

## Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape



Brendan K. Hobart<sup>a,\*</sup>, Kevin N. Roberts<sup>b</sup>, Brian P. Dotters<sup>b</sup>, William J. Berigan<sup>a</sup>,  
Sheila A. Whitmore<sup>a</sup>, Martin G. Raphael<sup>c</sup>, John J. Keane<sup>d</sup>, R.J. Gutiérrez<sup>a,e</sup>, M. Zachariah Peery<sup>a</sup>

<sup>a</sup> Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

<sup>b</sup> Sierra Pacific Industries, PO Box 496014, Redding, CA, USA

<sup>c</sup> USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA

<sup>d</sup> USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

<sup>e</sup> Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA

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### ABSTRACT

Biodiversity conservation in mixed-ownership landscapes often depends on contributions from privately-owned lands, where natural resource development can alter and produce novel habitat conditions for species of conservation concern. A lack of research on private lands stemming from access issues and concerns over regulatory outcomes, however, often limits evaluation of the impact of land management. The California spotted owl (*Strix occidentalis occidentalis*), for example, often occurs in mixed-ownership landscapes but research on this species has occurred primarily on public lands. Therefore, we conducted the first large-scale private-public cooperative and comparative analyses of California spotted owls inhabiting mixed-ownership landscapes in the Sierra Nevada, California, USA. We surveyed 151 spotted owl sites from 2013 to 2017 within two study systems: one comprised primarily of public lands (national forests) where the owl population has declined over the last ~20 years and a set of study areas comprised mostly of private lands on which relatively high estimates of site occupancy were recently reported. Multistate occupancy modeling indicated that the probability of occupancy and successful reproduction by owls depended on site status in the previous year, with both probabilities highest at sites where owls successfully reproduced in the previous year, intermediate at occupied sites where owls had not successfully reproduced, and lowest at previously unoccupied sites. Site occupancy probability was higher at low-elevation sites and lower at sites that contained more open area and younger forest. Successful reproduction by owls was also more likely at low-elevation sites and at sites with more north-facing slope and younger forest with high basal area of hardwoods. Study areas with more private lands tended to occur at lower elevations and have greater amounts of younger forest with high basal area of hardwoods, which may have contributed to higher occupancy and reproductive probabilities than the study area with more public land. Thus, differences in occupancy and reproductive probabilities between study areas appeared to be the result of differences in topographic and vegetation conditions that likely promote populations of key spotted owl prey species. Our results suggest that private lands in mixed-ownership landscapes may contribute to spotted owl conservation by conferring different benefits to owls than public lands and, more broadly, highlight the importance of including private lands in conservation research and planning.

### 1. Introduction

Privately-owned lands play an important role in biodiversity conservation (Kirby, 2003; Knight, 1999; Norton, 2000; Thomas, 2000). In the United States, about 72% of all land is private and the geographic ranges of approximately 80% of federally listed

threatened or endangered species occur at least partially on private lands (USFWS, 1997). Unlike publicly-owned lands, which are often managed for a balance of natural resource development, biodiversity conservation, and ecosystem services, resource extraction is often the priority on private lands (Bergmann and Bliss, 2004). Therefore, species conservation in mixed-ownership landscapes requires

\* Corresponding author at: 1630 Linden Drive, Madison, WI 53706, USA.

E-mail address: [bkhobart@wisc.edu](mailto:bkhobart@wisc.edu) (B.K. Hobart).

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strategies that maintain ecological integrity while allowing resource development to occur. Achieving this objective is challenging because resource development can alter habitat conditions for species of concern (Stanfield et al., 2002) and because mixed-ownership landscapes are typically characterized by complex landscape-scale patterns of landownership, habitat suitability, and species distributions (Dale et al., 2000; Mladenoff et al., 2007, 1997; Stanfield et al., 2002). Consequently, conservation success in mixed-ownership landscapes can hinge on understanding how species respond to varying and heterogeneous habitat conditions across multiple landownerships.

Effective conservation within mixed-ownership landscapes is often challenged by a lack of research on private lands resulting from restricted access, less funding, and landowner fear of regulatory restrictions resulting from research findings (Dale et al., 2000; Mir and Dick, 2012; Norton, 2000). Conversely, our understanding of species of conservation concern is typically based on research conducted primarily on public lands (e.g., carnivores; Peterson et al. 1998). For this reason, conservation scientists have largely focused on providing input about management issues on public lands (Knight, 1999). Nevertheless, failure to integrate private lands into conservation research and planning in mixed-ownership landscapes can lead to incorrect predictions about species responses to management, undesirable conservation outcomes, and increased tensions among stakeholders (Brook et al., 2003; Norton, 2000).

California spotted owls (*Strix occidentalis occidentalis*) occupy mixed-ownership landscapes throughout their range and have been studied extensively on public lands for decades, yet with relatively little attention paid to the influence of private lands (Stine and Manley, 2017; Verner et al., 1992). Until recently, it was assumed that the viability of this subspecies depended heavily on habitat conditions on public lands (Peery et al., 2017), whereas private lands were believed to make minimal contributions to the regional population based on studies demonstrating an avoidance of private lands for nesting, roosting, and foraging (Bias and Gutiérrez, 1992; Williams et al., 2014). Recent studies indicate that spotted owl populations are declining on three long-term national forest demographic study areas in the Sierra Nevada (Conner et al., 2016; Tempel and Gutiérrez, 2013), perhaps because of contemporary and historical loss of key nesting and roosting habitat elements (Jones et al., 2018; Tempel et al., 2014). In contrast, Roberts et al. (2017) reported high California spotted owl territory occupancy on mixed-ownership study areas (where private lands were managed primarily for timber production) relative to an adjacent national forest demographic study area. These different findings suggest that private lands, within a mixed-ownership context, may be more important for spotted owl populations in the Sierra Nevada than previously believed.

Because Roberts et al.'s (2017) comparison of spotted owl occupancy between public- and private-dominated landscapes was made in an *ad hoc* manner (e.g., potential differences in detection probabilities between study areas were not explicitly accounted for), we aimed to make comparisons among different studies more rigorous. In our study, we conducted the first large-scale, cooperative research effort between the U.S. Forest Service (USFS) and a large private landowner (Sierra Pacific Industries [SPI]) on California spotted owls inhabiting mixed-ownership landscapes in the Sierra Nevada, California, USA. By contrast, most previous studies of spotted owl populations have focused on the response of spotted owls to forest conditions without

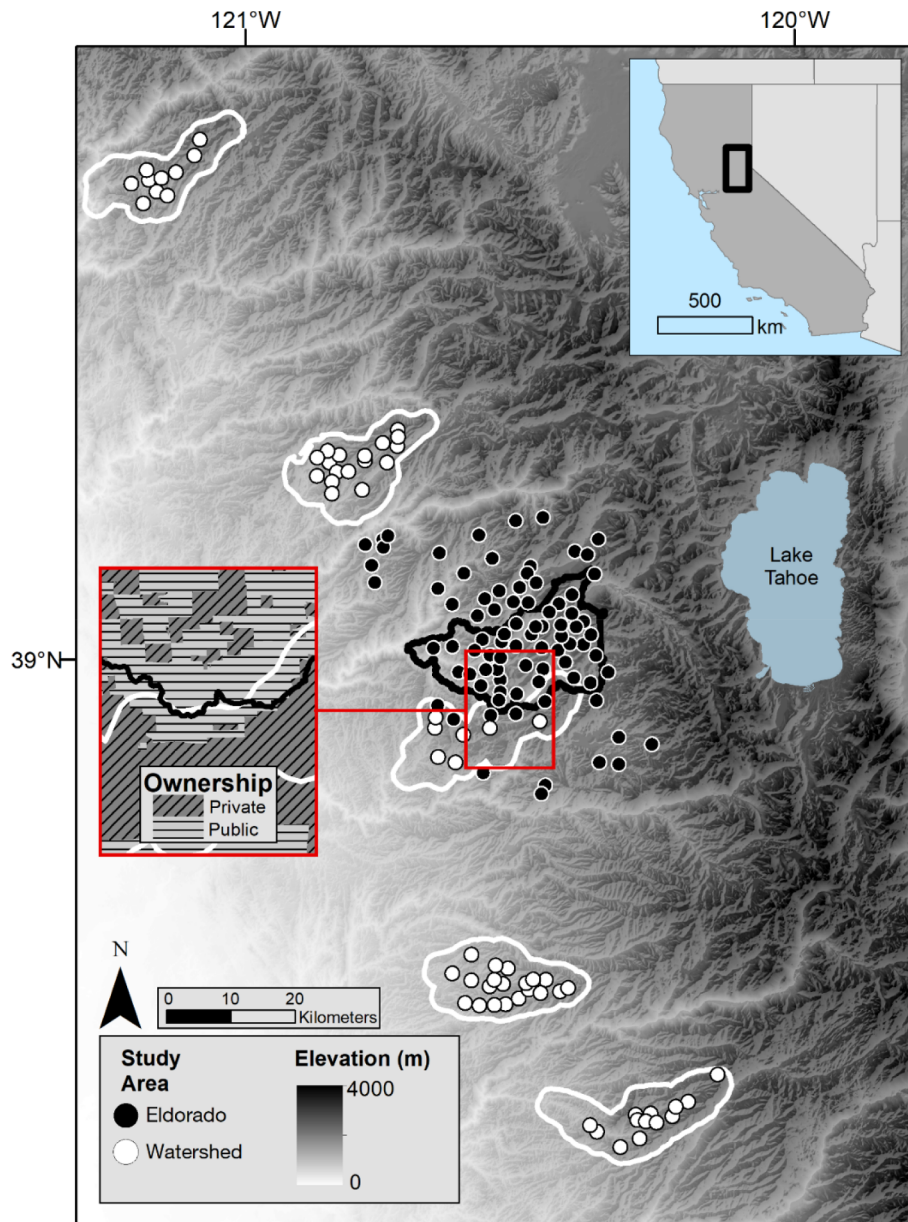
regard to ownership (e.g., Conner et al., 2016, Tempel et al., 2016; but see Dugger et al., 2016). Our primary objectives were to: (i) estimate spotted owl occupancy and reproductive dynamics in landscapes that varied in the proportion of public and private land; and (ii) assess the extent to which differences in site occupancy and reproduction among sites were a function of forest conditions, landownership, and other environmental factors. We used multistate occupancy modeling, which offers the opportunity to relate multiple life-history traits (e.g., site occupancy and reproductive state) to environmental conditions rather than simple species presence-absence (MacKenzie et al., 2009). Indeed, including information about multiple states may provide valuable insights because habitat components on various ownerships may have contrasting effects on different life-history traits (e.g., beneficial for occupancy but detrimental or unimportant for reproduction).

