Biological Conservation 296 (2024) 110701

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Changing fire regimes and nuanced impacts on a critically imperiled species

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ARTICLE INFO

Keywords:
Disturbance regimes
Northern spotted owl
Mark-recapture
Multistate models
Fire ecology
Population
Wildfire

ABSTRACT

Wildfire activity throughout western North America is increasing which can have important consequences for species persistence. Native species have evolved disturbance-adapted traits that confer resilience to natural disturbance provided disturbances operate within their historical range of variability. This resilience can erode as disturbance regimes change and begin operating outside this range. We assessed wildfire impacts during 1987–2018 on the northern spotted owl, an imperiled species with complex relationships with late and early seral forest in the Pacific Northwest, USA. We analyzed population- and individual-level wildfire impacts across the frequent-fire portion of the owl's geographic range at two spatial scales and uncovered important nuances involving wildfire risk. When comparing survival of owls on burned vs unburned territories, we detected no differences in apparent survival, and owls overwhelmingly remained on burned territories indicating no measurable population-level wildfire impacts. However, when including territory-scale fire characteristics we detected negative individual-level wildfire impacts that indicated apparent survival decreased and territory displacement increased with burn severity and extent within an owl's territory. Northern spotted owls were also more sensitive to fire effects within their core use area indicating that *where* fire burns is important for spotted owl conservation. These findings indicate nuance is required when discussing wildfire impacts to spotted owls, and that changing fire regimes in this portion of the northern spotted owl's range have not yet translated into negative population-wide impacts. However, dwindling populations and continued fire regime changes could exceed the adaptive capacity of remaining spotted owls, thereby resulting in negative population-wide impacts.

1. Introduction

Natural disturbances are discrete events that alter ecosystem structure by removing or rearranging resources or altering successional trajectories (White and Pickett, 1985; Turner, 2010). They play a crucial role in the long-term function of ecosystems by shaping and maintaining landscape patterns that species require as habitat and are characterized by their size, intensity, and frequency and have variable ecological impacts. There is a great deal of variability among individual disturbance events, and ecologists use the concept of a disturbance regime defined as the range of variability in individual disturbance traits (size, frequency, intensity, etc.; Turner, 2010) as a helpful way of classifying disturbances occurring over broad spatial and temporal scales. Therefore, a disturbance regime can be thought of as a distribution of individual disturbance events that includes the range of characteristics that reflect all the inherent variability of individual disturbances. Thus, species-specific inferences drawn from evaluating the impacts of one or a few disturbance events at the individual level may be different than inferences drawn from the impacts of a disturbance regime at the population level.

Native species have evolved with the natural disturbance regime of the region and developed a suite of disturbance-adaptive traits that are tuned to the historical range of variability (HRV) of the disturbance

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https://doi.org/10.1016/j.biocon.2024.110701
Received 10 November 2023; Received in revised form 21 June 2024; Accepted 24 June 2024

regime. These adaptations confer resilience (Rykiel, 1985; Seidl et al., 2014) to natural disturbances provided they operate within their historical range of variability. However, if disturbances begin operating outside of this range and result in conditions not experienced in their evolutionary past, a species' adaptive capacity may be exceeded thereby threatening species persistence and ecosystem function (Johnstone et al., 2016; Seidl et al., 2016; Hart et al., 2019). Alterations in vegetation structure and composition arising from disturbances can impact the habitat suitability and ultimately the components of fitness (e.g., survival, reproduction) of wildlife species because vegetation is a core component of habitat (Morrison et al., 2006). Species vital rate responses to disturbance may also vary depending on the spatial arrangement of post-disturbance vegetation structure, not just the total amount of remaining vegetation, because some species may require multiple different vegetation structures in particular arrangements to meet all of their life history traits (Franklin et al., 2002a). These considerations suggest that researchers can leverage the core concepts of disturbance regimes, disturbance-adaptive traits (i.e., resilience), and wildlife-habitat relationships to generate hypotheses about changing disturbance regimes while uncovering important individual-level impacts of disturbance events that highlight how individuals respond to disturbance (Bunnell, 1995).

There is widespread concern that wildfire regimes across western North America are changing due to the combined effects of climate change, fire suppression, and past and current land-use practices. These changes may exceed the adaptive capacity of native species and threaten their persistence. This concern has led to an increased focus on the impacts of changing disturbance regimes to native species and ecosystems (Turner, 2010; Halofsky et al., 2020). The frequent fire landscape of the Pacific Northwest (PNW) inhabited by the northern spotted owl (*Strix occidentalis caurina*) is a particularly useful system to address the question of changing disturbance regimes because: 1) range-wide estimates of the species' vital rates based on data collected on individuals over the last three decades are available (Franklin et al., 2021), 2) the northern spotted owl occurs within a range of forest types throughout the PNW, including landscapes characterized by different fire regimes (Spies et al., 2018; Reilly et al., 2021), 3) previous research has indicated northern spotted owls inhabiting the frequent fire landscape exhibit life history tradeoffs (Franklin et al., 2000, Olson et al., 2004) resulting from the complex patchwork of seral stages that historically resulted from repeated fires (Reilly et al., 2021), and 4) initial research suggests northern spotted owls respond to fire through a variety of mechanisms that have individual as well as population level consequences (Rockweit et al., 2017).

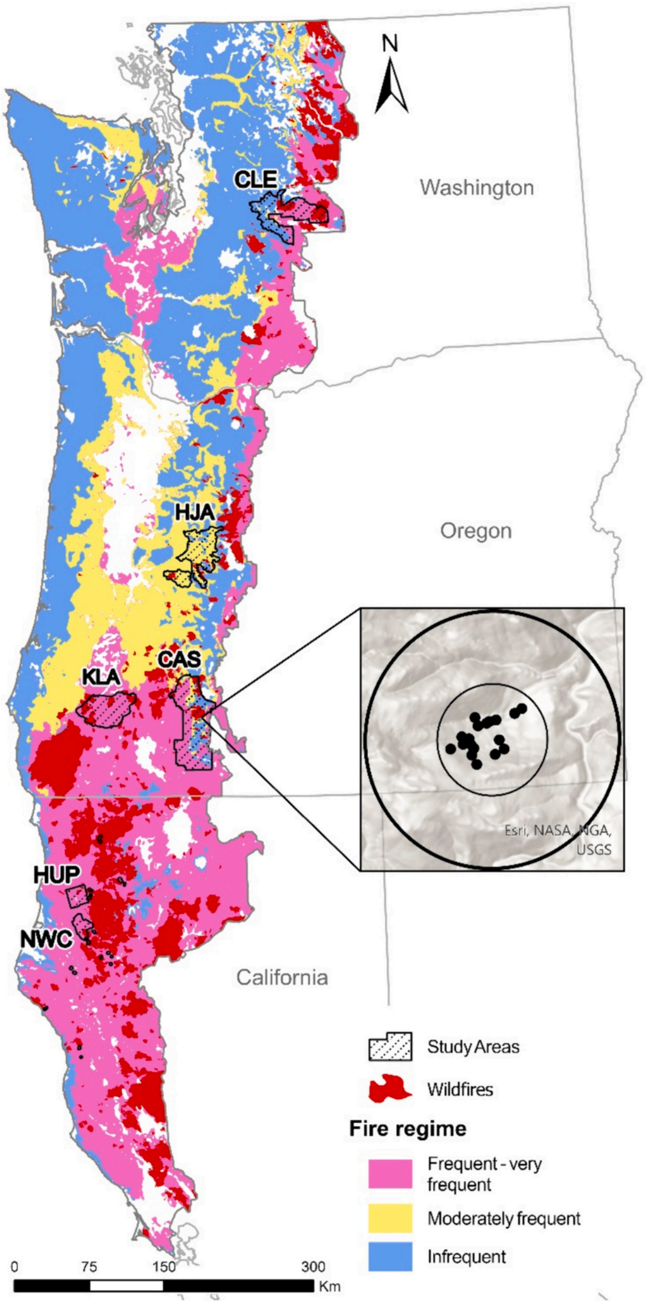

Fig. 1. Study areas used to assess wildfire impacts to northern spotted owls. Over 90 % of owls affected by fire occurred within the frequent – very frequent fire portion of the owl's geographic range. Inset map illustrates the accumulation of annual site centers with core use (inner circle) and home range (outer circle) buffers.

