occidentalis*). Photo by Rick Kuyper/USFWS.

Our primary objective was to understand whether forest heterogeneity generated by fuels reduction activities could be compatible with the conservation of spotted owls.

Materials and methods

Study area

The Tahoe-Central Sierra Initiative (TCSI) landscape is a 971 245-ha area in the central Sierra Nevada where state, federal, nonprofit and private institutions are partnering to increase the pace and scale of forest restoration and improve ecological and social resilience to wildfire (https://www.tahoecentralsierra.org/). Elevations in the TCSI landscape range from ~600 m on the west slope in the foothills of California to ~2700 m at the crest of the Sierra Nevada. The TCSI boundary follows watershed HUC-8 level boundaries to the north and south. The eastern boundary follows the Lake Tahoe Basin watershed and the California-Nevada state line for the Truckee River watershed. The western boundary is roughly uphill of the blue-oak foothill pine and blue-oak woodland vegetation types. TCSI includes portions of four National Forests (Plumas, Tahoe, Eldorado and Humboldt-Toiyabe National Forests) covering 70% of the area, private industrial and non-industrial forest land (15%), and other private land and water bodies (15%).

LANDIS-II model and calibration

To model change in owl habitat under climate change, wildfire and two forest management scenarios, we used the LANDIS-II model (Scheller *et al.*, 2007) with the NECN (v. 6.9) and the SCRPPLE extension (v.3.2.2) (Scheller *et al.*, 2019) following the methods of Maxwell *et al.* (2022). The model simulates forest succession and disturbance of species-age cohorts with multiple cohorts existing in a single cell (180 × 180 m or 3.24 ha), with the model being flexible in regard to spatial and temporal resolution. In order to run LANDIS, the model requires initial vegetation conditions, information about the species being modeled, spatial information about fires, rates of management and a ruleset for its application and daily weather data (including precipitation, temperature, humidity and wind). The outputs from the model include spatial projections of future vegetation conditions, wildfires and management activities. The NECN extension uses the CENTURY model to track above- and belowground carbon and nitrogen pools and fluxes (Scheller *et al.*, 2011). The SCRPPLE extension simulates both wildfire and prescribed fires across the landscape, with the fire effects determined at the species-age-cohort level by cell which drives changes within the carbon and nitrogen pools. We ran the model from 2020 to 2050 with ten replicates of two climate projections and two management scenarios to capture stochastic variation in wildfire and management. We did not examine potential effects of insect outbreaks and resulting patterns of tree mortality on spotted owls because little is understood about the effects of insect outbreaks on spotted owl habitat suitability.

The initial forest conditions that were entered into the LANDIS-II model were assembled by Natural Capital Exchange (NCX) and were based on the imputation of USDA Forest Service Forest Inventory and Analysis (FIA) plots across the study area using random forest methods involving biophysical variables and represented forest conditions of 2019 (Maxwell *et al.*, 2022). Initial live aboveground biomass stocks for the study area were 218 Mg $ha^{\hat{}-1}$ ± 91 Mg ha^{-1}, which are comparable against a similar FIA imputed model TREEMAP (mean 185 ± 159 Mg ha^{-1}). Forest growth and mortality within the model was calibrated against the MODIS 17A3 annual Net Primary Productivity (NPP) product (with modeled NPP of 532 ± 149 g C m^{-2} and observed NPP of 506 ± 145 g C m^{-2}) and the measured annual Net Ecosystem Exchange (NEE) value from the Sagehen Field Station, (with modeled −60 ± 140 g C m^{-2} compared to observed −66 ± 72 g C m^{-2}). Fire size and severity were based on the Monitoring Trends in Burn Severity (MTBS) dataset (Eidenshink *et al.*, 2007). The model was calibrated by running the initial conditions using the 2010 climate data (see below) through 2020 to approximate the empirical fire size and severity found in the MTBS dataset.

Climate change

We simulated two climate projections: one based on recent climate conditions from 2010 to 2020 taken from GridMET that were randomly resampled by year and one based on the multivariate adaptive constructed analogs downscaling of the MIROC5 model using uncontrolled emissions (relative concentration pathway 8.5) available online through USGS Geo Data Portal (https://cida.usgs.gov/gdp) (Abatzoglou & Brown, 2012). The climate data were spread across the landscape from their native 6-km grid to larger regions based on elevational gradients. We selected the 2010–2020 period because annual area burned during this period was higher than any other period in recorded history and included the 2014 King Fire, a large fire (39 545 ha) with the largest proportion of high-severity fire (58%) in the MTBS records for this study area. We selected the MIROC5 projections because it was the only climate projection that recreated recent droughts out of the five recommended by the state (Pierce, Kalansky, & Cayan, 2018; Maxwell *et al.*, 2022). We adjusted the calculation of the fire weather index based on expert recommendation specific to CMIP5 and the Sierra Nevada (D. Swain, pers. comm.). Specifically, instead of mean values for all the inputs, we used daily maximum temperature, daily minimum relative humidity and daily average wind speed multiplied by 1.5 to approximate the windiest few hours of each day (Goss *et al.*, 2020).