## 2. Materials and methods

### 2.1. Study areas and management history

Our study areas were located in the central and northern Sierra Nevada, California, USA (Fig. 1). Historical logging and fire suppression in the Sierra Nevada have shifted tree species composition towards shade-tolerant, fire-sensitive species (e.g., White fir [*Abies concolor*]), led to a deficit of large, old trees, and an increase in surface and ladder fuels (McKelvey and Johnston, 1992). Although national forests and private forests were historically managed similarly, concern over the status of the spotted owl in the early 1990's prompted the USFS to emphasize diameter-limited logging prescriptions (North et al., 2017; Verner et al., 1992). In contrast, even-aged timber harvest on private lands has increased relative to public forests (North et al., 2017). This history has resulted in dense, spatially homogenous national forests that lack large, old trees, and private forests that contain a mix of different conditions including recent clear cuts, plantations, and forests similar to those that occur on public lands.

We used data from two sources: the USFS Eldorado Study Area (EDSA) and SPI's five Watershed Study Areas (WSAs). The EDSA was 63% national forest and 37% private (largely non-SPI) lands, which included a core 355 km<sup>2</sup> "density" area and satellite territories surrounding the "density" area (Fig. 1). Conversely, on the five WSAs private landownership predominated (overall 69%, range 48 – 94%), with lesser amounts of national forest (mean 30%, range 6 – 52%). The 549 km<sup>2</sup> (range 86 – 137 km<sup>2</sup>) WSAs spanned a 145 km latitudinal gradient (Roberts et al., 2017). The locations of all study areas were selected nonrandomly. Primary vegetation on all study areas was Sierran mixed-conifer forest, with white fir, Douglas fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), and black oak (*Quercus kelloggii*) dominating at low and intermediate elevations, while red fir (*Abies magnifica*) dominated at high elevations. Climate on the study areas was Mediterranean, with cool, wet winters and warm, dry summers. Although barred owls (*Strix varia*) are common throughout the range of the northern spotted owl (*S. o. caurina*) and are increasing in the northern Sierra Nevada, their low abundance in our study areas indicate that barred owls did not have a substantial effect on the spotted owl populations studied here (Keane, 2017; Roberts et al., 2017).



**Fig. 1.** Location of California spotted owl sites included in occupancy analyses. White and black shapes outline the WSAs and EDSA “density” area, respectively. Inset map displays an example of typical configuration of public and private lands on our study areas.

## 2.2. Owl surveys

We surveyed for owls on both study areas from March 15 to August 31, 2013–2017. Although the EDSA has been surveyed annually since 1986, we included only 2013–2017 data because we aimed to make direct comparisons to the WSAs, for which reliable data was only available 2013–2017; spotted owl occupancy and reproductive rates can vary annually (Conner et al., 2016; Franklin et al., 2000) so including data for additional years may have biased comparisons of occupancy and reproduction estimates. Territory locations on the EDSA were identified during long-term demographic research (Tempel et al., 2016), while territory locations on the WSAs were identified using records of annual owl activity centers found in the California Natural Diversity Database and from SPI’s owl surveys (Roberts et al., 2017). On the EDSA, only land within the “density” area was surveyed entirely while all WSAs were surveyed entirely.

We conducted initial early-season diurnal/twilight surveys annually to identify occupied territories on both study areas; on the WSAs, these surveys included all territories, whereas on the EDSA only territories that

were recently occupied (i.e., within the past 2–3 years) received an initial diurnal survey. We surveyed all territories at night (except those where initial surveys resulted in detections) 3–4 times per season by imitating spotted owl vocalizations for 10 min at predetermined call stations spaced 0.8–1.0 km apart or while walking routes connecting such points. When owls were detected nocturnally, we conducted diurnal follow-up surveys within 72 h to assess reproduction, locate roosts and nests, identify marked owls, and mark new owls with unique color bands. If follow-up surveys did not result in a detection, we resumed nocturnal surveys. We determined sex of detected owls by the pitch of calls, and assigned one of four age classes based on plumage characteristics (Moen et al., 1991). We determined the number of juveniles fledged by successful nests by offering live mice to adult owls, observing the delivery of mice to juveniles by parents, and counting the number of young observed outside the nest.

## 2.3. Modeling approach

We used multi-season multistate occupancy models to assess occupancy and reproductive dynamics that followed the conditional

**Table 1**

Notation and description of parameters used in multistate multi-season occupancy models employed to investigate occupancy and reproduction dynamics of spotted owls. Note that  $m$  refers to site state in year  $t$ : unoccupied (“0”), occupied without successful reproduction (“1”), or occupied with successful reproduction (“2”).

Parameter	Description
$p^{(1)}$	Probability of detecting occupancy of non-reproducing owls
$p^{(2)}$	Probability of detecting occupancy of reproducing owls
$\delta$	Probability of correctly classifying reproduction, given occupancy
$\Psi_0$	Initial occupancy probability
$\Psi_{t+1}^{[m]}$	Probability of transitioning to occupied at time $t + 1$ , given state $m$ at time $t$
$R_0$	Initial reproduction probability (given occupancy)
$R_{t+1}^{[m]}$	Probability of transitioning to reproductively successful at time $t + 1$ , given state $m$ at time $t$

binomial parameterization initially developed by Nichols et al. (2007) for a single-season sampling design, which was later extended to multi-season designs by MacKenzie et al. (2009). In our model structure, a site’s true state was either unoccupied (“0”), occupied without successful reproduction (“1”), or occupied with successful reproduction (“2”). Thus, detection and classification parameters estimated the probabilities of detecting occupancy and reproduction, respectively (Table 1). State parameters estimated the probabilities of initial occupancy and reproduction, while a set of transition parameters estimated the probability of sites becoming occupied and reproductively successful in subsequent years (Table 1). Our notation followed MacKenzie et al. (2009) where occupancy and reproductive parameters with a superscript were transition probabilities (e.g.,  $\Psi_{t+1}^{[m]}$  and  $R_{t+1}^{[m]}$ ) and those lacking a superscript were state variables (e.g.,  $\Psi_0$  and  $R_0$ ).