Throughout most of their range, northern spotted owls are closely associated with dense, multi-layered coniferous forests for nesting and roosting (Forsman et al., 1984; Lahaye and Gutiérrez, 1999; Sovern et al., 2019); conditions typical of older coniferous forests in the PNW (Franklin et al., 1981). While nesting and roosting requirements are generally similar across their range, foraging habitat requirements are more variable. In the infrequent, high severity fire regime (Fig. 1), spotted owl foraging habitat requirements are more similar to habitat requirements for nesting and roosting (Forsman et al., 1984; Carey et al., 1990). Foraging habitat in the frequent fire regime areas includes older coniferous forests but also includes ecotones between older forests and areas of younger seral stages (Zabel et al., 1995; Ward and Noon, 1998) that historically resulted from a spatially heterogeneous patchwork of low, moderate and high severity fire effects. It has been hypothesized that this pattern of foraging results from the habitat requirements of the spotted owl's main prey resources that vary across the owl's geographic range (Zabel et al., 1995, Carey et al., 1999, Franklin et al., 2000). Northern spotted owls prey predominately on northern flying squirrels (*Glaucomys sabrinus*), red tree voles (*Arborimus longicaudus*), and bushy-tailed woodrats (*Neotoma cinerea*) that are generally associated with older forests in the infrequent, higher severity fire regime region. In the southern portion of the frequent, mixed-severity fire region, dusky-footed woodrats (*N. fuscipes*) are abundant in early seral stages and ecotones where they predominate in spotted owl diets (Ward and Noon, 1998; Forsman et al., 2004). Indeed, in the frequent fire regime areas, there is a tradeoff in spotted owl vital rates such that old forest positively influences survival, but moderate amounts of habitat heterogeneity positively influences fecundity (Franklin et al., 2000, Olson et al., 2004, Dugger et al., 2005). Spotted owls evolved in these pyrodiverse landscapes (Bowman et al., 2016; Jones and Tingley, 2021) where the post-fire mosaic of seral stages resulting from heterogenous burn patterns provide all of the habitat components required by spotted owls to meet all of their life history traits (Franklin et al. 2002a). Thus, it has been hypothesized that spotted owls residing in the frequent fire portion of their range display behavioral adaptations to fire to capitalize on the mosaic of seral stages created and maintained by fire (Franklin et al., 2000, Lesmeister et al., 2019) by nesting and roosting in areas that burn at low severity and are maintained as old forest ("fire-tended" old-growth; Meddens et al., 2018), and foraging along ecotones between old forest and younger seral stages where woodrats are more abundant. Indeed, recent studies on California spotted owls (*S. o. occidentalis*) inhabiting frequent fire landscapes have shown they make short distance forays into areas recently burned at higher severity when foraging (Jones et al., 2020; Kramer et al., 2021) and consume more woodrats in territories with more habitat heterogeneity (Kuntze et al., 2023) which is presumably a behavioral adaptation of spotted owls in a post-fire landscape; one that historically was more heterogeneous owing to an active fire regime that provided spotted owls with both older forests for nesting and roosting and high-quality foraging opportunities in areas burned at higher severity.

Therefore, we sought to address whether changing fire regimes throughout the frequent fire portion of the northern spotted owl's geographic range have resulted in negative population-wide impacts to spotted owls. We did this by leveraging a long-term (1987–2019) mark-recapture dataset from study areas located throughout the frequent-fire portion of the owl's range and using multi-state mark-recapture models (Brownie et al., 1993; Williams et al., 2002) to examine wildfire effects on population- and individual-level survival and movement rates. We draw inferences to fire effects on individuals and to the population as a whole by comparing models with and without fire effects covariates, respectively. Excluding fire effects covariates allowed for population-level inference because estimates of apparent survival were based on the overall mean population-level response (i.e., comparing mean survival estimates of owls on burned versus unburned sites). We then added covariates that described fire effects within owl territories which allowed us to make inference to wildfire impacts on individuals. The long-term nature of these studies and the occurrence of numerous wildfires allowed us to examine the potential impacts of a changing disturbance regime to northern spotted owls inhabiting the frequent fire portion of their range in a retrospective quasi-experimental context. In addition to the potential threat of changing fire regimes, northern spotted owls are also currently threatened by a number of well-known additional stressors including the effects of historical and current habitat loss and fragmentation due to logging and competitive exclusion by nonnative barred owls (*Strix varia*; Yackulic et al., 2019, Wiens et al., 2021), and they face an uncertain future (Franklin et al., 2021). Gaining an understanding of the potential impact of changing fire regimes to northern spotted owls is critical for identifying how future, predicted changes in wildfire regimes could affect persistence of northern spotted owls and their habitats.

2. Methods

We used data from 6 long-term, demographic study areas located throughout the fire prone regions of the owl's geographic range with a recent (since 1987) history of fire within owl territories (Fig. 1, Table 1). Three study areas (NWC, HUP, KLA) were located within the Klamath physiographic province in California and Oregon and 3 were in the Cascade Range in Oregon (CAS, HJA) and Washington (CLE), with elevations ranging from 160 m to 1700 m. Dominant forest cover on all study areas was primarily mixed-conifer or mixed evergreen (Whitakker, 1960; Franklin and Dyrness, 1988). Mean annual precipitation ranged from <120 cm on KLA to >200 cm on HJA with most precipitation falling as rain for study areas in the Klamath Province and as snow for study areas in the Cascades. For a more complete description of study areas, see Dugger et al. (2016; Appendix A).

Historical (pre-European settlement) fire regimes in the Klamath province fall within a continuum from very frequent (5–25 yrs) to frequent (25–50 yrs), low- to mixed-severity fire with smaller patches (10–1000 ha) of high severity fire intermixed (Spies et al., 2018; Reilly et al., 2021). Historical fire regimes for the Cascades study areas (CAS, HJA, CLE) included areas of frequent, low- and mixed-severity fire, but also included areas characterized by less frequent (50-200 yrs), and infrequent (>200 yrs), higher severity fire (Agee, 1993; Spies et al., 2018). This latter fire regime is mostly constrained to higher elevations outside the geographic range of northern spotted owls, but occasionally extends into lower elevation forests used by northern spotted owls during fires with concurrent strong east wind events (Agee, 1993; Reilly et al., 2021).

Table 1
Characteristics of wildfires that affected northern spotted owl territories on 6 demographic study areas located throughout the frequent fire portion of the Pacific Northwest (PNW).

Year	Occupied territories affected[b]	Area burned (ha)	Burn severity[a]		
			Low	Moderate	High
1987	17 (11)	51538	0.53	0.32	0.15
1988	1 (1)	2980	0.46	0.28	0.26
1999	5 (4)	57217	0.58	0.29	0.14
2003	5 (3)	38930	0.26	0.34	0.40
2004	9 (6)	3367	0.22	0.42	0.36
2005	1 (0)	591	0.31	0.45	0.25
2006	1 (0)	2910	0.38	0.36	0.26
2007	2 (2)	5746	0.41	0.42	0.17
2008	15 (12)	70533	0.44	0.34	0.22
2009	2 (2)	1163	0.49	0.34	0.17
2013	18 (15)	20355	0.35	0.33	0.32
2014	1 (0)	11123	0.52	0.36	0.12
2015	5 (5)	47600	0.42	0.33	0.25
2017	17 (9)	70732	0.39	0.33	0.28
2018	1 (1)	10001	0.49	0.28	0.23
Total	97 (71)	394787	0.42[c]	0.35[c]	0.24[c]

[a] Low (<25 % Basal Area (BA) mortality), Moderate (25–75 % BA mortality), High (>75 % BA mortality).

[b] Number affected at the home range (core use) scale.

[c] Mean proportion of burn severity.

Field surveys for owls were conducted annually during the breeding season (March–August) with the objectives of identifying individuals by vocally imitating owls to elicit a territorial response. Responding owls were either identified by a unique colorband combination on its leg, or, if not banded, by capturing and placing a locking U.S. Geological Survey band on one leg and a unique colorband combination on the other to facilitate subsequent identification (Franklin et al., 1996). Because northern spotted owls have high interannual site fidelity (Forsman et al., 2002; Jenkins et al., 2021), repeated visits across years provides high detectability of individual owls and robust mark-recapture data for estimation of apparent survival, movement probabilities between territories, and location data to define owl territories.