Wildfire

In the Social-Climate-Fire extension of the LANDIS-II model, wildfire is a function of climate, primarily mediated through the calculated daily Canadian fire weather index values and wind speed, human and/or lightning ignitions, fuels and topography (Scheller *et al.*, 2019). Simulating wildfires is a two-part process and involves calculating where and when a wildfire might start. This required deriving a probability surface for human caused and lightning caused ignitions, which were calculated from historical wildfire ignition data using a kernel density function (Short, 2022). From that surface, fires were allocated based on historical seasonality, with fire size and spread calibrated to the 2010–2021 period and including any past wildfires that intersected the TCSI boundary using fire data from MTBS and California Department of Fire Resource Assessment Program. Total area burned per decade was on average 150 675 ha for the calibration period, compared to 105 797 to 351 240 ha for the 2010–2020 LANDIS-II projection. The largest individual fire in the calibration period was the 2021 Caldor Fire at 89 773 ha, versus a 93 795-ha simulated fire under the 2010–2020 climate projection. The percent high-severity fire ranged from 7 to 73% in the historical period and was 3–96% in the 2010–2020 projection. The greatest proportion of high severity in an exceptionally large (Cova *et al.*, 2023) >40 000 ha fire (King Fire) in the calibration period was 58% and for a similar sized fire (50 000 ha) in the 2010–2020 climate projection it was 80%. A higher proportion of high severity in extremely large fires is reflective of recent 1985–2020 burn trends (Cova *et al.*, 2023).

Forest management scenarios

We identified two forest management scenarios that represented the bookends on a range of possible management futures from a 'minimal management' scenario to an 'accelerated management' scenario. The scenarios were designed to bracket the management-as-usual treatment rate from 2010 to 2019 (4348–11 786 ha per year) based on the U.S. Forest Service FACTS database and CalFire private lands database. We divided the TCSI area into seven management zones, five target disturbance return intervals and two slope classes to make forest treatments spatially explicit. The disturbance return interval, time between a wildfire or a treatment, was a range of years based on the mean historical fire return interval (van Wagtendonk *et al*., 2018) for different climate zones (Jeronimo *et al*., 2019). Both management scenarios included fire suppression that matched recent efforts based on fire manager input.

Under the minimal management scenario, timber harvest occurred on private industrial lands every 25 years, private non-industrial lands every 40 years, and on lands in the wildland urban interface (WUI) Defense zone, 402 m from development, based on a target disturbance return interval. Under the accelerated management scenario, forest treatments expanded beyond the private timber land and WUI Defense to the WUI Threat zone (2102 m from development), general forest and roadless areas. Treatments were triggered based on a minimum target disturbance return interval and a minimum biomass threshold (Maxwell *et al*., 2022). In the accelerated management scenario (Table 1), treatments matched the historical frequency of fire (20–40-year intervals). Treatments included clear cuts, mechanical thinning and hand thinning. It was assumed that thinning in the general forest and WUI threat zone would include prescribed fire underburn treatment following thinning to reduce surface fuels and increase forest resilience to subsequent wildfires (Prichard *et al*., 2020). Mechanical thinning followed by prescribed burning in our simulations reduced downed woody debris by 90% and soil organic material by 55%. Treatment prescriptions and fuels reduction percentages were based on expert opinion from forest fire specialists (Table 2). In either scenario, management-induced changes to forest structure were designed to produce conditions that were more resilient and resistant to wildfire (e.g. reduced fire-driven tree mortality)

Table 1 Distribution of simulated treatment prescriptions in the accelerated management scenario

Slopes <30%	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
Private non-industrial	–	–	100%*	–
Private industrial	100%*	–	–	–
Defense zone	–	–	100%*	–
Threat zone	–	40%	60%	–
General forest	–	30%	70%	–
Roadless area	–	–	–	100%
Slopes >30%	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
Private non-industrial	–	100%*	–	–
Private industrial	–	100%*	–	–
Defense	–	100%*	–	–
Threat	–	–	–	100%
General forest	–	–	–	100%
Roadless	–	–	–	100%

Values marked with an asterisk (*) are those that were implemented under the minimal management scenario. Defense zone = within 400 m of an urban area; Threat zone = between 400 m and 2000 m of an urban area; General forest = non-restricted publicly owned forest 2000 m from an urban area; Roadless area = restricted publicly owned forest.

Table 2 Treatment prescriptions based on species-age ranges

Common name	Scientific name	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
White fir	*Abies concolor*	All	All	All	1–70
Red fir	*Abies magnifica*	All	All	All	1–71
Jeffrey pine	*Pinus jeffreyi*	All	1–68	1–140	1–68
Sugar pine	*Pinus lambertiana*	All	1–57	1–125	1–64
Lodgepole pine	*Pinus contorta*	All	1–68	1–200	1–88
Western white pine	*Pinus monticola*	All	1–81	1–200	1–88
Whitebark pine	*Pinus albicaulis*	All	1–79	1–200	1–87
Ponderosa pine	*Pinus ponderosa*	All	1–59	1–125	1–68
Washoe pine	*Pinus washoensis*	All	1–59	1–125	1–60
Douglas fir	*Pseudotsuga menziesii*	All	All	All	1–56
Incense cedar	*Calocedrus decurrens*	All	All	All	1–78
Mountain hemlock	*Tsuga mertensiana*	All	All	All	1–71
California foothill pine	*Pinus sabiniana*	All	1–50	1–125	1–64

and more representative of historical forest structure compared to present day conditions.