Our sampling unit of analysis was the owl territory (hereafter site), defined here as a circle with a radius equal to 1/2 nearest neighbor distance (NND) centered on a site’s activity center. One-half NND is a metric commonly used to denote areas of use for highly territorial species such as the spotted owl. We estimated site activity centers as the among-year spatial mean of nest locations when available and the within-year mean of roost locations for non-nesting years. We then calculated a single NND across all study areas (1.12 km). Although spotted owl site NND can vary with latitude (e.g., Tempel et al., 2016), the latitudinal range of our sites was relatively small, which justified the use of a single NND. We defined primary sampling periods as annual breeding seasons and secondary sampling periods as the 11 biweekly periods between March 15 and August 31. When we surveyed a site  $\geq 30$  min within a secondary sampling period, we assigned one of three survey results: no detection of owls, detection of at least one adult owl but no fledged juveniles, or detection of at least one fledged juvenile. We used a strict definition of “detection” to limit false-positives:

**Table 2**

Site-level covariates included in multistate models to explain variation in occupancy and reproduction dynamics of spotted owls on the EDSA and WSAs. Predicted effects were: positive (+) relationship between covariate and parameter; negative (–) relationship between covariate and parameter; and no specific prediction (x).

Covariate	Abbreviation	Description	Predicted effect on:	
			$\Psi_0, \Psi_{t+1}^{[m]}$	$R_0, R_{t+1}^{[m]}$
Open area	OPEN	Proportion of a site containing area with canopy cover < 40%	–	–
Younger forest	YF	Proportion of a site containing forest with QMD < 30 cm and canopy cover > 40%	+ / –	+ / –
Older forest	OF	Proportion of a site containing forest with QMD > 61 cm and canopy cover > 70%	+	+
Shannon’s evenness index	EVEN	Calculated based on OPEN, YF, and OF covariates (unitless)	+	+
Diameter diversity index	DDI	Measure of forest structural diversity (unitless)	+	+
Basal area of hardwoods	BAHW	Mean live area of hardwoods (m <sup>2</sup> /ha, divided by 25 to scale for analysis)	+	+
Study area	SA	Binary indicator: WSAs = 1; EDSA = 0	+	x
SPI-owned land	SPI	Proportion of a site with SPI-owned land	x	x
USFS-managed land	USFS	Proportion of a site with USFS-managed land	x	x
Elevation	ELEV	Elevation (km) at a site-center	x	x
North-facing slope	NFS	Proportion of a site with slope aspect within $\pm 45^\circ$ of geographic north	+	+

we included observations as detections only if they occurred diurnally or involved identification of known adult resident owls by resighting their uniquely-colored leg bands (Berigan et al., 2018). We defined diurnal as the time between (and including) the hours of civil twilight in the morning and civil twilight in the evening, which varied by study area and year.

In September 2014, the King Fire burned 39,545 ha in the central Sierra Nevada, including spotted owl sites on the EDSA and WSAs (Jones et al., 2016a). Jones et al. (2016a) demonstrated that owl sites that burned > 50% by area at high-severity (> 75% canopy cover loss) had significantly higher extinction probabilities following the fire, while sites that experienced < 50% high severity fire did not. Thus, to limit the potential confounding effects of wildfire on our comparisons, we censored 15 owl sites from 2015 to 2017 that experienced > 50% high severity fire (14 on the EDSA and one on the WSAs).

2.4. Site-level covariates

We included a suite of *a priori* covariates in occupancy models that fell into three broad categories: land cover, ownership, and topography (Table 2). We constructed land cover covariates using gradient nearest neighbor (GNN) forest structure maps produced by the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) group (Oregon State University, Corvallis, OR, USA). Briefly, GNN data estimates forest conditions at 30 m resolution based on extensive forest-inventory plots and Landsat imagery (Ohmann and Gregory, 2002). We averaged 2013–2016 GNN data, except for owl sites that were severely burned > 50% in the King Fire, in which case we averaged only data from 2013 and 2014. Our three forest class covariates were open areas and sparse forests (hereafter “open areas”), younger forest, and older forest. We limited our analyses of cover classes to these three to reduce the number of models run, avoid spurious relationships, and focus on specific *a priori* hypotheses of interest. Open area was calculated as the proportion of pixels in an owl site that had canopy cover less than 40%. Younger forest was calculated as the proportion of pixels in an owl site with canopy cover greater than 40% and quadratic mean diameter of dominant and codominant trees (QMD) less than 30 cm. Older forest was calculated as the proportion of pixels in an owl site with canopy cover greater than 70% and QMD greater than 61 cm. We selected these criteria based on patterns of land cover in our study areas, previous work on spotted owl-habitat relations, and the reasonable correspondence of these classes to National Agriculture Imagery Program (NAIP) imagery (60 cm resolution; Fig. 2). Pixels with less than 40% canopy cover described low canopy cover forests and areas recently cleared as part of even-aged management practices, so we predicted that occupancy and reproduction would be lower at sites with more open area based on the importance of older forest for spotted owls (Tempel et al., 2016). Pixels with canopy cover greater than 40% and QMD less than

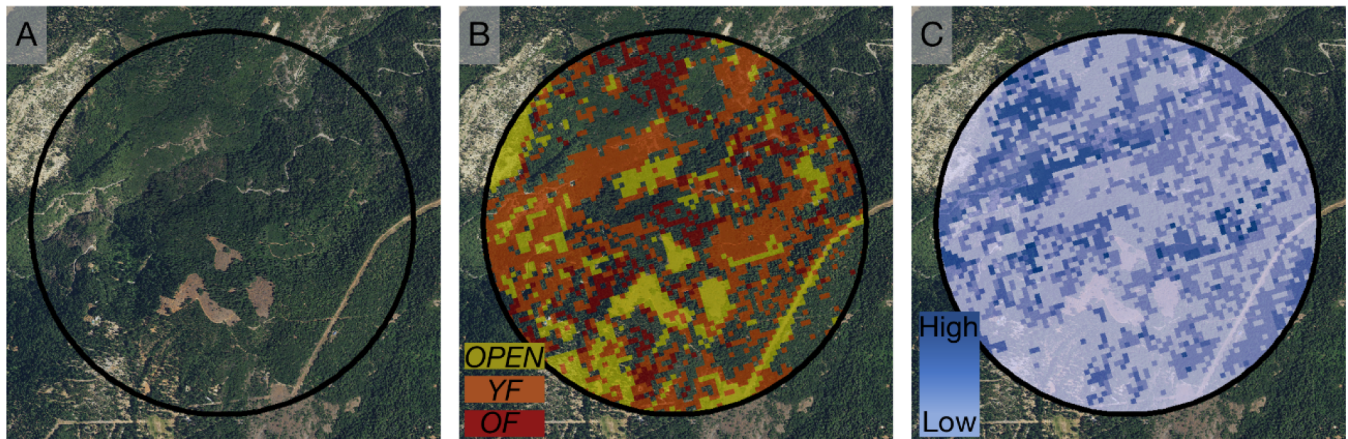


Fig. 2. Depiction of a typical spotted owl site visualized with (A) NAIP imagery, (B) GNN-derived covariates open area, younger forest, and older forest, and (C) GNN-derived basal area of live hardwoods.

30 cm typically corresponded to closed-canopy forests with sapling and pole-sized trees, which represents potential habitat for the dusky-footed woodrat (*Neotoma fuscipes*), an important spotted owl prey species (Hamm and Diller, 2009; Sakai and Noon, 1993). However, because spotted owls require older forests for nesting and roosting, we predicted that the relationship between younger forest and occupancy and reproduction could be positive or negative. Finally, forest with canopy cover greater than 70% and QMD greater than 61 cm was recently demonstrated to be strongly positively correlated with spotted owl occupancy in the Sierra Nevada (Jones et al., 2018; Moen and Gutiérrez, 1997), so we predicted that sites with more older forest would have higher occupancy and reproduction. We also included Shannon's evenness index calculated for the three preceding classes to describe site-level uniformity of forest conditions, which we predicted to be positively associated with occupancy and reproduction based on previous work demonstrating the importance of multiple forest cover types for spotted owl life-history traits (Franklin et al., 2000).

Other GNN-derived covariates included mean diameter diversity index (DDI; Spies et al., 2007) and mean basal area of hardwoods (Fig. 2). DDI is a unitless measure of stand-level forest structural diversity based on densities of different tree size classes and tends to increase with stand age. Thus, we predicted that spotted owl occupancy and reproduction would be greater at sites with higher average DDI, given the reliance of spotted owls on old forest conditions (Jones et al., 2018). We included mean basal area of live hardwoods because of the importance of hardwoods for woodrat habitat (Hamm et al., 2007) and predicted that sites with more hardwoods would have greater occupancy and reproduction, given the frequent consumption of woodrats by spotted owls (Thraillkill and Bias, 1989).