We defined owl territories based on the accumulation of historical, annual owl locations from field surveys. We selected one location per year based on the following hierarchical ranking: 1) location of nest, 2) location of young if no nest found, 3) daytime roost location, and lastly 4) night-time detection within 1 h of dusk or dawn. If no locations fit these criteria, no location was used for that year. The resulting annual territory centers from all years of the study were then used to generate Theissen polygons to represent territories using a bandwidth equal to the study area-specific ½ median nearest neighbor distances (Dugger et al., 2016). We then determined the centroid of each polygon and created two buffers around those centroids; one based on ½ median nearest neighbor distances (core use scale), and one based on home range estimates for each study area (Dugger et al., 2016; home range scale). We created two buffer sizes because sensitivity to fire effects could vary with distance from site center (e.g., Dugger et al., 2005). We used a static site centroid instead of annually varying centroids because nest and roost locations within a territory are typically tightly clustered and in most cases our core use areas encompassed nearly all of the annual nest and roost locations within a territory. While home range estimates acquired from GPS tracking might have been a better approximation of shorter-term spotted owl space use, we feel our circular buffers capture the general long-term space use patterns of northern spotted owls, especially at the territory core scale (Fig. 1. Hereafter, we use the term 'territory' for discussions relevant to either scale.

We used multistate, mark-recapture models to assess population- and individual-level impacts of wildfire on spotted owl apparent survival (S) and transition probabilities (Ψ) among states. Multistate models are an extension of Cormack-Jolly-Seber open population models that allow for the movement of individuals among states (e.g., burned, unburned), where state is user-defined (Brownie et al., 1993). This allows for estimation of state-specific recapture (p) and apparent survival (S) probabilities along with estimates of the probability of transitioning among states. We defined 3 states based on the burned status of the territory upon which owls resided in any given year, with owls residing on unburned sites assigned to state UB (unburned), owls residing on sites the year it burned assigned to state JB (just-burned), and owls residing on sites burned >1 year ago to state PB (previously-burned). Multistate models are parameterized such that state-specific apparent survival is estimated at the start of the capture interval. These models assume that individuals survive first and then transition immediately prior to the subsequent capture occasion. Therefore, individual survival is estimated for the state at the start of the capture interval and then individuals transition to a new state. This means that care must be taken when assigning individuals to states to ensure these assumptions are met. In our case, we assigned owls to the just-burned state (JB) in year t if it occupied a territory that burned in year t, and to the previously-burned (PB) state in all years $>t$ if it remained on a burned site. We used program MARK to build models and generate parameter estimates and model selection results (White and Burnham, 1999).

We investigated population-level fire impacts by comparing estimates of state-specific apparent survival among our 3 states while including time- and site-specific covariates to account for known sources of variation in spotted owl vital rates (e.g., barred owls), but excluded covariates that described fire effects to individual owl territories. These estimates represent the effect of fire averaged over all individuals within each population of individuals (i.e., states) and as such can be thought of as population-level impacts. To investigate the effect of fire on spotted owl survival and movement at the individual level, we used time-varying, individual covariates that described: 1) the extent and severity of wildfire within northern spotted owl core use areas and home ranges, 2) the proportion of an owl's core use area or home range composed of nesting and roosting (NR) forest, 3) the proportion of post-fire salvage logging that occurred within core use areas and home ranges, 4) detection/nondetection of barred owls within spotted owl territories, and 5) time since fire (Table 2). We used time-varying, individual covariates so we could account for movement of individual owls between territories and the spatial and temporal variability of wildfire effects on spotted owl apparent survival and movement rates.

Table 2
Covariates included in the analysis of fire effects on northern spotted owl apparent survival rates. We did not combine fire effects covariates in the same model.

Acronym	Description
NR.pre	Proportion of analysis area composed of nesting and roosting (NR) forest 1 yr before fire
NR.post	Proportion of analysis area composed of NR forest 1 yr after fire
LOW	Proportion of NR forest in analysis area burned at low severity
MODERATE	Proportion of NR forest in analysis area burned at moderate severity
HIGH	Proportion of NR forest in analysis area burned at high severity
HIGHER	Proportion of NR forest in analysis area burned at moderate or high severity
SALV	Proportion of analysis area post-fire salvage logged.
TSF	Time (in years) since fire
BO	Binary year- and site-specific variable indicating if a barred owl(s) was detected in the analysis area in year t.

Northern spotted owls require a minimum amount of NR forest to meet their life history traits (Bart and Forsman, 1992). Therefore, we calculated the annual proportion of NR forest within an owl's core use area and home range to include in our analysis using maps of NR forest developed by Davis et al. (2016). We also included covariates that described the extent and severity of wildfire within spotted owl territories. We acquired data for all large fires (>404 ha) that occurred from 1987 to 2018 from the Monitoring Trends in Burn Severity project (Eidenshink et al., 2007) and classified burn severities based on a relationship between the relativized difference in the normalized burn ratio and % basal area mortality for the region (Reilly et al., 2017). We defined low, moderate, high, and higher burn severity as <25 %, 25 %–75 %, >75 %, and >25 % basal area mortality, respectively and developed covariates that described the proportion of NR forest within an owl's territory that burned at these severities. We included the higher burn severity (>25 % basal area mortality) covariate because previous research indicated this was more informative than moderate or high severity alone (Rockweit et al., 2017) and the broad ecological definition of moderate burn severity (25 % - 75 % basal area mortality) suggests there is uncertainty in how it might affect spotted owls. Satellite-based fire severity mapping cannot distinguish truly unburned patches from very low or low severity fire effects because intact tree canopies obstruct the satellite sensor's 'view' of the ground (Meddens et al., 2016). Accordingly, our low severity fire effects covariates included areas burned at low severity plus areas within the burn perimeter that were truly unburned. For cases in which wildfires reburned a portion of a previously burned territory, we overlayed the two burn severity maps and used the maximum burn severity value of the overlapping pixels.

Post-fire salvage logging effects are spatially and temporally confounded with fire effects (McIver and Starr, 2001). To address this confounding, we included a covariate that described the proportion of territory that was post-fire salvage logged, which we defined as any timber harvest occurring within a burn perimeter ≤3 years post-fire. We acquired salvage data from the U.S Forest Service Forest Activity Tracking System (USDA Forest Service, 2020), the Bureau of Land Management Data Portal (USDI Bureau of Land Management, 2021), and a public disclosure request to the state of Washington. We also digitized evidence of post-fire salvage logging on private lands in Google Earth by overlaying fire perimeters onto the base imagery to identify areas with visual evidence of post-fire salvage logging. Through time and in the absence of repeat disturbance, successional processes result in the reestablishment of NR forest (Franklin et al., 2002b). To account for these processes, we developed a covariate that was the time (years) since fire occurred on a given territory.

Lastly, we included a binary site- and year-specific covariate of detection/nondetection of at least 1 barred owl within a spotted owl territory during surveys for spotted owls. Because our covariates referred to the condition of the territory upon which an individual owl resided, we carried forward covariate values from the last known spotted owl location for cases in which we had missing data (e.g., 0's in the encounter history). The time period of our study (1987–2019) slightly overlapped with a barred owl removal study on 2 study areas (2015–2019 for CLE and 2013–2019 for HUP) designed to estimate impacts of barred owl on northern spotted owl vital rates (Wiens et al., 2021). While this created the potential for confounding our results, we think that our inclusion of a site- and year-specific barred owl covariate and the fact that only 3 occupied territories that burned were within the removal area minimized this potential.

We assessed model goodness-of-fit with program U-CARE (Choquet et al., 2009), which tests for several sources of overdispersion including trap dependence, transience, and state memory. Program U-CARE indicated significant overdispersion at both spatial scales arising from the increased probability of detecting an owl in year t, if it was also detected in year t-1 (i.e., trap dependence), as well as some overdispersion arising from state memory. We conservatively addressed overdispersion by, 1) creating a time-varying, individual covariate when modeling recapture rates (p) that was 1 if an individual was recaptured in year *t-1*, and 0 otherwise to account for trap dependence and 2) adjusting the overdispersion parameter ($\widehat{c}$) to 1.12 to account for the 'left over' overdispersion not accounted for by our trap dependence covariate.

We created an a priori model set that represented competing hypotheses of the impacts of wildfire on northern spotted owl populations and individuals (Table S1) using a build-up approach within a secondary candidate set strategy following Morin et al. (2020). Using this approach, we initially determined the top, competitive model structures for the recapture parameter, p, while keeping the non-focal parameters, S and Ψ at a consistent model structure that accounted for some spatial and temporal variation. After determining the set of competitive models for the recapture parameter, we repeated this process for S and Ψ until we had 3 sets of competitive "submodels" for our 3 parameters of interest. During the final, combined modeling stage we examined all possible combinations of these competitive submodels to determine our final set of models from which we drew inference. This modeling approach is particularly useful when simultaneously modeling several parameters and has been found to be effective at capturing the top set of competitively ranked models (Morin et al., 2020).