Summarizing vegetation change

We summarized changes in forest and shrub habitat using the California Wildlife Habitat Relationships (CWHR) classification scheme for habitat types. Habitat is based on dominant vegetation type, size measured as the mean diameter at breast height of the predominant trees and canopy cover. We translated species-age-biomass outputs from the LANDIS-II model into CWHR habitat types following recent work (White *et al.*, 2022; Zeller *et al.*, 2023) with a modification to allow for large tree sizes and 0–10% canopy cover. This modification allowed for cells to contain large trees post-fire with very low canopy cover and for larger trees not found in the reference condition.

We classified trees into 5 size classes: seedlings (size class 1: <2.5 cm), sapling (size class 2: 2.5–15 cm), pole trees (size class 3: 15–28 cm), small trees (size class 4: 28–61 cm) and medium/large trees (size class 5: >61 cm). Canopy cover was classified into 5 classes: limited cover (L: 0–10%), sparse cover (S: 10–25%), open cover (P: 25–40%), moderate cover (M: 40–60%) and dense cover (D: >60%). Our classification differs from CWHR habitat types by including the limited cover class, which we did intentionally to capture burned areas with low canopy cover and a few remaining large trees.

Owl habitat summaries

We used classifications of the CWHR database (https://wildlife.ca.gov/data/cwhr) to develop vegetation types that are associated with owl habitat to track during LANDIS-II simulations (Table 3). Specifically, we considered all forests falling into 5D, 5M and 5P CWHR classifications to be features associated with California spotted owl nest/roost habitat. We note that CHWR class 5P is typically not considered to be suitable nesting/roosting habitat for California spotted owls; for example, it is not included as suitable in the 2019 California Spotted Owl Conservation Strategy (USDA, 2019).

Table 3 Description of California Wildlife Habitat Relationships (CWHR) classes that were used to track nesting/roosting and foraging habitat during the Landis-II simulations

Habitat type	CWHR classification code	Tree size	Canopy closure
Nesting/ roosting	5P	>24″ DBH	25–40%
	5M	>24″ DBH	40–60%
	5D	>24″ DBH	>60%
Foraging	2P, 3P	<11″ DBH	25–40%
	2M, 3M	<11″ DBH	40–60%
	2D, 3D	<11″ DBH	>60%
	4P	11–24″ DBH	25–40%
	1S, 2S, 3S, 4S, 5S	Any DBH	<25%

DBH, diameter at breast height.

However, we view 5P as having a strong potential to serve as nesting/roosting habitat, since it contains large-diameter trees, which are believed to be the primary factor limiting spotted owl populations (Ganey *et al.*, 2017). We think one reason very few contemporary spotted owl nests/roost are found in this vegetation type is simply because it is extremely rare on the landscape, but we predict that owls could use it as it becomes more available in the future. We further considered all mixed chaparral, forests with smaller diameter trees (<11″ dbh) with >25% canopy cover, forests with intermediate-sized trees (11–24″ dbh) with 25–40% canopy cover, and all forests with <25% canopy cover to represent features associated with California spotted owl foraging habitat, particularly at lower elevations (see below) (Sakai & Noon, 1997; Innes *et al.*, 2007; Kuntze *et al.*, 2023). We tracked these two habitat types (nest/roost and foraging) over the simulation period. We also tracked the co-occurrence of these two habitat types, given that co-occurring nest/roost and foraging habitat are needed to satisfy multiple resource needs of owls.

We reported the area of each habitat type and the extent of co-occurrence across 1857 territory-sized summary units (400 ha) to reflect spotted owl biological needs. Specifically, we tallied the number of 400 ha hexagons (the approximate size of a spotted owl territory; Tempel *et al.*, 2014) that contained at least 20% spotted owl nest/roost habitat, 20% foraging habitat and 20% of both (i.e. 20% of each nest/roost and foraging habitat). We used 20% as a target because previous work has suggested that local territory extinction rates decline substantially when ~20% of the territory contains large, old trees (Jones *et al.*, 2018). We performed a sensitivity analysis to explore robustness of results to threshold selection, examining 5, 10, 15, 20, 30 and 40% as alternative thresholds, but we found to qualitative differences in inferences, so we proceeded with our literature-informed 20% threshold. We further divided summaries of spotted owl habitat into two elevational bins: >5000 ft (1000 hexagons) and <5000 ft (738 hexagons). In the lower elevational zone (<5000 ft.), a mosaic of younger and mature forest has been demonstrated to increase woodrat capture rates and the biomass of prey delivered by spotted owls to their nests (Zulla *et al.*, 2022, 2023; Kuntze *et al.*, 2023). By contrast, at higher elevations (>5000 ft.), mature forest-associated flying squirrels are the dominant prey item (Waters & Zabel, 1995; Kramer *et al.*, 2021) and tend to be captured by spotted owls in areas with large trees (Zulla *et al.*, 2022). Thus, we specifically tracked woodrat foraging habitat at lower elevations and assumed that flying squirrel habitat was consistent with spotted owl nest/roost features at higher elevations.

Finally, we summarized changes in spotted owl habitat in relation to the minimal management scenario. Specifically, we present habitat projections as changes in number of spotted owl territories resulting from accelerated management, relative to the minimal management scenario. This permits clearer visualization of the relative effects of the management alternative and can also lead to more robust interpretations than when using absolute effects in simulations (e.g. in population viability analyses; Beissinger & Westphal, 1998).