Our remaining covariates described study area, ownership, and topography. We specified study area as "0" for the EDSA and "1" for the WSAs. Based on Roberts et al. (2017), we predicted that occupancy would be higher on the WSAs but made no specific prediction about reproduction. We also used a proprietary ownership map (SPI, unpublished data) to estimate the proportion of owl sites on SPI and USFS ownership, each of which constituted a covariate. Finally, we included elevation (of activity centers) and north-facing slope (proportion of sites within  $\pm 45^\circ$  of geographic north) as covariates because of their relationship to a suite of biotic and abiotic conditions including microclimate, mean temperature, prey availability, and forest conditions (Jones et al., 2016b). We made no specific *a priori* hypotheses regarding the relationship between elevation and occupancy and reproductive parameters. We did, however, predict that sites with more north-facing slope would have greater occupancy and reproduction because north-facing slopes create favorable microclimatic conditions for both spotted owls (Barrows, 1981; North et al., 2000) and flying squirrels (*Glaucomys oregonensis*), which are important prey (Pyare and Longland, 2002).

## 2.5. Model selection

We used program PRESENCE 12.6 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit multi-season multistate occupancy models to our detection history data in a multistage hierarchical process. We ranked models within each of seven stages using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and progressed the best model structure from each stage forward to the next stage. We did not investigate interactions between covariates as doing so would have required fitting an excessive number of models, which can result in the selection of models describing spurious relationships. Additionally, we did not include covariates in model statements together if they were highly correlated ( $|r| > 0.60$ ; Table S1). The seven stages in our modeling framework were conducted as follows:

**Stage 1.** We determined the best within-year structure of  $p^{[1]}$ ,  $p^{[2]}$ , and  $\delta$  while holding their among-year structures fully time varying, and holding  $\Psi_{t+1}^{[m]}$  and  $R_{t+1}^{[m]}$  in a *state + year* structure (*state* refers to site status in the previous year). Within-year structures included: a "null" model where probabilities were constant among secondary sampling periods ("."); a site-specific "initial" response where the probability of detection/classification varied before and after the initial detection of occupancy/reproduction; an "early" effect, where the probability of classifying sites as reproductively successful varied before and after July 1st each year; and a within-year linear time trend ("T"). Note that  $p^{[1]}$  and  $p^{[2]}$  were always modeled separately but with the same structure, based on strong *a priori* knowledge that spotted owls are more detectable when reproducing than when not reproducing (Tempel et al., 2016).

**Stage 2.** We compared among-year and among-study area structures of  $p^{[1]}$ ,  $p^{[2]}$ , and  $\delta$  while holding  $\Psi_{t+1}^{[m]}$  and  $R_{t+1}^{[m]}$  in a *state + year* structure. Among-year structures included: a "null" model where all years were given the same coefficient; a linear time trend; a log-linear time trend ("lnT"); a full time-varying year effect ("year"); and a study area effect in which probabilities varied between the EDSA, the WSAs in 2013, and the WSAs 2014–2017 ("SAdet"). Because 2013 was the first full-effort field season on the WSAs, we predicted that detection and classification may have been relatively low in that year.

**Stage 3.** Prior to including site-level covariates, we assessed whether  $\Psi_{t+1}^{[m]}$  and  $R_{t+1}^{[m]}$  depended on state in the previous year, varied annually, varied in an additive *state + year* relationship, or neither (i.e., a "null" model).

**Stage 4.** We modeled the effects of site-level covariates on  $\Psi_0$ , using separate model suites for forest covariates (Stage 4.1), ownership covariates (Stage 4.2), and topographic covariates (Stage 4.3). We then compared and combined the top models from these sub-stages

**Table 3**  
Mean values (SD) for site-level covariates used to model variability in spotted owl occupancy and reproduction dynamics.

	Overall	EDSA	WSAs
<i>OPEN</i> <sup>A</sup>	0.15 (0.10)	0.16 (0.12)	0.13 (0.06)
<i>YF</i> <sup>A</sup>	0.24 (0.09)	0.23 (0.09)	0.24 (0.10)
<i>OF</i> <sup>A</sup>	0.07 (0.06)	0.06 (0.05)	0.07 (0.07)
<i>EVEN</i> <sup>B</sup>	0.66 (0.09)	0.66 (0.09)	0.66 (0.09)
<i>DDF</i> <sup>B</sup>	0.49 (0.06)	0.50 (0.07)	0.49 (0.05)
<i>BAHW</i> (m <sup>2</sup> /ha)*	7.54 (4.56)	6.81 (4.63)	8.46 (4.34)
<i>USFS</i> <sup>A</sup> ***	0.53 (0.37)	0.77 (0.22)	0.22 (0.27)
<i>SPI</i> <sup>A</sup> ***	0.31 (0.35)	0.07 (0.14)	0.60 (0.31)
<i>ELEV</i> (km) *	1.32 (0.27)	1.44 (0.22)	1.17 (0.24)
<i>NFS</i> <sup>A</sup>	0.27 (0.13)	0.28 (0.14)	0.25 (0.12)
<i>Post hoc covariates:</i>			
<i>YF low-BAHW</i> <sup>A</sup> ***	0.10 (0.05)	0.11 (0.04)	0.08 (0.05)
<i>YF high-BAHW</i> <sup>A</sup> *	0.14 (0.10)	0.12 (0.09)	0.16 (0.12)
<i>non-YF high-BAHW</i> <sup>A</sup> ***	0.30 (0.16)	0.26 (0.15)	0.37 (0.15)

Result of *t*-test comparing EDSA to WSAs: \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001.

<sup>A</sup> Covariate values are the proportion of an owl site.

<sup>B</sup> Unitless index.

to determine the best model for  $\Psi_0$  (Stage 4.4).

**Stage 5.** We modeled the effects of site-level covariates on  $\Psi_{t+1}^{[m]}$ , using separate model suites for forest covariates (Stage 5.1), ownership covariates (Stage 5.2), and topographic covariates (Stage 5.3). We then compared and combined the top models from these sub-stages to determine the best model for  $\Psi_{t+1}^{[m]}$  (Stage 5.4).

**Stage 6.** We modeled the effects of site-level covariates on  $R_0$ , using separate model suites for forest covariates (Stage 6.1), ownership covariates (Stage 6.2), and topographic covariates (Stage 6.3). We then compared and combined the top models from these sub-stages to determine the best model for  $R_0$  (Stage 6.4).

**Stage 7.** We modeled the effects of site-level covariates on  $R_{t+1}^{[m]}$ , using separate model suites for forest covariates (Stage 7.1), ownership covariates (Stage 7.2), and topographic covariates (Stage 7.3). We then compared and combined the top models from these sub-stages to determine the best model for  $R_{t+1}^{[m]}$  (Stage 7.4).

### 3. Results

#### 3.1. Survey effort and covariate distributions

We surveyed 151 individual spotted owl sites (84 on the EDSA and 67 on the WSAs) from 2013 to 2017 (mean = 136 sites/year; range:

**Table 4**

Beta coefficients (SE) for the top-ranked model resulting from multi-stage model selection (Table S8). Cells with “0” indicate that a covariate was not modeled for a given parameter. Parameters and covariates follow notation from Table 1 and Table 2, respectively. Bold font values indicate that the respective 95% confidence interval did not overlap zero.

<i>Detection probability parameters</i>						
	<i>initial</i>	<i>T</i>	<i>early</i> <sup>A</sup>	<i>late</i> <sup>A</sup>	<i>WSA 13</i>	<i>WSA 14–17</i>
$p^{[1]}$	<b>1.18 (0.17)</b>	+	0	0	0	0
$p^{[2]}$	<b>0.91 (0.22)</b>	+	0	0	0	0
$\delta$	0	0	<b>-1.63 (0.20)</b>	<b>1.29 (0.23)</b>	<b>-2.53 (0.45)</b>	<b>-0.55 (0.26)</b>
<i>Detection and reproduction parameters</i>						
	<i>ELEV</i>	<i>NFS</i>	<i>OPEN</i>	<i>YF</i>	<i>BAHW</i>	
$\Psi_0$	<b>-2.78 (0.96)</b>	0	0	0	0	
$\Psi_{t+1}^{[m]}$	<b>-1.91 (0.96)</b>	0	-4.13 (2.42)	<b>-7.30 (3.00)</b>	0	
$R_0$	-2.62 (1.40)	<b>4.53 (2.27)</b>	0	0	0	
$R_{t+1}^{[m]}$	0	2.16 (1.38)	0	0	1.71 (1.06)	

+ separate beta coefficients for each year; not listed.

<sup>A</sup> intercept term.