Within the submodeling approach for survival, we built up model complexity by comparing models that represented competing hypotheses of the impacts of wildfire on northern spotted owl apparent survival (Table S1). This process began by comparing models that represented competing hypotheses of whether or not apparent survival varied by study area (Table S1, step 2.1). We then added structure that represented several competing hypotheses of chronic ($S_{UB} \neq S_{JB} = S_{PB}$), acute ($S_{UB} = S_{JB} \neq S_{PB}$), or no fire effects ($S_{UB} = S_{JB} = S_{PB}$) based on our 3 defined states (stage 2.2). We then added time and barred owl effects to the set of competitive models in stage 1. The set of hypotheses comparing estimates of state-specific apparent survival from stage 1 without time-varying, individual covariates of fire effects at the territory scale represented our assessment of population-level impacts of fire to spotted owl apparent survival. During stage 2 of our apparent survival modeling, we added time-varying, individual covariates of fire effects and salvage logging which represented various hypotheses of such effects on northern spotted owl apparent survival at the territory scale. Incorporating individual covariates with program MARK allowed us to partition some of the process variation attributable to fire and salvage logging effects among individuals within the population. Thus the sampling unit from which we draw inferences to for our stage 2 models is the individual and not the population (Franklin et al., 2000). The resulting set of competitive models from stage 2 represented our assessment of individual-level impacts of fire and salvage logging. To disentangle fire effects from salvage logging effects, we compared models representing only fire effects to models representing only salvage logging effects, and to models including both fire and salvage logging effects (Table S1). We did not combine multiple fire effects covariates in the same models.

We also used a build-up strategy when modeling Ψ (Table S1, Ψ models), which required extra consideration. We used the multinomial logit link function to constrain all transition estimates originating from the same starting state to sum to ≤ 1 ($\widehat{\Psi}^{JB\ to\ UB} + \widehat{\Psi}^{JB\ to\ PB} + \widehat{\Psi}^{JB\ to\ JB} \leq 1$) because owls must transition to one of these states. This constraint, however, imparts a dependency among all transitions that originate from the same starting state which can be problematic especially when including time-varying, individual covariates. We were most interested in how fire affects territory displacement (e.g., $\widehat{\Psi}^{JB\ to\ UB}$ and $\widehat{\Psi}^{PB\ to\ UB}$), so we only included covariates on transitions that described territory displacement and left the transition that describes territory fidelity (e.g., $\widehat{\Psi}^{JB\ to\ PB}$ and $\widehat{\Psi}^{PB\ to\ PB}$) without covariates. Because of this dependency in transition probabilities, program MARK only estimates $m - 1$ possible transitions originating from the same starting states and estimates the last by subtraction (i.e., it is not modeled directly). We set our states to estimate via subtraction to $\widehat{\Psi}^{JB\ to\ JB}$ for transitions from state JB and to $\widehat{\Psi}^{PB\ to\ JB}$ for the transitions from state PB so we could estimate covariate effects for the transitions of interest (i.e., $\widehat{\Psi}^{JB\ to\ UB}$ and $\widehat{\Psi}^{PB\ to\ UB}$). We did not add covariates to transitions from the unburned state (UB) because they were not the focus of this study.

We also modeled immediate ($\widehat{\Psi}^{JB\ to\ UB}$) and delayed ($\widehat{\Psi}^{PB\ to\ UB}$) displacement separately and applied a different set of covariates to each model. As with our modeling of apparent survival, we make inferences to population-level impacts based on displacement models without time-varying, individual covariates, and inferences to individual-level impacts from models that include territory-specific fire, salvage, and post-fire NR forest covariates. We used covariates for fire and salvage logging effects when modeling immediate displacement, and post-fire NR and salvage logging covariates when modeling delayed displacement. We hypothesized that spotted owls would immediately respond to fire effects and the decision to stay on a burned site would depend on the amount of NR forest that persisted after the fire. Because our variables are likely dependent on each other (e.g., burn severity influences post-fire NR and may also influence salvage logging), we took a conservative approach when including covariates by comparing single variable models with combined variable models and relied on variable precision and model ranking to assess model performance (Table S1).

We used a version of Akaike's Information Criterion (QAIC$_c$) that corrects for small sample-sizes and overdispersion when assessing model ranking. In general, we considered models within 5 $QAIC_c$ of the top-ranked model as competitive when modeling each of the submodels, but then constrained this criterion to models within 2 $QAIC_c$ of the top-ranked model when determining our final competitive model set from which we draw our inferences. In general, we discarded any models that contained covariates considered spurious or uninformative (sensu Arnold, 2010), except in a few cases where covariates that have consistently been found to influence northern spotted owl vital rates in previous studies, but whose 95 % confidence interval (CI) during initial modeling stages may have slightly overlapped 0.

3. Results

We estimated fire effects on spotted owl survival and movement rates based on 3427 individuals occupying 727 territories. We present all results for both scales of analysis as: home range (core area) unless otherwise specified. During our study period, 54 (45) large wildfires (>404 ha) burned through all or portions of 279 (219) owl territories at least once during our study period and 60 (33) owl territories were burned more than once. Mean fire return interval for territories burned more than once was 14.5 years. However, not all territories were occupied when fires occurred, resulting in 166 (121) owls directly affected by fire (state JB [just-burned]), 490 (352) owls indirectly affected by fire (state PB [previously-burned]), and 2771 (2954) owls unaffected by fire (state UB [unburned])). Approximately 90 % of all owls affected by fire were located in the 4 southernmost study areas (CAS, KLA, HUP, NWC) and were thus largely responsible for driving the observed relationships. While several of our study area boundaries contained areas characterized by an infrequent fire regime type, all of the spotted owl territories affected by fire in our study were within areas characterized by a historically frequent fire regime (Fig. 1).

3.1. *Wildfire impacts to northern spotted owl populations*

Initial modeling of apparent survival on burned vs unburned territories (Stage 1, Table S1) indicated there were no differences in apparent survival among the 3 states ($S_{UB} = S_{JB} = S_{PB}$) at either the core use or home range scale, or across time. This result suggested fire did not have a measurable population-wide effect on spotted owl survival during the study period, although point estimates for S_{JB} were slightly lower and more variable than estimates for S_{UB} and S_{PB} at both scales of analysis

(Fig. 2a). Estimates of apparent survival from our stage 1 models were: $S_{UB} = 0.846$; SE = 0.003 (0.845; SE = 0.003), $S_{JB} = 0.837$; SE = 0.036 (0.808; SE = 0.042), and $S_{PB} = 0.836$; SE = 0.009 (0.832; SE = 0.012).

Estimates of immediate (first year post-fire) and delayed (>1 yr post-fire) movement rates when not accounting for fire effects indicated owls were much more likely to remain on burned territories than move to an unburned territory, regardless of spatial scale (Fig. 2b). The probability of an owl remaining on a just-burned territory from year t to year $t + 1$ ($\widehat{\Psi}^{JB\ to\ PB}$) was 0.91; SE = 0.029 (0.88, SE = 0.037), and the probability of remaining on a previously-burned territory ($\widehat{\Psi}^{PB\ to\ PB}$) was 0.95, SE = 0.006 (0.94, SE = 0.008). The probability of being immediately displaced by fire ($\widehat{\Psi}^{JB\ to\ UB}$) was 0.07; SE = 0.025 (0.08; SE = 0.032), and the probability of delayed displacement (>1 yr post-fire; $\widehat{\Psi}^{PB\ to\ UB}$) was 0.03, SE = 0.005 (0.04, SE = 0.007).

3.2. Wildfire impacts to northern spotted owl individuals

Subsequent modeling of apparent survival with fire and salvage covariates (stage 2, Table S1) indicated apparent survival of spotted owls at both scales decreased as the extent and severity of fire increased, and that spotted owls were more sensitive to fire- and salvage-based disturbances occurring within their core use area than their home range (Table 3). The same fire effect covariates appeared in competitive models at both spatial scales (moderate and higher), but fire effects were additive and negative at the core use scale (Table 4, Fig. 3a), whereas fire effects at the home range scale were somewhat ameliorated by the proportion of pre-fire NR forest (i.e., an interaction effect; Table 5, Fig. 3b). Spotted owl apparent survival also appeared more sensitive to post-fire salvage logging within their core use area, but not their home range as this covariate was only supported at the core use scale (Table 3). Analyses at both spatial scales suggested the effect of time since fire was positive, which suggested post-fire apparent survival gradually increased with time (Tables 4, 5). The presence of barred owls had an additive, negative effect on spotted owl apparent survival at both spatial scales (Tables 3–5).