Results

The area treated in the accelerated management scenario was greatest in the first decade and decreased slightly over the next 20 years (Fig. 2). The cumulative area treated under the accelerated management scenario (~370 000 ha) was ~12 times higher than the minimal management scenario (~30 500 ha) (Figs 2 and 3). Compared to the minimal management scenario, total fire area was lower on average under accelerated management, but this result was dependent on climate scenario and time period under consideration. That is, simulations using the 2010–2020 climate scenario generally showed decreases in area burned compared to the minimal management scenario across all time periods, but the MIROC climate tended to show increased area burned relative to the minimal management scenario, except for in earlier decades at high elevations (Fig. 2). Projected high-severity fire showed similar idiosyncrasies. At higher elevations, accelerated management appeared to reduce projected high-severity burned area relative to the minimal management scenario, although we observed a high degree of prediction uncertainty. At lower elevations, we observed a

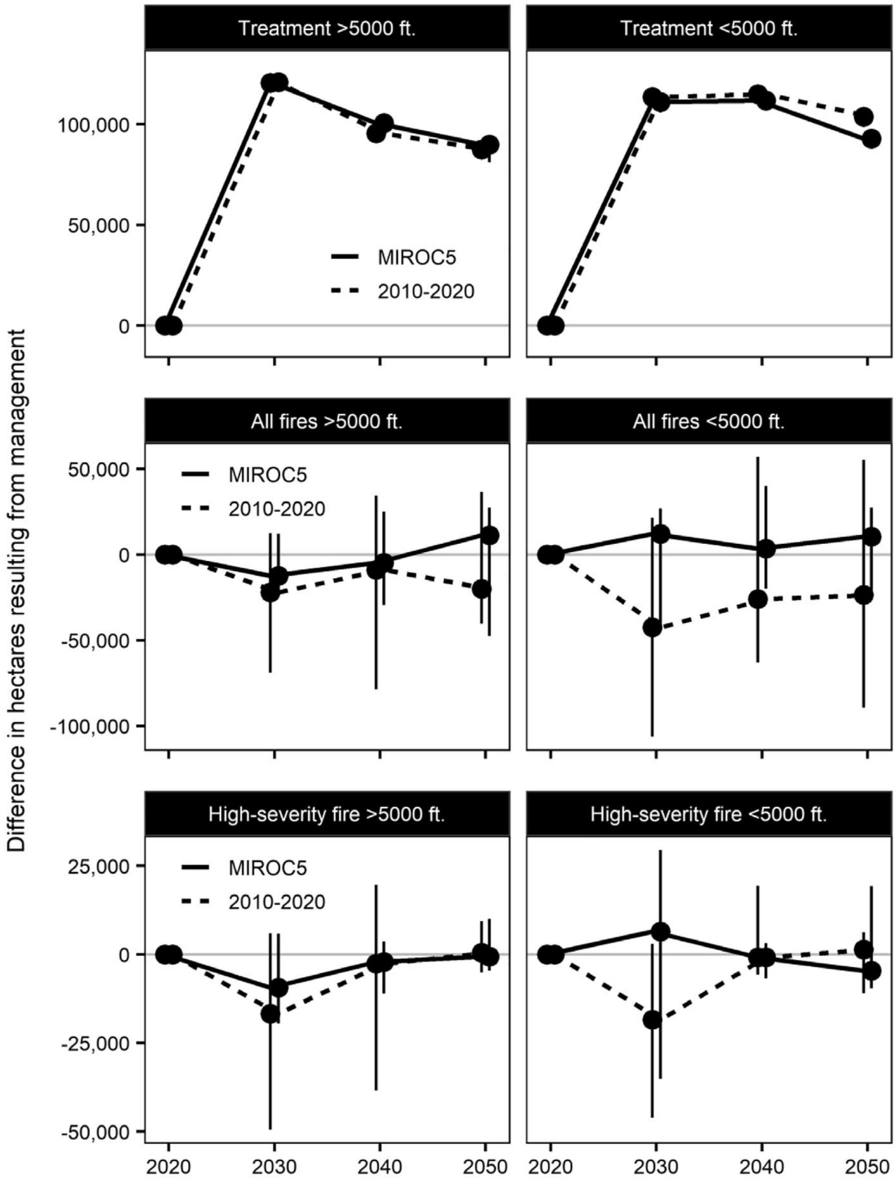

Figure 2 Predictions of future treatments (top row), fire area (middle row) and high-severity fire area (bottom row) relative to the minimal management scenario (gray horizontal line). Lines represent the difference between accelerated management and minimal management scenarios. Vertical error bars indicate the 80% prediction interval based on 10 LANDIS-II replicates, and circles represent the median value across replicates.