128 – 150). We detected occupancy at an average of 86 sites annually (range: 83 – 91) and successful reproduction at an average of 25 sites annually (range: 6 – 43). Basal area of hardwoods (*BAHW*), *USFS*, *SPI*, and *ELEV* were the only site-level covariates that differed significantly between the two study areas (all *p*'s < 0.05; Table 3). Four pairwise sets of covariates were highly correlated ( $|r| > 0.60$ , Table S1) and were thus only included in separate model statements.

#### 3.2. Stagewise modeling results

Modeling *stage 1* indicated that within-year detection of non-reproductive ( $p^{[1]}$ ) and reproductive adults ( $p^{[2]}$ ) was higher after owls were initially detected at a site ( $w_i = 1.0$ , Table S2, Table 4, Fig. 3A, B). Similarly, classification of successful reproduction ( $\delta$ ) was higher after July 1st ( $w_i = 1.0$ ; Table S2; Table 4; Fig. 3C). *Stage 2* modeling indicated that detection of non-reproductive adults ( $p^{[1]}$ ) increased linearly among years while detection of reproductive adults ( $p^{[2]}$ ) decreased linearly among years ( $w_i = 0.42$ ; Table S3; Table 4; Fig. 3A, B). Classification of successful reproduction ( $\delta$ ) was lowest on the WSAs in 2013, intermediate on the WSAs 2014–2017, and highest on the EDSA ( $w_i = 0.42$ ; Table S3; Table 4; Fig. 3C).

*Stage 3* indicated that the probability of a site becoming or remaining occupied ( $\Psi_{t+1}^{[m]}$ ) did not vary among years and was lowest when previously unoccupied, intermediate when previously occupied without successful reproduction, and highest when previously occupied with successful reproduction (i.e.,  $\Psi_{t+1}^{[0]} < \Psi_{t+1}^{[1]} < \Psi_{t+1}^{[2]}$ ;  $w_i = 0.91$ ; Table S4; Fig. 4A). The probability of a site having reproductively successful owls in a given year ( $R_{t+1}^{[m]}$ ) varied annually and followed the same previous-status relationship as occupancy (i.e.,  $R_{t+1}^{[0]} < R_{t+1}^{[1]} < R_{t+1}^{[2]}$ ;  $w_i = 0.91$ ; Table S4; Fig. 4B).

*Stage 4* indicated that initial site occupancy ( $\Psi_0$ ) declined as elevation increased ( $w_i = 0.33$ ; Table S5; Table 4; Fig. 5A). *Stage 5* indicated that the probability of a site becoming or remaining occupied ( $\Psi_{t+1}^{[m]}$ ) declined with increasing elevation, younger forest, and open area ( $w_i = 0.77$ ; Table S6; Table 4; Fig. 5B).

*Stage 6* indicated that initial reproduction ( $R_0$ ) decreased as elevation increased but was higher at sites with more north-facing slope ( $w_i = 0.26$ ; Table S7; Table 4; Fig. 6A). In modeling reproductive transitions (*stage 7*), two models received virtually identical support (both  $w_i = 0.12$ ;  $\Delta AIC = 0.02$ ; Table S8). Together, they indicated that the probability of a site having reproductively successful owls in a given year ( $R_{t+1}^{[m]}$ ) was higher at sites containing more north-facing slope and either more basal area of hardwoods or more younger forest (Table S8; Table 4;  $\beta_{YF} = 3.39$ , 95% CI = -0.82 – 7.60). Note, however, that

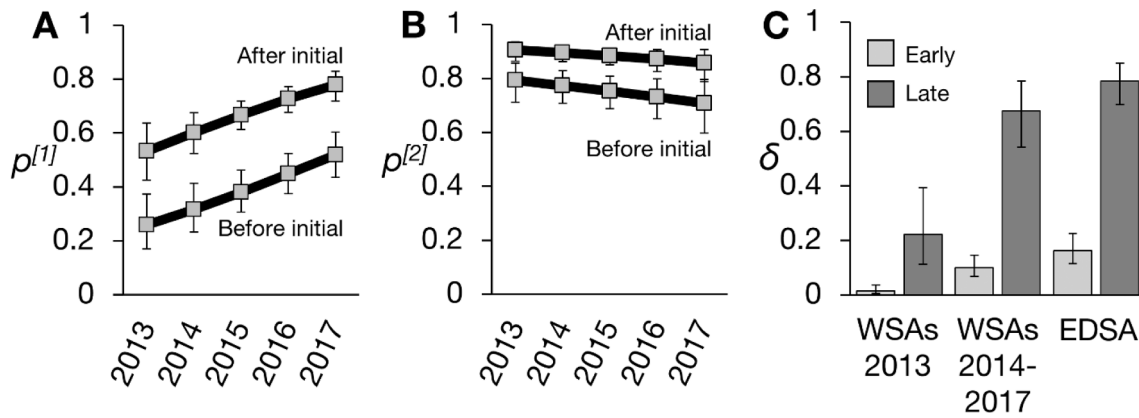


Fig. 3. Estimates of detection probabilities  $p^{[1]}$  (A) and  $p^{[2]}$  (B), and classification probability  $\delta$  (C) for California spotted owls based on model  $p^{[1]}(T, initial)$ ,  $p^{[2]}(T, initial)$ ,  $\delta(SAdet, early)$  (Table S8). Error bars correspond to approximate 95% confidence intervals.

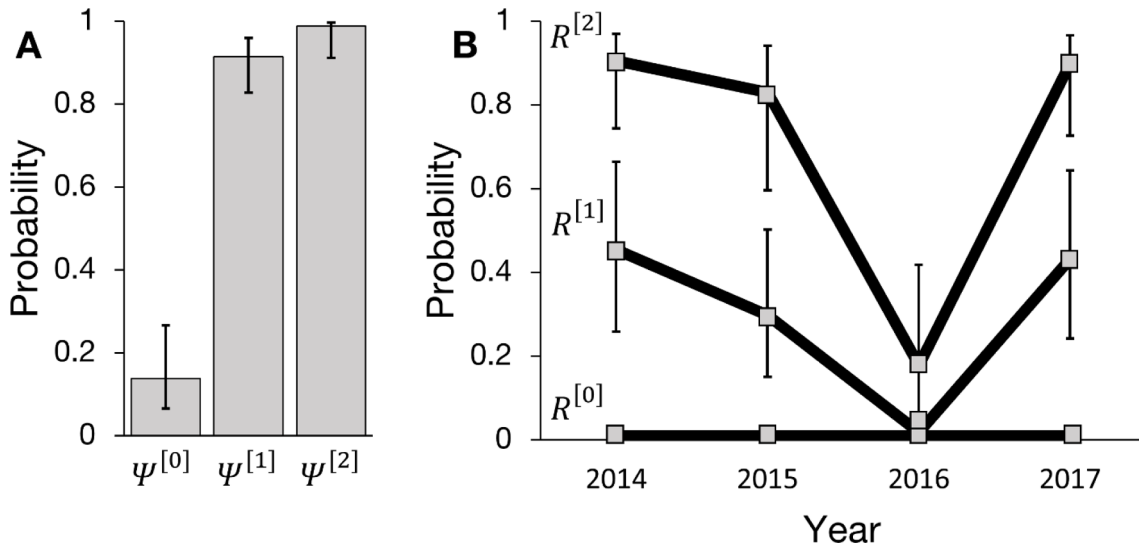


Fig. 4. Estimates of (A) occupancy and (B) reproduction transition probabilities for California spotted owls based on model  $\Psi_{t+1}^{[m]}(OPEN + YF + ELEV + state)$ ,  $R_{t+1}^{[m]}(state + year + BAHW + NFS)$  with all site-level covariates held constant at their mean values (Table S8). Error bars correspond to approximate 95% confidence intervals and were omitted for  $R_{t+1}^{[0]}$  estimates for clarity.

younger forest and basal area of hardwoods were positively correlated ( $r = 0.72$ ; Table S1). Furthermore, all models in stage 7.4 were within 2 AIC of the top model, including the “null” model, and AIC weight was distributed relatively equally among models indicating that a considerable amount of variability in reproductive data was not described by our covariates (Table S8).