Immediate post-fire territory displacement ($\widehat{\Psi}^{JB\ to\ UB}$) was more likely as the extent and severity of fire within a spotted owl's core use area or home range increased (Tables 4, 5). The same fire effect covariate (high) was supported at both spatial scales and was the only covariate in competitive models with the exception of one model at the core use scale that included the effect of higher burn severity (Table 3b). Initial modeling of salvage logging on territory displacement indicated data were too sparse to reliably estimate salvage logging effects on immediate territory displacement, so we only included this effect relative to delayed territory displacement. Delayed post-fire territory displacement ($\widehat{\Psi}^{PB\ to\ UB}$) increased at the core use scale as the proportion of post-fire NR forest decreased (Table 4). A model describing salvage effects on delayed displacement at the core use scale performed poorly and was ranked >6 QAICc units below the top-ranked model and was not considered further. No other covariates were useful for explaining delayed territory displacement at the core use scale. None of our covariates for delayed territory displacement at the home range scale were informative. Initial modeling of delayed displacement at the home range scale ranked models that included salvage logging and post-fire NR forest in our set of competitive models, however the point estimate of salvage logging on delayed displacement at the home range scale was the opposite of our prediction and imprecise $\left(\widehat{B}_{salvage} = -5.14, SE = 3.93, 95\%\text{CI} : -12.845 - 2.546\right)$, and this model ranked only 0.20 QAIC$_c$ units lower than (i.e., above) the intercept-only model for delayed displacement indicating poor predictive power. The point estimate for post-fire NR forest on delayed displacement was also imprecise $\left(\widehat{B}_{NR.post} = -1.09, SE = 1.19, 95\%\text{CI} : -3.429 - 1.233\right)$ and ranked 1.2 QAICc units lower than the intercept-only model.

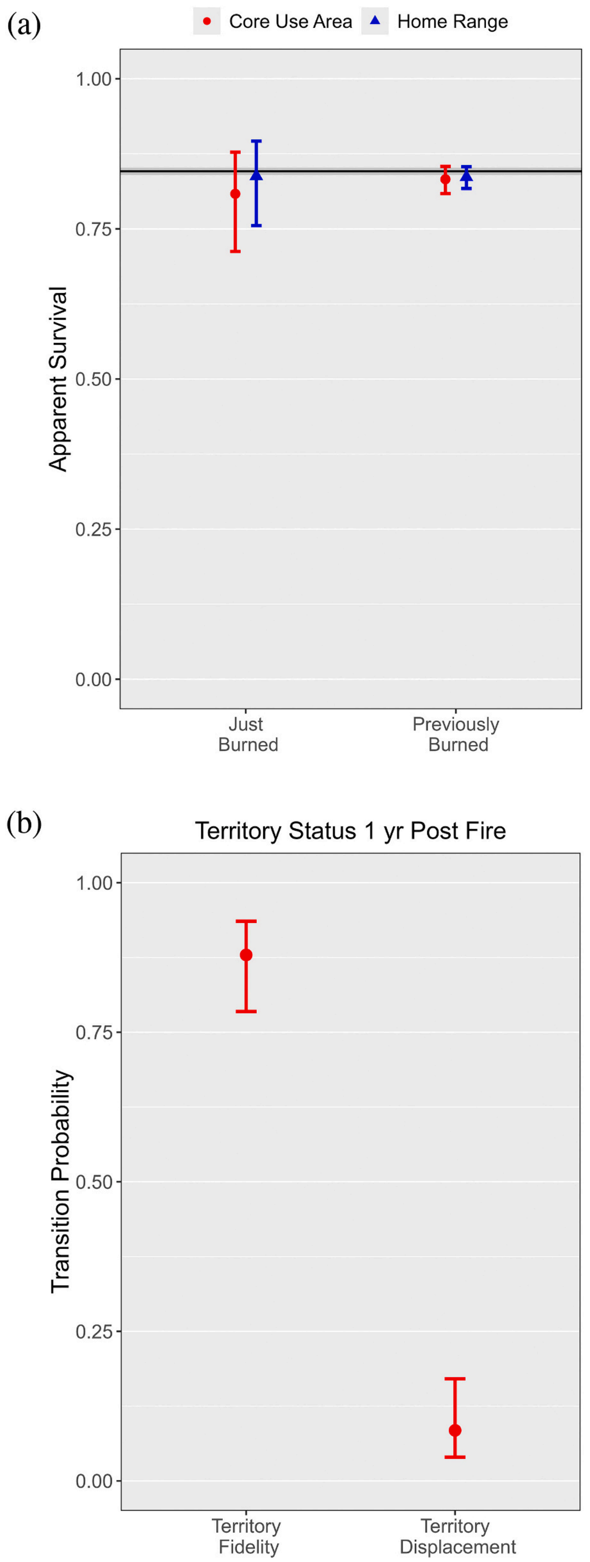

Fig. 2. Population-level estimates of (a) state-specific apparent survival at the core use and home range scales compared to owls not affected by fire (state = UN; horizontal shaded line), and (b) transition probabilities at the core use scale. Estimates of territory fidelity and displacement at the home range scale (not shown) were similar to estimates at the core use scale (shown here).

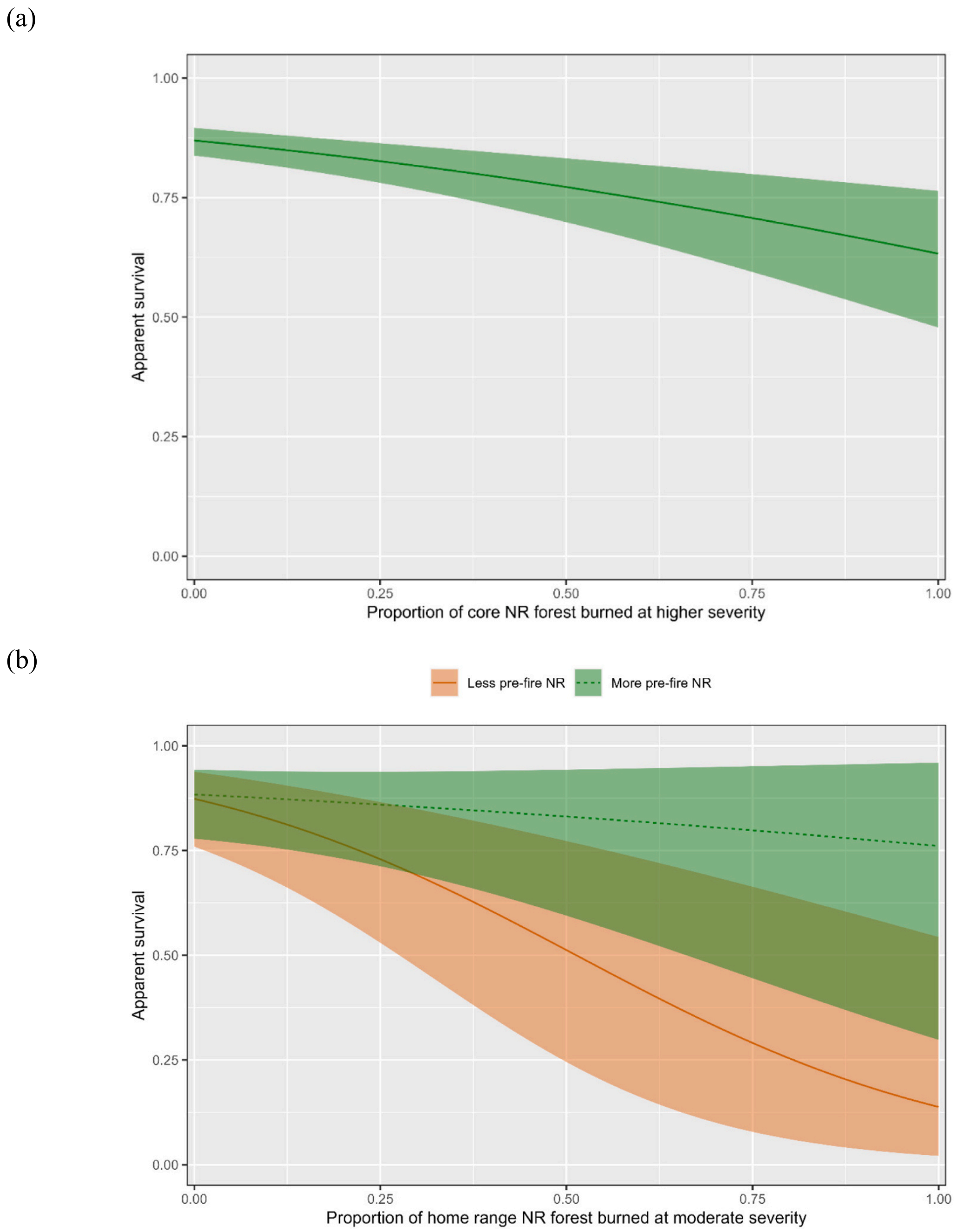

Fig. 3. Results from our top models of fire effects on northern spotted owl apparent survival indicating modeled relationships between apparent survival and the proportion of nesting and roosting (NR) forest burned higher severity within an owl's core use area (a), and the proportion of NR forest burned at moderate severity within their home range (b). Fire effects within an owl's broader home range were ameliorated to some degree depending on the amount of pre-fire NR forest (an interaction between severity and pre-fire NR), whereas fire effects within an owl's core use area were not ameliorated by the amount of pre-fire NR (additive effect only).