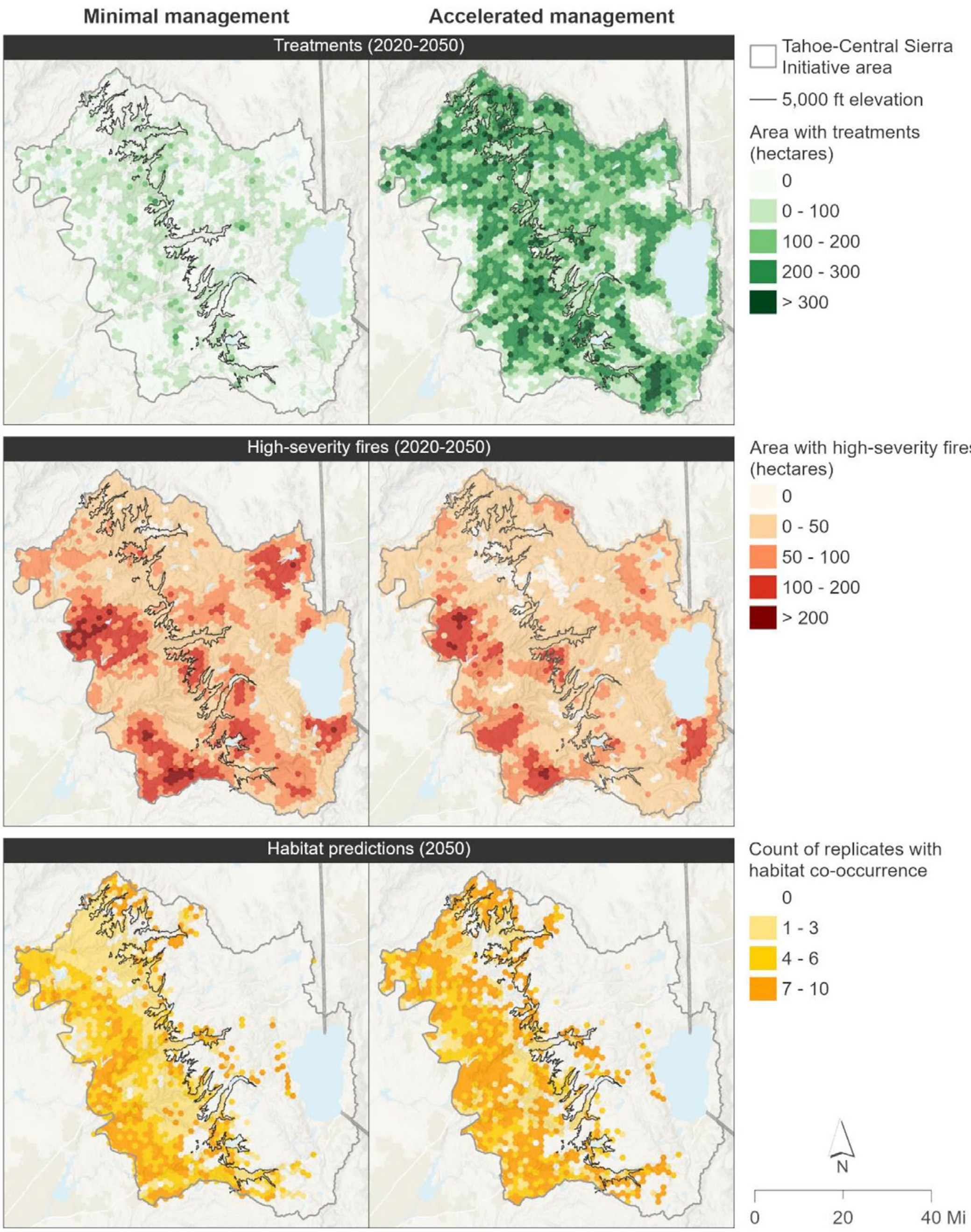

Figure 3 Spatial predictions of treatments (top row), high-severity fire extent (middle row) and landscape complementarity (bottom row) over our simulation period 2020–2050 under the minimal management scenario (left column) and the accelerated management scenario (right column). In the first and second rows, the mean area (of treatments and high-severity fire, respectively) in hectares is shown in each hexagon across 10 LANDIS-II replicates. In the bottom row, the number of LANDIS-II replicates (maximum of 10) showing landscape complementation within a given hexagon is shown.

similar trend, except for an apparent increase in high-severity fire in the second simulation decade under the MIROC climate scenario (Fig. 2). The cumulative area burned by wildfire was 2–3 times greater on average in the MIROC5 projection than the 2010–2020 projection while the area of high-severity fire was similar. In general, the lower amount of high-severity fire in the first decade of the simulation corresponded with increased treatment during that same decade (Fig. 2) and resulted in considerably less cumulative high-severity burned area over the modeling period (Fig. 3). Yet, because of the wide prediction intervals across the LANDIS-II replicates, differences in high-severity fire and fire at any severity due to treatment were not clearly distinguishable from the minimal management scenario.

In general, treatments across the TCSI landscape resulted in modest to no changes to spotted owl nest/roost habitat conditions at both high and low elevations relative to a minimal management scenario (Fig. 4). Through 2040, treatments resulted in no measurable changes to nest/roost habitat, but modest negative effects emerged by 2050 (median of ~16 potential territories lost) at higher elevations under one climate scenario (Fig. 4, top left). At lower elevations, there was more variation in predicted gains and losses through time, but by 2040 and 2050 the average prediction showed declines in nest/roost habitat (~10 to 34 potential territories lost) (Fig. 4, top right). However, considerable variation across LANDIS-II replicates indicates that potential gains or longer-term losses were not statistically distinguishable from the minimal management scenario; outcomes in the 80% prediction interval ranged from a gain of 56 territories to a loss of 86 territories by 2050. These results remained relatively consistent across both climate scenarios examined.

At lower elevations, treatment across the TCSI landscape resulted in rapid and large increases in the amount of potential woodrat habitat in spotted owl territories. By 2050, the number of spotted owl territories containing at least 20% woodrat habitat increased by a median of 108 and 146 (depending on the climate scenario used) compared to the minimal management scenario. Across LANDIS-II replicates, these increases were statistically distinguishable from a null result of zero difference in one of two climate scenarios (Fig. 4, bottom left).