### 3.3. Post hoc analysis

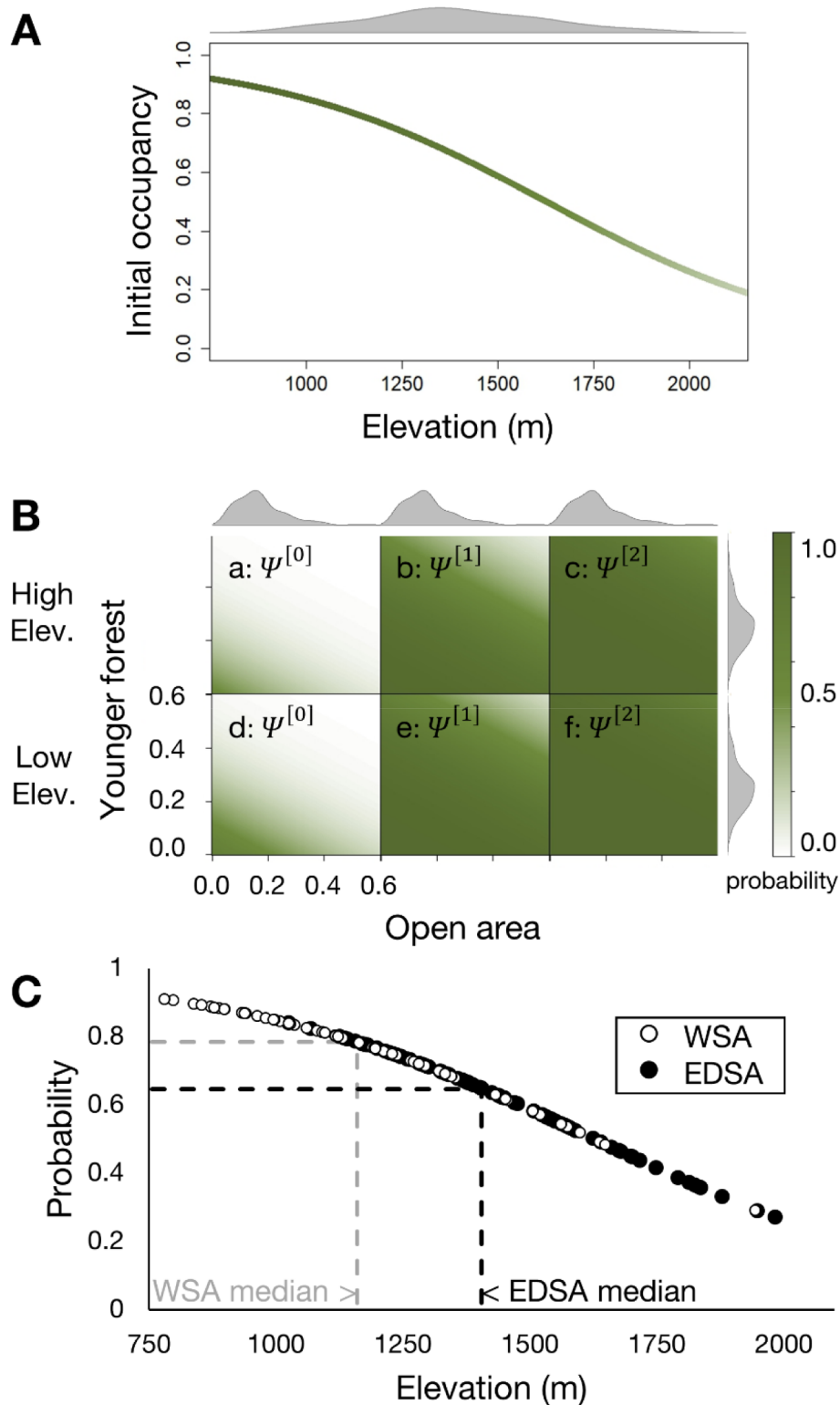
Because younger forest and basal area of hardwoods were essentially equally supported in stage 7.4 (Table S8) and were highly correlated at the site level (Table S1), we conducted a post hoc analysis to assess their relative importance for spotted owl reproduction. To do so, we defined three new site-level covariates: (i) younger forest with low basal area of hardwoods (YF low-BAHW), (ii) younger forest with high basal area of hardwoods (YF high-BAHW), and (iii) non-younger forest with high basal area of hardwoods (non-YF high-BAHW). We defined younger forest using our original criteria (QMD < 30 cm and canopy cover > 40%). We used the mean value of basal area of hardwoods at the pixel scale within sites (4.5 m<sup>2</sup>/ha) to distinguish between low and high levels of hardwoods. The new covariates, then, were the proportions of pixels within sites meeting these criteria. All three covariates differed significantly between the EDSA and the WSAs (all  $P < 0.05$ ;

Table 3) but were not significantly correlated with one another (Table S1). We proceeded to model reproductive transition probabilities ( $R_{t+1}^{[m]}$ ) as a function of north-facing slope (which occurred in the original top model) and each of the three new covariates (in additive relationships), with all other parameters held at their previously-determined best structure. We compared these models to one another and to a null (“.”) model. Our post hoc analysis indicated that the probability of successful reproduction in a given year ( $R_{t+1}^{[m]}$ ) was higher at sites containing more north-facing slope and more younger forest with high basal area of hardwoods ( $w_t = 0.51$ ; Table S9;  $\beta_{YFhigh-BAHW} = 3.07$ , 95% CI = -0.72 – 6.85; Fig. 6B).

## 4. Discussion

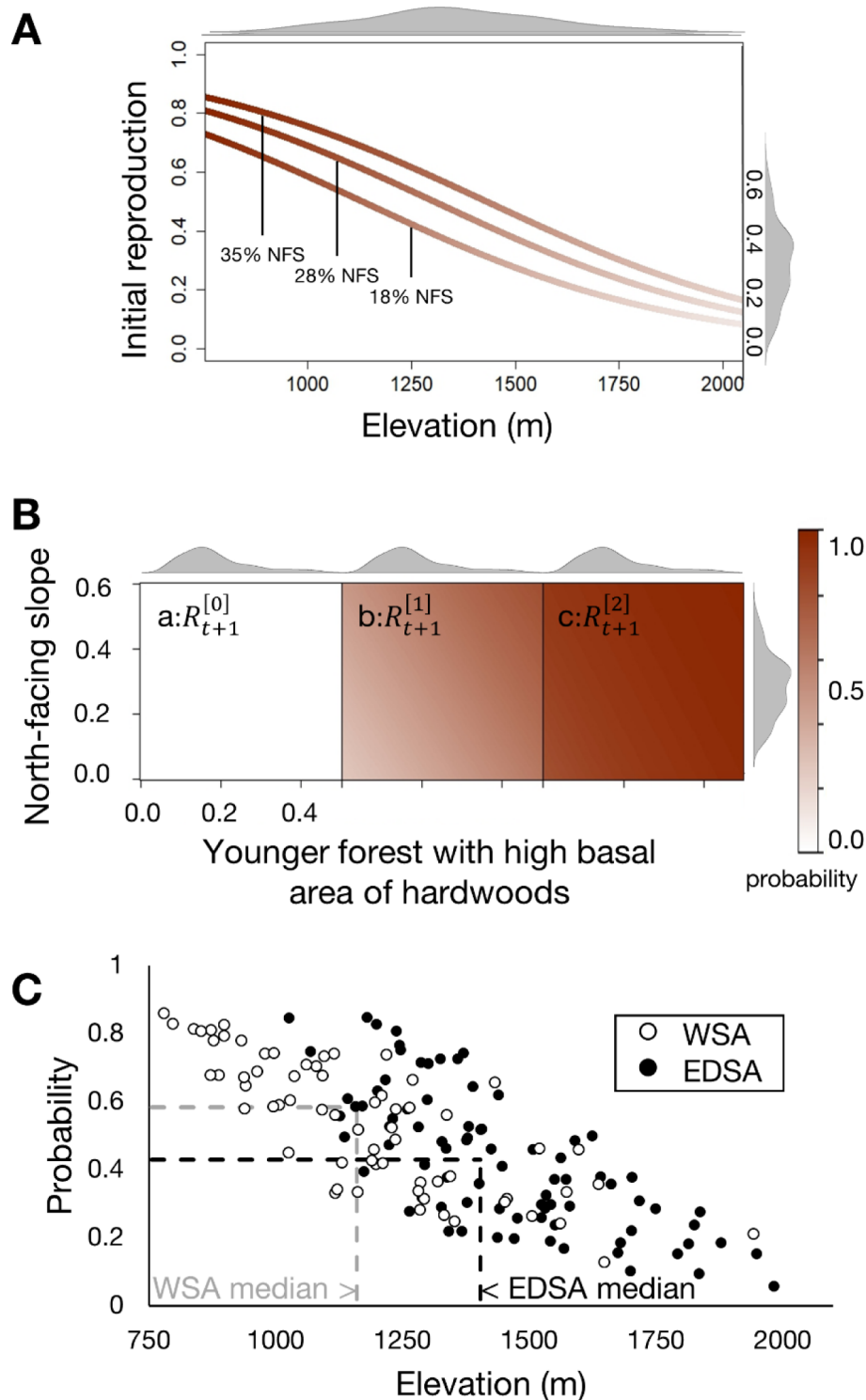
### 4.1. State-dependency of spotted owl occupancy and reproductive dynamics