4. Discussion

Our results indicated that nuance is required when assessing the impacts of wildfire to northern spotted owls and that inferences can diverge based on the scale of the analysis and the characteristics of the fires used in the analyses. By including multiple samples (i.e., fires) we better captured the range of fire attributes (size, intensity, frequency, etc.; Fig. 4) that compose a fire regime. In addition, we were better able to assess the overall impacts of changing fire regimes to the population of northern spotted owls inhabiting the frequent fire portion of their geographic range. At the territory (individual) scale, our analysis indicated that wildfire can have important, negative impacts to individuals that depends on *how* and *where* wildfire effects occur. Northern spotted owl apparent survival decreased and territory displacement increased as the extent and severity of fire within an owl's territory increased, and owls were more sensitive to fire effects occurring within their core use area than their broader home range where fire effects could be ameliorated to some degree depending on the amount of pre-fire NR forest (proportion of NR forest lost on occupied territories ranged from 0.0 to 0.66 at the home range scale to 0.0–0.93 at the core use scale; Fig. 4). However, when examining wildfire impacts at the population scale (stage 1 of our analysis), our data indicated that during the course of this study (1987–2019), wildfires had not measurably impacted northern spotted owls at the population level as apparent survival for

Table 3

Final, top-ranked models of fire effects at the home range (a) and core use (b) scales on northern spotted owl apparent survival and movement rates.

(a)	Home range models					
Survival	Immediate displacement[a]	Delayed displacement[a]	k	QAIC$_c$	Δ QAIC$_c$	w_i
BO + NR.pre × MODERATE + TSF	High	–	60	26,787.93	0	0.201
BO + NR.pre × HIGHER + TSF	High	–	60	26,788.87	0.94	0.125
BO + HIGHER + TSF	High	–	58	26,789.00	1.07	0.118
BO + NR.pre × MODERATE + TSF	–	–	59	26,789.73	1.80	0.082
BO + MODERATE + TSF	High	–	58	26,789.91	1.98	0.075

(b)	Core use models					
Survival	Immediate displacement	Delayed displacement	k	QAICc	Δ QAICc	w_i
BO + HIGHER + SALVAGE + TSF	High	NR.post	60	26,252.1	0	0.211
BO + MODERATE + SALVAGE + TSF	High	NR.post	60	26,252.61	0.51	0.163
BO + HIGHER + TSF	High	NR.post	59	26,253.24	1.13	0.120
BO + MODERATE + TSF	High	NR.post	59	26,253.65	1.55	0.097
BO + HIGHER + SALVAGE + TSF	Higher	NR.post	60	26,253.92	1.82	0.085

Table acronyms are as follows: BO = barred owl presence, NR.pre = pre-fire nesting/roosting forest, NR.post = post-fire nesting/roosting forest, MODERATE = moderate burn severity, HIGH = high burn severity, HIGHER = moderate + high burn severity, TSF = time since fire, k = number of model parameters, QAIC$_c$ = Akaike's Information Criterion corrected for small sample sizes and overdispersion; Δ QAIC$_c$ = difference in QAIC$_c$ between top-ranked model and focal model; w_i = Akaike weights.

[a] Hyphen indicates intercept only structure on immediate or delayed displacement.

Table 4

Estimates of model coefficients ($\widehat{\beta}$), standard errors (SE) and 95 % confidence intervals (lower: LCI, upper: UCI) for the top-ranked model at the core use scale. Psi models were evaluated using separate intercepts for each transition, but we only present estimates for territory displacement.

Covariate	$\widehat{\beta}$	SE	LCI	UCI
Survival				
Intercept				
BO	−0.216	0.080	−0.373	−0.058
HIGHER	−1.353	0.301	−1.943	−0.762
SALVAGE	−1.294	0.703	−2.673	0.085
TSF	0.021	0.007	0.007	0.036
Immediate displacement				
Intercept	0.232	0.814	−1.364	1.828
HIGH	3.968	1.658	0.719	7.218
Delayed displacement				
Intercept	2.478	0.550	1.400	3.555
NR.post	−2.614	0.889	−4.356	−0.872

Table 5

Estimates of model coefficients ($\widehat{\beta}$), standard errors (SE) and 95 % confidence intervals (lower: LCI, upper: UCI) for the top-ranked model at the home range scale. Psi models were evaluated using separate intercepts for each transition, but we only present estimates for territory displacement.

Covariate	$\widehat{\beta}$	SE	LCI	UCI
Survival				
Intercept	2.853	1.139	0.620	5.086
BO	−0.129	0.062	−0.250	−0.008
NR.pre	0.217	0.158	−0.093	0.527
MODERATE	−5.759	2.106	−9.888	−1.630
NR.pre × MODERATE	6.381	3.777	−1.022	13.783
TSF	0.017	0.006	0.006	0.028
Immediate displacement				
Intercept	0.411	0.803	−1.162	1.984
High	5.095	2.347	0.495	9.696
Delayed displacement				
Intercept	0.717	0.269	0.189	1.245

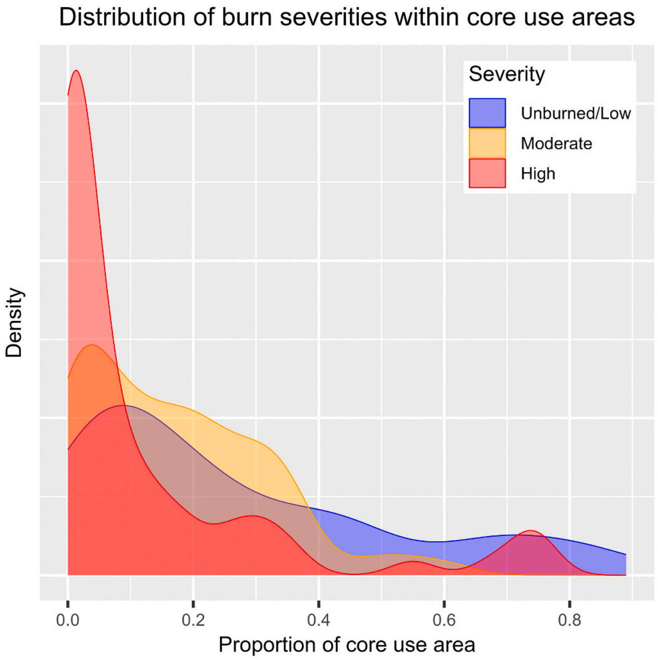

Fig. 4. Kernel densities of the proportion of NR forest within northern spotted owl core use areas that burned at unburned/low, moderate, and high severity. Most core use areas experienced low proportions of high burn severity and few core use areas experienced large proportions of high burn severity. The lack of a population-wide impact of fire on northern spotted owls in this region suggests that the observed patterns of burn severities within owl core use areas is likely within the bounds of the historical range of variability of the fire regime in this region.

owls residing on unburned, just-burned, or previously-burned territories did not differ. In addition, population-level estimates of territory displacement indicated owls were more likely to remain on burned territories. It has been well documented that northern spotted owls require sufficient amounts of older forests throughout most of their geographic range for nesting and roosting (Bart and Forsman, 1992, Bart, 1995, Franklin et al., 2000, Dugger et al., 2005). This suggests that, on average, the fires used in our analysis did not remove a sufficient amount of NR forest to render the territory unsuitable for spotted owls and that not enough spotted owl individuals had been negatively affected by fire to translate into negative population-wide impacts. Indeed, one year post-fire, owl home ranges had lost a median of 7.5 %, and owl core areas lost a median of 9.7 % of their pre-fire NR forest cover due to fire (Fig. 4). This pattern of important, negative fire effects to some individuals, but generally benign fire effects to the population as a whole likely mirrors the historical range of variability of the region's fire regime. A regime that is characterized by frequent, mixed-severity fire driven by the complex interplay of bottom-up and top-down drivers that results in a mosaic of post-fire seral stages that includes patches of persistent old forest that owls use for nesting and roosting; and less common higher severity fires when extreme weather conditions overwhelm bottom-up drivers and remove the otherwise persistent old forest stands (Agee, 1993; Abatzoglou et al., 2021). Our results indicated: 1) how and where fire effects occur within owl territories can have negative impacts to individuals, 2) during the course of this study most, but not all, territories burned with generally lower severity fire effects (Fig. 4), such that, 3) not enough individuals were negatively impacted by fire to translate into negative population-wide impacts, and 4) that our data suggests that changing fire regimes have not yet shifted enough to result in measurable impacts at the population level despite the occasional higher-severity fire that negatively affects some individuals.