At lower elevations, treatment increased the extent of co-occurrence of nest/roost conditions with woodrat habitat within potential spotted owl territories; that is, increased landscape complementation. By 2030, these increases were modest or close to zero (with the 80% prediction interval ranging from a gain of 18 territories to a loss of 12 territories), but thereafter the number increased through 2050. By 2050, we predicted an average increase of 90 to 118 spotted owl territories containing 20% of both nest/roost and woodrat habitat, depending on the climate scenario (Fig. 4, bottom right). Moreover, these differences were statistically distinguishable from the minimal management scenario based on the prediction intervals of LANDIS-II replicates.

Discussion

Results from our analysis suggest a broad compatibility between forest restoration objectives and spotted owl habitat

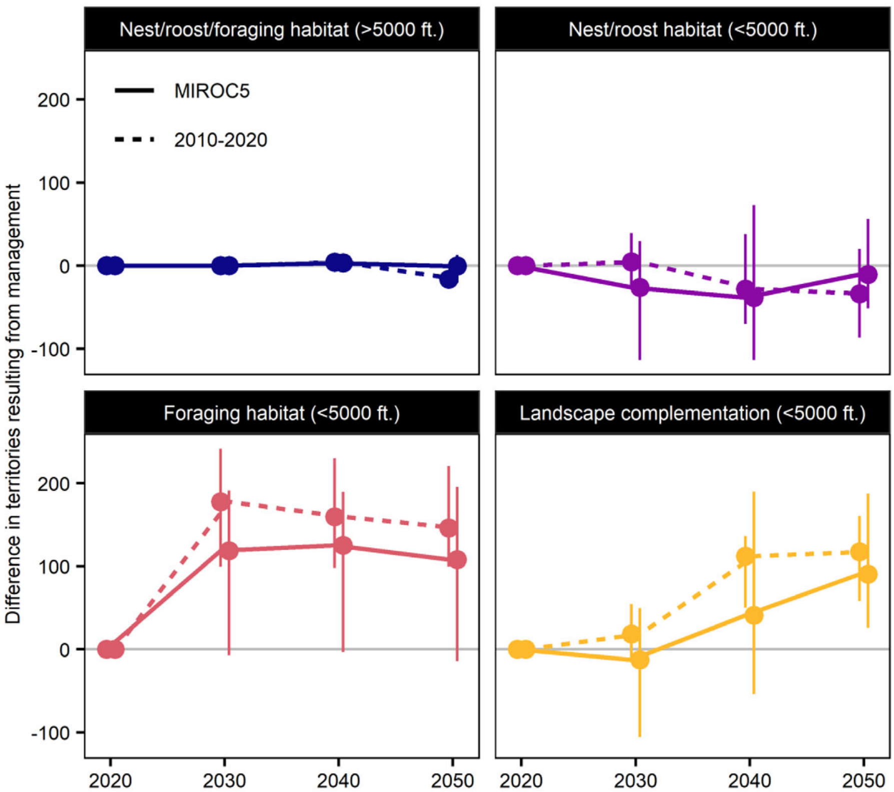

Figure 4 Predictions of spotted owl nest/roost habitat at high (upper left) and low (upper right) elevations; predictions of woodrat habitat at lower elevations (lower left); and predictions of the co-occurrence of nest/roost habitat and woodrat habitat at lower elevations (lower right) on the TCSI landscape. Units are the number of potential spotted owl territories (~400 ha hexagons) containing at least 20% of the noted cover type compared to the minimal management scenario. Vertical error bars indicate the 80% prediction interval based on 10 LANDIS-II replicates, and circles represent the median value across replicates.

conservation in the Sierra Nevada. Most importantly, our habitat projections showed (1) relatively large increases in woodrat habitat (brushy habitat, early-seral conditions and open forests) at lower elevations and (2) increased co-occurrence of spotted owl nest/roost habitat with woodrat habitat at lower elevations compared to the minimal management scenario. This increased co-occurrence of nest/roost habitat with foraging habitat at lower elevations is expected to provide net benefits to spotted owls, suggesting that accelerated management that includes thinning followed by under-burning could benefit spotted owl populations within the TCSI landscape.

One reason we focused on summarizing the co-occurrence of nest/roost habitat with woodrat habitat at lower elevations is that recent research has emphasized that this juxtaposition (i.e. landscape complementation) is important in habitat selection, behavioral ecology, movement, occupancy and fitness of spotted owls in the Sierra Nevada. For example, the mixture of older and younger forest types within a spotted owl territory (Fig. 5) increases the likelihood of capturing woodrats (Wilkinson *et al*., 2022; Zulla *et al*., 2022), increases the dietary proportion of woodrats (Hobart *et al*., 2019), results in higher rates of biomass delivery to nestlings (Wilkinson *et al*., 2022; Zulla *et al*., 2023) and yields higher reproductive output (Wilkinson *et al*., 2022, Zulla *et al*., 2023). Higher consumption rates of woodrats, driven by vegetation heterogeneity, has been shown to reduce territory extinction rates and promote population stability (Hobart *et al*., 2019). Other species of management concern inhabiting the Sierra Nevada have shown similar proclivity to landscape complementation, suggesting a broader applicability of our results for conservation. For example, the black-backed woodpecker (*Picoides arcticus*), a species emblematic of post-fire specialization, has recently been shown to be more dependent on burned/unburned forest interfaces than previously thought (e.g. Hutto, 2008). The landscape complementation of recently burned forests with adjacent unburned ('green') forests provides access to both critical nesting habitat (burned forest) as well as refugia for juvenile woodpeckers once they fledge the nest (green forests) (Stillman *et al*., 2019, 2021).