Spotted owl site occupancy and reproduction exhibited strong autocorrelation: occupancy and reproductive success in year  $t + 1$  were dependent on state in year  $t$  and this structure explained a large amount of variability in the data. Specifically, occupancy was highest at sites that were occupied with successful reproduction in the previous year, intermediate at sites that were occupied without successful reproduction in the previous year, and lowest at sites that were unoccupied in the previous year. This finding supports the general understanding that



**Fig. 5.** A: Relationship between the probability of initial occupancy ( $\Psi_0$ ) and elevation for California spotted owls based on model  $\Psi_0(ELEV)$  (Table S8). The gray subplot above the main plot displays the frequency distribution of elevation of owl sites. B: Heat plots relating occupancy transition probabilities ( $\Psi_{t+1}^{[m]}$ ; color scale) to younger forest and open area for California spotted owls based on model  $\Psi_{t+1}^{[m]}(OPEN + YF + ELEV + state)$  (Table S8). Individual panels represent the probability of site occupancy at time  $t + 1$ , given it was unoccupied at time  $t$  (a, d), occupied without reproduction at time  $t$  (b, e), and occupied with reproduction at time  $t$  (c, f). Panels a-c represent the relationship with elevation held constant at its 3rd quartile (1.52 km) while panels d-f represent the relationship with elevation held constant at its 1st quartile (1.15 km). The gray subplots above and to right of main plots display the frequency distributions of open area and younger forest (respectively) at owl sites. C: Site-level estimates of initial occupancy probability for spotted owl sites on the EDSA and WSAs. Study area is denoted by color of points. Dashed lines indicate median elevation for each study area and corresponding initial occupancy estimates.





**Fig. 6.** A: Relationship between the probability of initial reproduction ( $R_0$ ) and elevation for California spotted owls based on model  $R_0(ELEV + NFS)$  (Table S8). Individual lines represent the relationship at different levels of north-facing slope (from bottom: 1st quartile, median, and 3rd quartile). Gray subplots above and to right of the main plot display frequency distributions of elevation and north-facing slope (respectively) at owl sites. B: Heat plots relating reproduction transition probabilities ( $R_{t+1}^{[m]}$ ; color scale) to north-facing slope and younger forest with high basal area of hardwoods for California spotted owls based on model  $R_{t+1}^{[m]} state + year + YF\ high-BAHW + NFS$  (Table S9). Individual panels represent the probability of a site successfully reproducing at time  $t + 1$ , given it was (a) unoccupied at time  $t$ , (b) occupied without reproduction at time  $t$ , and (c) occupied with reproduction at time  $t$ . Note that these probabilities varied annually; the relationships shown here are for the first transition (i.e.,  $t = 2013$ ,  $t + 1 = 2014$ ). The gray subplots above and to right of main plots depict the frequency distributions of basal area of hardwoods and north-facing slope (respectively) across owl sites. C: Site-level estimates of initial reproduction probability for spotted owl sites on the EDSA and WSAs. Study area is denoted by color of points. Dashed lines indicate median elevation for each study area and corresponding initial reproduction estimates.

spotted owls have high site fidelity and the observation that California spotted owl pairs are less likely to disperse from sites at which successful reproduction occurs (Blakesley et al., 2006; Gutiérrez et al., 2011). Because others have previously reported similar patterns in state-dependency for spotted owl occupancy, these processes likely apply to the species in general (e.g., MacKenzie et al. 2009, Lee and Bond 2015). Although the probability of successful reproduction fluctuated among years, it varied by state in the same pattern as occupancy: successful reproduction in year  $t + 1$  was most likely if reproduction occurred in year  $t$ . Autocorrelation in reproduction at a given site occurred despite previous evidence of the tendency for reproductive individuals to have a slightly reduced likelihood of breeding the following year (Stoelting et al., 2015). Thus, some owl sites appeared to be consistently high quality and may serve as population sources (Pulliam 1988). Predicting and identifying such high quality sites may be particularly important for prioritizing owl sites for habitat retention or forest restoration activities (Wood et al., 2018).

#### 4.2. Associations of site occupancy and reproduction with forest conditions and topography

Spotted owl occupancy and reproductive probabilities were associated with topographic and vegetation conditions at individual sites. Occupancy and initial reproduction were greater at low elevation sites, perhaps because the dusky-footed woodrat (*Neotoma fuscipes*), an important spotted owl prey species, is more common at lower elevations in the Sierra Nevada (Roberts, 2017). Indeed, woodrats are large in size and reach high population densities, which could promote occupancy and increase the likelihood of successful reproduction by spotted owls at lower elevation sites (Smith et al., 1999). Alternatively, Jones et al. (2016b) showed that owls at high-elevation sites in the central Sierra Nevada were more adversely affected by warm summer temperatures than at low-elevation sites. They suggested that warm, drought conditions may negatively impact flying squirrels – the primary prey of spotted owls at high elevations – by reducing hypogeous fungi biomass, which is the primary summer food of flying squirrels. Because our study occurred largely under drought conditions, declines in flying squirrel populations may also have contributed to the negative relationships between elevation and owl demographic parameters. Thus, elevational patterns in spotted owl demography may be related to underlying patterns in the abundance and distribution of prey resources.

As predicted, owl sites with more north-facing slope had higher probabilities of reproduction. North-facing slopes are generally cooler than south-facing slopes and may provide thermal refugia for spotted owls, a relatively cold-adapted species with limited ability to dissipate heat (Barrows, 1981; Ganey et al., 1993; Weathers et al., 2001). Barrows (1981) suggested that spotted owls reduced heat stress by selecting for roost locations on north-facing slopes. Additionally, because north-facing slopes tend to contain relatively more old forest with complex canopy structure (North et al., 2009), they may afford juvenile spotted owls greater protection from aerial predation than the surrounding landscape, which could positively impact reproductive rates (Franklin et al., 2000; Gutiérrez and Carey, 1985). Finally, mature forests on north-facing slopes may provide favorable habitat conditions for flying squirrels (Pyare and Longland, 2002), which are consumed relatively more frequently by reproducing owls than non-reproducing individuals (Thrailkill and Bias, 1989). Further research would be required to disentangle the relative contributions of microclimatic refugia, protection from predation, and prey availability to successful spotted owl reproduction.

Spotted owl site occupancy tended to be less likely at sites that contained more open area and greater amounts of younger forests. Younger forests and open areas are warmer than neighboring mature forests (Chen et al., 1995) and are also habitats for great horned owls (*Bubo virginianus*; Johnson 1992, Gutiérrez et al. 1995), which may increase the chances of either heat stress or predation, respectively.

Although younger forests and open areas may contain high densities of potential prey, younger forests may be too densely vegetated to allow hunting by owls and open areas often lack large branches from which spotted owls perch while hunting (Gutiérrez et al., 1995). Thus, there are several ecologically plausible mechanisms that may explain the observed negative associations between occupancy and open areas and younger forests.

In contrast to our occupancy results, our *post-hoc* analysis indicated that successful spotted owl reproduction tended to be more likely at sites containing a greater area of younger forest with high basal area of hardwoods. While previous studies have shown that spotted owls selectively forage in or near forests containing hardwoods (Irwin et al., 2007; Ward et al., 1998; Zabel et al., 1995), ours is the first to report a positive association between reproduction and younger forest with high basal area of hardwoods. This relationship may have been a function of prey abundance and availability: dusky-footed woodrat densities are highest in brushy, early-seral forests with an ample supply of downed logs and in the presence of mast-producing hardwoods such as large California black oaks (Innes et al., 2007; Sakai and Noon, 1993). Thus, patches of younger forest with high basal area of hardwoods within territories may provide owls with more woodrat prey, the consumption of which is positively associated with California spotted owl reproductive success (Smith et al., 1999). The juxtaposition of younger forest with high basal area of hardwoods with other cover types is likely an important consideration (Franklin et al., 2000); spotted owls forage in younger forests in proportion to its availability but selectively forage in older forests (Atuo et al., 2019; Blakey et al., 2019) and thus may benefit from the “spillover” of small mammals from younger forests into older forests (Sakai and Noon, 1993). We did not, however, investigate the relationship between forest spatial configuration and occupancy or reproduction because fine-scale inferences based on GNN data are not appropriate (D. Bell, personal communication). Furthermore, because GNN data is remotely-sensed, we could not systematically identify the most important hardwood species. A subjective, opportunistic ground-based evaluation indicated that the younger forest with high basal area of hardwoods cover type, as we defined it based on GNN data, was both floristically and structurally variable and often included: (i) brushy openings containing a variety of species such as deerbrush (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), and black oaks (Fig. S1A), and (ii) younger conifer forests containing a similar mix of hardwoods (Fig. S1B). Interpreting the relationship between spotted owl reproduction and younger forest with high basal area of hardwoods (as defined here) is further complicated by the fact that GNN appeared to sometimes misclassify this cover type: both our ground-based evaluation (Fig. S1C) and NAIP imagery inspection (Fig. S2) revealed that older forests were sometimes classified as younger forests with high basal area of hardwoods. Thus, additional work is required to establish which species and under what forest conditions (e.g., age) hardwoods benefit California spotted owl reproduction.