In addition to population- and individual-level distinctions, we also observed relevant differences in owl responses depending on where fire occurred within a territory. Northern spotted owls were more sensitive to disturbances that occurred within their core use area relative to those occurring throughout their larger home range. Higher severity fire effects that occurred within an owl's core use area negatively affected apparent survival, whereas higher severity fire effects occurring within the larger home range could be ameliorated to some degree on territories that contained higher amounts of pre-fire NR forest. Additionally, salvage logging that occurred within an owl's core use area likely negatively affected apparent survival, whereas we did not find an effect of salvage logging within an owl's broader home range. Delayed territory displacement ($\widehat{\Psi}^{PB\ to\ UB}$) increased as the post-fire proportion of NR forest decreased at the core use scale, but not the home range scale, yielding further evidence of enhanced sensitivity to forest disturbance within their core use areas. We used annual maps of NR forest in our analysis which captured some of the secondary fire effects associated with post-fire delayed tree mortality that was not captured in our fire effects covariates (which only represent initial fire effects). Additionally, spotted owls are known to exhibit high site fidelity (Forsman et al., 2002; Jenkins et al., 2021), and may remain site faithful even when post-fire territory conditions are marginal. We suggest a combination of the owl's high site fidelity and post-fire delayed tree mortality may result in situations in which owls are likely to remain on burned territories with marginal amounts of NR forest until the cumulative impacts of initial and secondary fire effects reduces NR forest cover below some threshold for territory fidelity, at which point owls disperse.

Core use areas represent locations of concentrated use within a home range and are usually tied to certain critical resources such as food or shelter (Samuel et al., 1985). For spotted owls, core use areas represent the majority of nest and roost locations within a territory (Berigan et al., 2012; Fig. 1), which are closely associated with a closed, multilayered canopy of large trees generally located on lower slope positions (Lahaye and Gutiérrez, 1999; Forsman et al., 2015; Sovern et al., 2015). It is hypothesized that this close association is tied to the protection this forest type provides from inclement weather, including both late season winter storms as well as excessively hot summer weather (Barrows, 1981), and there is both experimental and observational data that supports this hypothesis (Forsman et al., 1984; Ganey et al., 1993; Ting, 1998; Weathers et al., 2001; McGinn et al., 2023). Spotted owls have relatively narrow thermoneutral zones and easily suffer heat stress (Ganey et al., 1993; Weathers et al., 2001; Mikkelsen et al., 2022), which can affect long-term survival (Mikkelsen et al., 2023). During hot summer months northern spotted owls roost low to the ground beneath understory vegetation (Barrows and Barrows, 1978; Forsman et al., 1984) and maintain ambient roosting temperatures lower than the surrounding forest (Ting, 1998). Older coniferous forests in topographically-sheltered locations provide microclimates that are buffered or decoupled from the surrounding landscape and provide cooler and moister locations for spotted owls to roost and nest (Frey et al., 2016; Davis et al., 2019). During inclement winter weather northern spotted owls utilize a different strategy by roosting mid-canopy near the bole of large trees where the dense canopy reduces wind speeds, intercepts rainfall, and reduces radiative heat loss (Gates, 1980). Any disturbances occurring to this forest type within core use areas likely reduces its protective benefit and may negatively impact its suitability for northern spotted owls.

Conversely, spotted owls appeared less sensitive to fire effects at the broader home range scale. Areas of territories outside core use areas are mostly comprised of foraging locations. Northern spotted owls in the southern portion of their range utilize a broader range of vegetation conditions for foraging than their northern counterparts (Forsman et al., 1984; Zabel et al., 1995), including young forest and complex early seral stages, which is likely tied to the occurrence of the dusky-footed woodrat whose geographic range is limited to the southern portion of the spotted owl's range (Carey et al., 1999). Dusky-footed woodrats can occur in high densities in early seral forest (Sakai and Noon, 1993; Hamm, 1995; Kuntze et al., 2023) and are the largest prey item for northern spotted owls by dietary biomass (Ward and Noon, 1998). Spotted owls in this region forage along ecotones between old forest and younger stands where woodrats are more abundant (Zabel et al., 1995; Ward and Noon, 1998). Indeed, northern spotted owls appear to benefit from a mosaic of seral stages that includes large amounts of old forest in their core use area and more variable forest structure outside their core area (Franklin et al., 2000, Olson et al., 2004, Dugger et al., 2005). It has been hypothesized this mosaic of seral stages that was historically created and maintained by frequent, mixed-severity fire is the key mechanism responsible for creating the conditions that maximize territory fitness because old forest maximizes survival while heterogeneous forest maximizes reproduction (Franklin et al., 2000, Dugger et al., 2005). This tradeoff between survival and reproduction could represent a disturbance-adaptive trait of spotted owls where frequent fire and dusky-footed woodrats co-occur by allowing them to capitalize on the patchwork of seral stages maintained by mixed-severity fire. Thus, provided there is a sufficient amount of NR forest that persists through fire within an owl's core use area, more variable fire effects throughout their broader home range appear to have less of an effect on vital rates of spotted owls, and may provide the forest heterogeneity that promotes territory fitness of northern spotted owls in frequent-fire landscapes (Franklin et al., 2000, Olson et al., 2004).

Native wildlife species can be useful for assessing the implications of changing disturbance regimes because they can experience disturbance at multiple spatial scales and may be sensitive to both how and where those disturbance effects occur. Disturbances significantly alter vegetation structure and composition, which are core components of wildlife habitat and these alterations can affect a species' vital rates in different ways depending on the disturbance attributes. Because native wildlife is adapted to the HRV of the natural disturbance regime, they are able to cope with, recover from, or take advantage of the post-disturbance vegetation conditions. Disturbances that depart from the HRV may result in novel vegetation conditions not experienced in a species' evolutionary history and may erode species resilience by exceeding their adaptive capacity resulting in negative impacts to a species' vital rates. By leveraging these concepts of the HRV of disturbance regimes, adaptative capacity, and habitat use to model long-term species vital rate responses to numerous disturbance events occurring over three decades, we were able to assess the implications of changing fire regimes in a more ecologically informed way (Bunnell, 1995; Berry et al., 2016).

Nonetheless, despite our findings that support no population level impacts of fire within the frequent fire portion of the geographic range of the northern spotted owl, populations continue to decline (e.g., Franklin et al., 2021) and concern for the species long-term persistence is warranted. In addition to the ongoing threat of increasing wildfire activity, several external factors may contribute to an uncertain future for northern spotted owl populations. First and foremost, our study was retrospective and analyzed the effects of past wildfire activity on spotted owls, whereas future fire effects will depend on the nature of those wildfires. Wildfire severity in NR forest in this region has not yet increased appreciably during the decades of our study (Miller et al., 2012; Reilly et al., 2017; Lesmeister et al., 2021), but more frequent extreme fire weather conditions associated with climate change could result in fires with larger patches of high severity fire effects (Westerling, 2016; Parks and Abatzoglou, 2020). Furthermore, over a century of fire exclusion has increased the threat of severe fire by altering landscape vegetation patterns by homogenizing forest structure (i.e., fuels) over large spatial scales (Stephens et al., 2013), which has eroded the self-reinforcing pattern of burn severities that is evident in these frequent fire landscapes (Downing et al., 2021). Similar to other studies, we found that large high severity fires negatively impacted spotted owls (Roberts et al., 2011; Jones et al., 2016; Rockweit et al., 2017; Schofield et al., 2020). The influence of these weather-driven fires on NR forest cannot be overlooked because they can take centuries to develop from early seral stages (Franklin et al., 2002b). Indeed just 2 years after the conclusion of our study, the 2020 Labor Day fires in western Oregon burned ~340,000 ha at mostly high severity, including forests used by spotted owls for nesting and roosting. Prolonged hot and dry weather followed by a strong east wind event created conditions of rapid, high intensity fire growth (Abatzoglou et al., 2021; Reilly et al., 2022) that resulted in the loss of about 1510 km^2 of NR forest within those fire perimeters (R. J. Davis, unpublished data). Based on our findings, and those of other researchers (Jones et al., 2016, 2020; Rockweit et al., 2017; Eyes et al., 2017; Schofield et al., 2020) it is likely that spotted owls residing within the perimeters of those Labor Day fires were either displaced, killed, or took refuge in the few remaining pockets of old forest that may have persisted in topographically sheltered locations (Krawchuk et al., 2016). If our study included large wind-driven fires like the 2020 Labor Day fires, we would have been more likely to observe negative, population-level impacts of fire.