While the black-backed woodpecker has often been considered an early-seral specialist, spotted owls are often considered to be an old-forest dependent species (Jones *et al*., 2018). Yet the existence of landscape complementarity (Dunning *et al*., 1992) may be more important than extensive tracts of mature forest at lower and mid elevations for spotted owls. For example, woodrat abundance was ~2.5 times greater in spotted owl territories with a mixture of vegetation types compared to territories with extensive mature forest, and this increased abundance translated into greater rates of woodrat consumption (and overall biomass consumption; 30% higher) by spotted owls (Kuntze *et al*., 2023). The idea that heterogeneity in forest cover could benefit individual spotted owl fitness and population growth rates is not new (Franklin *et al*., 2000), but we are now uncovering one of the key mechanisms for its benefits; landscape complementation. The spatial configuration and patch sizes of foraging habitat are likely important, but we did not explore those factors here. Previous work has shown that in post-fire landscapes, spotted owls preferred to hunt in smaller patches (< 10 ha) of severely burned forest, which simultaneously provide relatively complete access to forest openings as well as abundant perches to use while searching for prey (Jones *et al*., 2020). When fuels reduction and forest restoration activities can mimic these smaller patches of early-seral forest openings through either mechanical thinning or mechanical thinning followed by prescribed fire treatments (Fig. 5), we predict that spotted owls will similarly prefer these over larger, homogenous patches of early-seral and open forest conditions.

One potentially counterintuitive result worthy of further exploration is the fact that accelerated management appeared to result in an increased abundance of woodrat habitat in our LANDIS-II simulations (Fig. 4). At least initially, thinning, mastication and prescribed fire would be expected to reduce the abundance of 'brushy' conditions typically associated with woodrats (Collins, Moghaddas, & Stephens, 2007). While shrub abundance has been shown to initially decrease in dry and moist mixed-conifer forests following mechanical treatments, it can increase thereafter, sometimes exceeding initial levels 8-years post-treatment (Vaillant *et al*., 2015). This could partly explain increased woodrat habitat in our simulations. However, in addition to brushy chaparral conditions, our definition of potential woodrat habitat included sparsely treed forests (those with <25% canopy cover even of larger size classes) and early-seral forests made up of smaller tree size classes and higher canopy cover that woodrats are known to occupy (Sakai & Noon, 1997; Innes *et al*., 2007; Kuntze *et al*., 2023). These conditions may be entirely expected to increase in abundance under accelerated fuels reduction scenarios, as the contemporary landscape-scale homogenous dominance of mid-seral conditions gives way to an increase in distributed gaps and openings and lower-density forest conditions produced by mechanical thinning, and as prescribed and managed fire periodically reset local forest succession (Hessburg *et al*., 2021). Given that treatment area was the main distinguishing feature between the minimal and accelerated management scenarios (Fig. 2), fuels reduction and forest restoration treatments appear to have played an important role in creating and maintaining a landscape-scale shifting mosaic of woodrat habitat over our simulation period.

Yet, it is widely held that the primary factor limiting spotted owl populations is the availability of high-quality nesting habitat (Ganey *et al*., 2017; Peery *et al*., 2017). That is, forests dominated by very large, old trees, structural decadence and multi-layered canopies (Gutiérrez, Franklin, & Lahaye, 1995; Jones *et al*., 2018). As such, it might appear concerning that our simulations indicated that accelerated management would have essentially no effect on recruiting this critical nest/roost habitat across all elevations compared to the minimal management scenario (Fig. 4). However, in absolute terms, our simulation showed a substantial increase in forests that spotted owls use for nesting and roosting (CWHR classes 5D, 5M and 5P). From 2020 to 2050, the abundance of 5D (>24″ dbh trees, >60% canopy cover), 5M