#### 4.3. Synthesizing population-habitat linkages in California spotted owls

Our current study is one of several that relate California spotted owl demographics to environmental conditions within territories and, in general, our results corroborate other such studies. For example, previous studies have indicated that spotted owl occupancy and reproduction were higher at sites with relatively large amounts of high canopy cover and older forests (Blakesley et al., 2005; Cade et al., 2017; Jones et al., 2016b, 2018, Tempel et al., 2014, 2016). Although older forest – which on average accounted for 7% of the area in our owl sites – was not supported in our final models for occupancy or reproduction, it did have a positive coefficient when present in models and generally outperformed intercept-only models. The negative associations of occupancy and reproduction with open areas were also consistent with previous studies and indicated that such habitats are less suitable for spotted owls (Blakesley et al., 2005; Gutiérrez et al., 1995; Tempel

et al., 2014). Thus, our research was consistent with previous studies that indicated California spotted owl populations may benefit from older and closed-canopy forests and can be adversely affected by younger seral stages within their territories.

Nevertheless, remaining uncertainties – and differences in results among studies regarding associations between spotted owl demography and habitat conditions – will challenge the translation of science into effective conservation and forest management. For example, Blakesley et al. (2005) reported lower occupancy and reproduction probabilities at sites with more younger forest, but Franklin et al. (2000) found that a broad category of cover types (“other,” which included younger forest) was correlated with higher owl reproduction. Our results reflect this uncertainty given that occupancy and reproduction were negatively and positively associated with younger forest, respectively. Differences in vegetation mapping and classification may account for some variability among studies associating spotted owl demographics and young forest. Indeed, previous studies have not quantified the prevalence of hardwoods (e.g., Blakesley et al., 2005; Franklin et al., 2000) – which likely provide important food resources for small mammal populations. And, as described above, some younger forest with high basal area of hardwoods (as classified in this study) may have contained older forests; as such, it is uncertain whether hardwoods or younger forest *per se* promoted high spotted owl reproduction. Future work that incorporates rigorous, ground-based measures of vegetation conditions – and ideally experimental manipulations of the hardwood component – may help resolve this and other uncertainties regarding spotted owl habitat requirements.

#### 4.4. Role of private lands in California spotted owl conservation

Despite decades of research, the importance of private lands for California spotted owl conservation has been uncertain. Although previous research demonstrated avoidance of private lands by spotted owls at both the territory (Bias and Gutiérrez, 1992) and foraging-site (Williams et al., 2014) scales, recent evidence suggested that landscapes containing relatively high proportions of private lands (the WSAs studied here) had higher site occupancy rates than landscapes containing more public land (the EDSA) and thus likely contribute to spotted owl conservation (Roberts et al., 2017). Here we found that spotted owl site occupancy and reproduction were best-explained by forest conditions and topography, with relatively little support for ownership covariates at either the site scale (proportion of territory in USFS versus SPI ownership) or landscape scale (EDSA versus WSAs). Yet, several important covariates differed significantly between sites occurring on the EDSA and WSAs: WSA sites, on average, occurred at lower elevations and contained more younger forest with high basal area of hardwoods (Table 3). Given our reported results for elevation and younger forest with high basal areas of hardwoods, these differences appeared to result in higher average site-level estimates of initial occupancy and reproduction probabilities on the WSAs (Fig. 5C and 6C). Of note, we observed these differences in occupancy and reproduction between study areas despite the prevalence of private lands on the WSAs, where even-aged forest management practices generate open and younger forest habitats, which our and previous work found reduced spotted owl occupancy (see above). As described below, the cause of this apparent discrepancy may hinge on the issues of cover type and prey species distributions.

A recent study indicated that GPS-tagged owls residing in the same mixed-ownership landscape studied here preferentially foraged in older forest near territory centers, but selected for diverse cover types (seral stages) at the periphery of territories (Atuo et al., 2019). These results suggest that outside of territory centers, a mix of stand conditions at fine spatial scales may provide foraging opportunities for spotted owls – even if some of those cover types are detrimental for nesting and roosting when considered at the territory scale. Given our and Atuo et al.’s (2019) results, management aimed at promoting a diversity of

cover types, maintaining adequate levels of older forest, and recruiting hardwoods (particularly mast-producing species like black oaks) following forest disturbance events (e.g., fire and harvest) may help concurrently conserve spotted owl populations and benefit forest ecosystems.

An alternative explanation for observed differences in patterns of occupancy and reproduction between study areas is that spotted owls occupying higher-elevation national forest-dominated sites (e.g., on the EDSA) may be more sensitive to forest thinning or logging that alters flying squirrels’ mature forest habitat – even when such practices retain more vertical structure than even-aged management systems (Jones et al., 2016b). By contrast, although reductions in closed canopy forests at lower elevations can also reduce spotted owl occupancy (Jones et al., 2016b), woodrats – a key spotted owl prey species at lower elevations – are less sensitive to forest management activities, particularly when some large living oaks are not harvested, hardwood regeneration is promoted, and residual snags and downed logs are retained (Innes et al., 2007). Further, differences in abundance of open and younger forests between the EDSA and WSAs – both of which contain mixed-ownership landscapes – were modest such that these habitat types did not disproportionately reduce occupancy on the WSAs relative to EDSAs (Table 3). Regardless, our results corroborate the finding of Roberts et al. (2017) that site occupancy tended to be greater on the WSAs than the EDSA and suggest that private lands like those studied here can contribute to spotted owl conservation in the Sierra Nevada depending on site conditions and management strategies/objectives.

#### 4.5. Conclusions

Spatial heterogeneity in ecological conditions – such as the juxtaposition of older forest nesting and roosting habitat interspersed with other cover types like younger forests with high basal area of hardwoods – may create opportunities for California spotted owl conservation in mixed-ownership landscapes with relatively high proportions of private lands, particularly at low elevations. Our study, however, had several important limitations: (i) we surveyed owl sites primarily on landscapes dominated by SPI-owned and USFS-managed land, with little inclusion of either national parks or other private ownerships; and (ii) our study areas did not extend into the southern Sierra Nevada. Thus, we limit our inferences to SPI/USFS mixed-ownership landscapes in the central and northern Sierra Nevada, as conditions may differ dramatically because of natural (e.g., drought-induced tree mortality in the southern Sierra Nevada) or anthropogenic (e.g., different management regimes) factors. Further research could extend the generality of the associations we described here, and, more importantly, elucidate ecological mechanisms (e.g., prey availability, microclimate) responsible for relationships between spotted owl demographics and landscape conditions.

Our research raises several considerations related to ecology and conservation in mixed-ownership landscapes. First, this work underscores the importance of overcoming barriers to research on private lands and in mixed-ownership landscapes, which may offer novel insights into species ecology and conservation. Second, landownership is not inherently beneficial or detrimental to biodiversity conservation. Given that the distribution of ownerships across landscapes is often nonrandom with respect to topographic and ecological characteristics (Drouilly et al., 2018; Scott et al., 2001), private lands may contain ecologically important and unique portions of species’ ranges. Third, our results exemplify the context-dependent nature of conservation in mixed-ownership landscapes: habitat conditions associated with private land management may provide benefits to species of conservation concern primarily under specific ecological conditions. Thus, because public and private lands may incur different benefits to species of concern, undertaking collaborative research that considers the full breadth of ecological conditions upon which species depend is vital to the success of conservation in mixed-ownership landscapes.

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## Declaration of interest

BKH, WJB, SAW, JJK, RJG, and MZP declare no conflicts of interest. KNR and BPD are currently employed by Sierra Pacific Industries, a private landowner. MGR is an ecological consultant currently contracted by Sierra Pacific Industries.

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## Animal rights

All research complied with University of Wisconsin – Madison Institutional Animal Care and Use Committee guidelines.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.01.028>.

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