In addition, contemporary wildfires are occurring in forested landscapes that have greatly departed from their historical condition (Demeo et al., 2018). Whereas, pre-European settlement, a spotted owl displaced by wildfire may have had a reasonable chance of finding a new territory, contemporary spotted owls displaced by fire face additional stressors. Human land use practices and land ownership patterns have fragmented and reduced the amount of suitable forest cover which increases the threat of higher severity wildfire (Zald and Dunn, 2018; Levine et al., 2022), and causes dispersing spotted owls to traverse farther distances through a fragmented landscape before finding a suitable territory (Jenkins et al., 2019). It is also likely that the added stress of prospecting in a highly fragmented landscape increases fitness costs of those individuals who must disperse (Dickie et al., 2017). In addition, barred owls now occur throughout the entire geographic range of the northern spotted owl and are significant contributors to the rapid decline in spotted owl populations, now occupying most historical spotted owl territories (Franklin et al., 2021; Jenkins et al., 2021; Wiens et al., 2021). Indeed, northern spotted owls throughout their geographic range are dispersing more frequently and are moving farther now than they were when long-term demographic studies began (Forsman et al., 2002, Jenkins et al., 2021), exemplifying the increasingly inhospitable landscape spotted owls now inhabit. Thus, contemporary spotted owls displaced by fire must navigate a vastly different landscape compared to historical counterparts and these increased impediments to successful territory recolonization likely have important, negative implications for displaced spotted owls that we were unable to document in this study.

Our results beg the question, "what would it take for individual-level impacts to translate into negative population-wide impacts?". As populations continue to decline, demographic and environmental stochasticity coupled with the increasing threat of wildfire could have a disproportionate impact to remaining owl populations. The most recent population assessment indicated northern spotted owl populations have declined >75 % in Washington, >60 % in Oregon, and >50 % in California (Franklin et al., 2021). Current remaining population strongholds exist in parts of the southern Oregon Cascades and the Klamath Province of southwestern Oregon and northwestern California. These population strongholds occur in regions that are predicted to experience increased risk of large fires associated with over a century of fire exclusion and climate change (Davis et al., 2017). If large, weather-driven fire events like the 2020 Labor Day fires occur within these remaining population strongholds, they could remove a large proportion of the remaining spotted owl population.

Our state definitions allowed us to equate transition probabilities with movement probabilities (Nichols and Kendall, 1995), except in cases where owls remained on burned territories ($\widehat{\Psi}^{JB\ to\ PB}$ and $\widehat{\Psi}^{PB\ to\ PB}$) because this transition could arise from an owl either staying on the same territory that burned (a passive transition) or by an owl moving to a different burned territory (an active transition). Regardless, both cases represent owls remaining on burned territories and most northern spotted owls in our study that were affected by fire remained on a burned territory. Nonetheless, the probability of immediate displacement increased as the extent and severity of fire within either their core use area or their home range increased. This relationship (increased territory displacement following severe fire) is probably partly responsible for some of our observed decline in apparent survival because open population Cormack-Jolly-Seber models will underestimate true survival as the proportion of individuals that permanently emigrate from the study area increases because it cannot be differentiated from mortality (White et al., 1982). In this case, some of the owls that permanently emigrated outside of our study areas after fire would have shown up as reductions in apparent survival. While we do not know what proportion of our apparent survival estimate is composed of individuals that permanently emigrated, we suspect owls displaced by fire have lower survival rates than owls not displaced by fire for the reasons previously discussed.

Our results also demonstrated that movement rates of spotted owls varied depending on disturbance intensity and time since disturbance as owls were nearly twice as likely to move immediately following fire than anytime thereafter and movement rates varied depending on the proportion of NR forest burned at higher severity. Variation in animal movements following landscape perturbations is not uncommon (Driscoll et al., 2012; Brown et al., 2014; Finnegan et al., 2021; Barrile et al., 2022), and it is reasonable to suggest that pre-fire movement rates differ from post-fire movement rates. Using mark-recapture methods allowed us to directly measure movement rates because individual owls were identifiable, however, this source of heterogeneity is often overlooked when assessing impacts of large landscape perturbations using detection/non-detection methods (Rockweit et al., 2017). Accounting for this source of variation by separately modeling pre- and post-disturbance recapture rates may be important when conducting analyses designed to address the impacts of large-scale landscape perturbations.

5. Conclusion

By examining numerous wildfires across a broad spatial and temporal scale we were able to address the question of whether or not changing fire regimes throughout the frequent-fire portion of the northern spotted owl's geographic range are negatively impacting the species' population. While there is mounting evidence of altered fire regimes from over a century of fire exclusion (Agee and Skinner, 2005;

Taylor et al., 2021) with climate change threatening to alter it even more (Hanan et al., 2021), our retrospective analysis indicated that during our study period changing fire regimes in the region have not yet translated into negative population-wide impacts to northern spotted owls. Our results also highlight the importance of nuance when assessing disturbance effects (fire in this case) on native species because disturbance is an inherently variable process with variable outcomes depending on the attributes (intensity, size, frequency, location, etc.) of each disturbance event. At the individual level, we noted that *how* and *where* fire effects occur within an owl's territory can have negative effects on apparent survival and territory displacement. Northern spotted owls were more sensitive to wildfire effects occurring within their core use area compared to outside their core use area which probably reflects historical patterns of burn severity and habitat use that reflect the evolution of fire-adapted traits by spotted owls (Jones et al., 2020). However, our data also suggested that during the course of this study, not enough individuals were negatively affected by fire at the territory scale to translate into negative population-wide impacts, as evidenced by our comparison of state-specific apparent survival which measured the mean effect of fire on the population of owls (i.e., differences among states). Our study represents a comprehensive analysis of wildfire effects on northern spotted owl apparent survival and movement rates to date and incorporates fire effects from all large fires (>404 ha) that occurred from 1987 through 2018 within the frequent fire portion of the owl's geographic range. Despite our finding of no measurable negative population-wide impacts to northern spotted owls during our study, the northern spotted owl remains critically imperiled and faces an uncertain future. While our findings indicated that changing fire regimes have not yet negatively impacted northern spotted owl populations, future fire regime change impacts remain uncertain and we urge caution drawing inferences about future fire effects from this retrospective study. Indeed, with future predicted increases the number of extreme fire weather days throughout much of the region (Jones et al., 2022), it is likely that individual-level impacts may translate into population-level impacts, adding yet another stressor facing northern spotted owl populations as well as other old forest obligate species.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110701.

CRediT authorship contribution statement

Jeremy T. Rockweit: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Katie M. Dugger:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Damon B. Lesmeister:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Raymond J. Davis:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Alan B. Franklin:** Writing – review & editing, Resources, Methodology, Conceptualization. **J. Mark Higley:** Writing – review & editing, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

Acknowledgements

All animal use activities associated with the data used in this project were approved by Oregon State University's Institutional Animal Care and Use Committee. All data on NWC, KLA, CAS, HJA, and CLE were collected under animal use protocols approved by Oregon State University's and Colorado State University's Institutional Animal Care and Use Committees. Funding for the northern spotted owl data collection on federally-administered public lands was provided by the U.S. Department of Agriculture Forest Service, and U.S. Department of the Interior, U.S. Bureau of Land Management. Funding for studies on non-federal lands came from the Hoopa Tribe. Funding support for JTR was provided by the U.S. Department of Agriculture Forest Service, U.S. Geological Survey Northwest Climate Adaptation Science Center, the Department of Fisheries, Wildlife, and Conservation Sciences at Oregon State University, and the Oregon Cooperative Fish and Wildlife Research Unit. This research was funded in part by a U.S. Geological Survey Northwest Climate Adaptation Science Center award G17AC00218 to Jeremy Rockweit. At the time of publication, data were not publicly available from USDA Forest Service (RJ Davis, Raymond.davis@usda.gov) or the Hoopa Tribe (M Higley, mhigley@hoopa-nsn.gov). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflicts of interest.

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