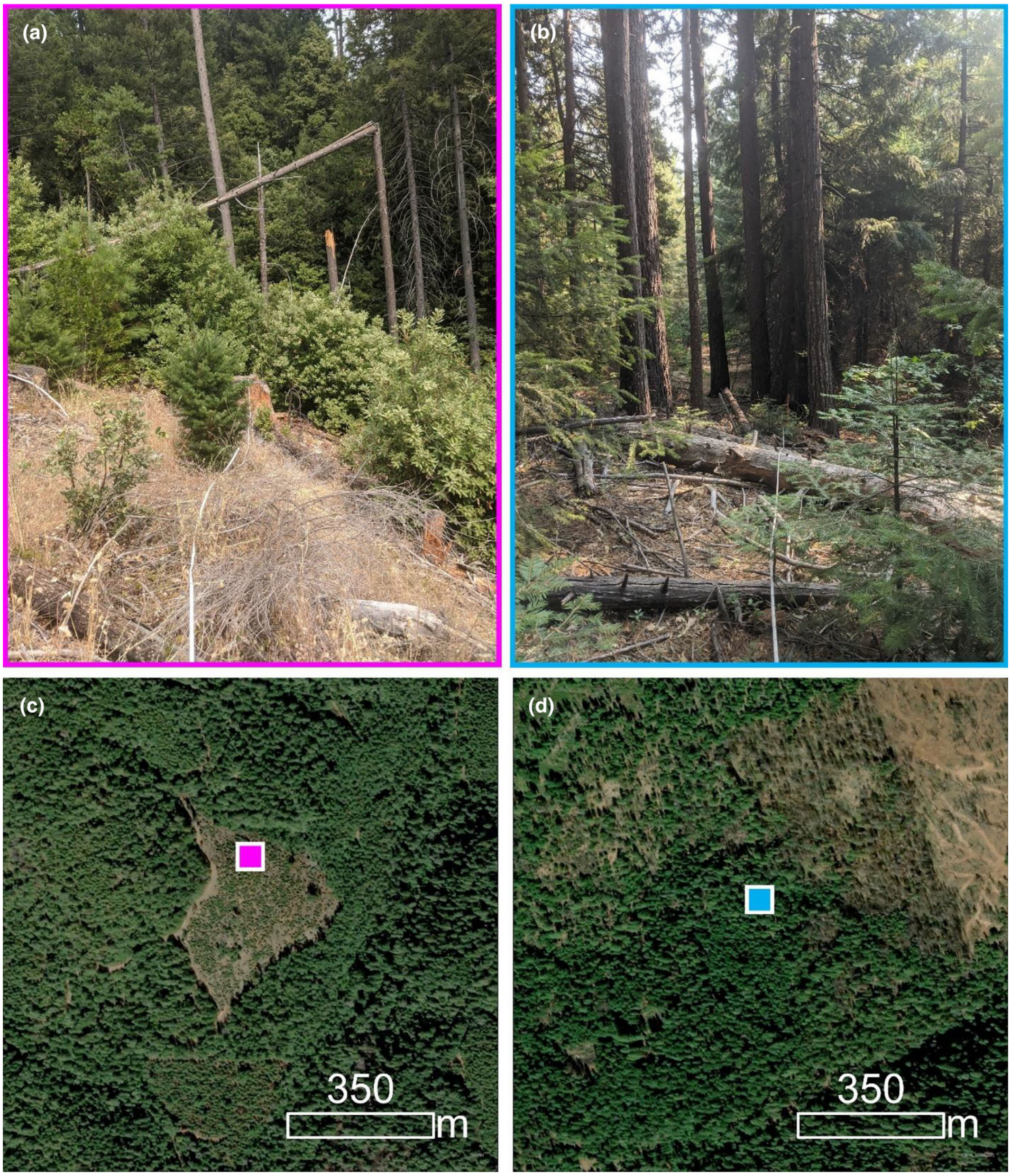

Figure 5 Examples of landscape complementation at an (a) intermediate patch scale and (b) micro-site scale on the Eldorado National Forest, California. Both photos show the juxtaposition of open, early-seral or brushy conditions that tend to be associated with woodrat habitat in the foreground, and later-seral, closed-canopy habitat in the background. Moreover, woodrats were captured at both sites in a different study (Kuntze *et al.*, 2023). The photo in (a) was taken at the location indicated by the pink square in (c), which occurred in a 10-hectare commercially harvested unit that had been recently replanted. The photo in (b) was taken at the blue square located in (d), which was a small forest gap (several meters wide) surrounded by continuous forest cover, but within ~150 m of more open forest conditions. Photo credits for (a) and (b): Corbin Kuntze, used with permission. Images in (c) and (d) obtained from National Agriculture Imagery Program.

(>24″ dbh trees, 40–60% canopy cover) and 5P (>24″ dbh trees, 25–40% canopy cover) increased by an average of nearly 243 000 ha in the minimal management scenario and nearly 222 000 ha in the accelerated management scenario. Thus, in both the minimal and accelerated management scenarios, many more large trees were simulated to occur in our study region by 2050, and this increase appears to be more driven by intrinsic forest recruitment processes and climate than management. Given the very high abundance of trees in intermediate size classes (11–24″ dbh) at the start of our simulation period (636 698 ha), it is unsurprising that so many trees in this class recruited into the larger size class (>24″ dbh) by 2050. Encouragingly, from the perspective of meeting forest restoration goals, it appears that even under an accelerated management scenario that specifically targets removal of trees in this intermediate size class, the very high initial abundance of intermediate-sized trees means that the overall recruitment into a larger size class was almost entirely unaffected (Fig. 4).

Concluding remarks

Our work demonstrates the importance of considering landscape complementation in habitat modeling efforts. Had we simply considered the changing abundance of typical nest/roost habitat and not the spatial juxtaposition of nest/roost habitat with foraging habitat, we may have concluded that the accelerated management scenario offered no benefits, or even net costs, to spotted owls. In contrast, our results suggest that on our study landscape, accelerated implementation of fuels reduction and forest restoration treatments could benefit spotted owl populations by generating landscape complementation (the co-occurrence of nest/roost with foraging habitat) within territories, particularly at lower elevations. This result is consistent with emerging science suggesting the benefits of landscape heterogeneity to owls, from individual to population scales. There is an increasing recognition that animal movements that produce landscape complementation represent a critical population process, mediating animal responses to rapid landscape changes (Nimmo *et al*., 2019). Our work provides a simple and generalizable approach for modeling landscape complementation to understand the influence of management interventions on rare or threatened species.

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Author contributions

All authors conceived of the ideas, designed the methodology and participated in numerous discussions about project ideas; CM developed and executed the forest simulations; KNW and CKS summarized and interpreted forest simulation output; GMJ and MZP developed interpretations of the forest simulation model in light of spotted owl ecology; GMJ wrote the first draft of the manuscript and developed most of the data visualizations; CKS developed and produced the maps; all authors contributed to manuscript revisions.

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