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Declining old-forest species as a legacy of large trees lost

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Abstract

Aim: Global declines in large old trees from selective logging have degraded old-forest ecosystems, which could lead to delayed declines or losses of old-forest-associated wildlife populations (i.e., extinction debt). We applied the declining population paradigm and explored potential evidence for extinction debt in an old-forest dependent species across landscapes with different histories of large tree logging.

Location: Montane forests of the Sierra Nevada, California, USA.

Methods: We tested hypotheses about the influence of forest structure on territory extinction dynamics of the spotted owl (*Strix occidentalis*) using detection/non-detection data from 1993 to 2011 across two land tenures: national forests, which experienced extensive large tree logging over the past century, and national parks, which did not.

Results: Large tree/high canopy cover forest was the best predictor of extinction rates and explained 26%–77% of model deviance. Owl territories with more large tree/high canopy cover forest had lower extinction rates, and this forest type was ~4 times more prevalent within owl territories in national parks ($\bar{x}$ = 19% of territory) than national forests ($\bar{x}$ = 4% of territory). As such, predicted extinction probability for an average owl territory was ~2.5 times greater in national forests than national parks, where occupancy was declining ($\hat{\hat{\lambda}} < 1$) and stable ($\hat{\hat{\lambda}} = 1$), respectively. Large tree/high canopy cover forest remained consistently low, but did not decline, during the study period on national forests while owl declines were ongoing—an observation consistent with an extinction debt.

Main conclusions: In identifying a linkage between large trees and spotted owl dynamics at a regional scale, we provide evidence suggesting past logging of large old trees may have contributed to contemporary declines in an old-forest species. Strengthening protections for remaining large old trees and promoting their recruitment in the future will be critical for biodiversity conservation in the world's forests.

KEYWORDS
declining population paradigm, forest management, forest restoration, logging, occupancy modelling, spotted owl

1 | INTRODUCTION

Large old trees have declined across nearly all global ecosystems, in part because their high commercial value has led to logging pressure that outpaces sometimes centuries-long recruitment and development (Lindenmayer, Laurance, & Franklin, 2012). Agriculture (Laurance, Sayer, & Cassman, 2014), fire (Jones, Gutiérrez, Tempel, Whitmore et al., 2016; Westerling, 2016) and disproportionate drought susceptibility (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015) also increasingly threaten large old trees and conservation of old-forest ecosystems (Lindenmayer & Laurance, 2017). Loss of large old trees is a major contributor to habitat loss for many globally endangered old-forest-dependent (hereafter "old-forest") species such as the orangutan (*Pongo spp.*) in South-East Asia (Wich et al., 2003), the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) in western North America (Noon & Blakesley, 2006; Raphael, 2006), the Leadbeater's possum (*Gymnobelideus leadbeateri*) in south-east Australia (Lindenmayer et al., 2013) and the Blakiston's fish owl (*Bubo blakistoni*) in the Russian Far East and Japan (Slaght, Surmach, & Gutiérrez, 2013).

Like large old trees, many old-forest species have "slow" life histories with long generation times and high adult survival, which increases vulnerability when environments change rapidly (Webb, Brook, & Shine, 2002). Long-lived individuals may persist for many years in marginal or degraded forests long after critical breeding habitat elements such as large old trees are lost or substantially reduced, but gradually these individuals die off and may not be replaced. Delayed population declines or local extinctions resulting from prior habitat loss or degradation is termed "extinction debt," which can be assessed across different levels of organization (e.g., individual species vs. community) and may be evaluated at spatial scales ranging from local extirpation within a habitat patch to regional or global extinction of a species. Extinction debt challenges the ability of scientists to establish causal links between habitat loss and population declines of individual species (Kuussaari et al., 2009). Uncertainty about population status or causes of decline, then, could delay implementing conservation measures for old-forest species and the restoration of degraded old-forest ecosystems. Moreover, this uncertainty creates political opportunities to undermine governmental or social responses to make corrective changes (Oreskes & Conway, 2010).

Global challenges facing the conservation of large old trees and old-forest-associated species (Lindenmayer & Laurance, 2016) have led some to propose new and more rigorous policies for ensuring their protection and improving conservation outcomes (Lindenmayer et al., 2014). Nevertheless, if an extinction debt has already been created, population declines of old-forest species may continue to occur long after policies protecting large old trees are put into place. Here, we studied the potential long-term (multi-generational) impacts of large tree loss on an old-forest species, the spotted owl (*S. occidentalis*), across a large mountain ecosystem by comparing forest conditions and population dynamics between national parks (long-established protected areas) and national forests (areas that experienced widespread large tree logging but more recent protections). Following a century of extensive, intensive and selective logging of very large trees on national forests (Laudenslayer & Darr, 1990; Stephens, Lydersen, Collins, Fry, & Meyer, 2015), forest policy was enacted immediately prior to our study to conserve remaining old-forest elements such as large trees and multi-layered canopy around spotted owl activity centres (Verner et al., 1992).

Despite these recent protections, we hypothesized that this historical loss of large trees on national forests could be associated with contemporary population declines, or an extinction debt, for spotted owls. In testing this hypothesis, we treated protected areas (national parks) as "contemporary reference landscapes" (Collins et al., 2016; Meyer, 2015; Miller et al., 2016), because prohibition of logging within national park boundaries over the past century has largely preserved historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). Thus, in principle, contemporary forests characteristics in spotted owl territories on national parks (e.g., large trees) might more closely represent forests characteristics that might have existed on national forests if protections for large trees had been established long ago.

Comparing spotted owl populations on national forests and national parks, then, allowed us to diagnose causes of decline (Caughley, 1994; Green, 1995; Peery, Beissinger, Newman, Burkett, & Williams, 2004) for a species considered to be a barometer of old-forest wildlife community health in western North America (Simberloff, 1998). Despite the fact that the spotted owl is one of the most intensively studied species in the world with 40 years of demographic and ecological research across its range, no definitive causal link between ongoing owl declines and changes in habitat has been established. Here, we offer insight into this elusive question by applying the concept of extinction debt and provide an unprecedented case study about the potential ecological legacies of large tree loss on increasingly rare global old-forest species and ecosystems (Lindenmayer et al., 2012, 2014).

2 | METHODS

2.1 | Study areas and logging histories

Four spotted owl study areas—Lassen (LAS), Eldorado (ELD), Sierra (SIE) and Sequoia-Kings Canyon (SKC)—span nearly the entire latitudinal range of California's Sierra Nevada (Figure 1). Elevations range

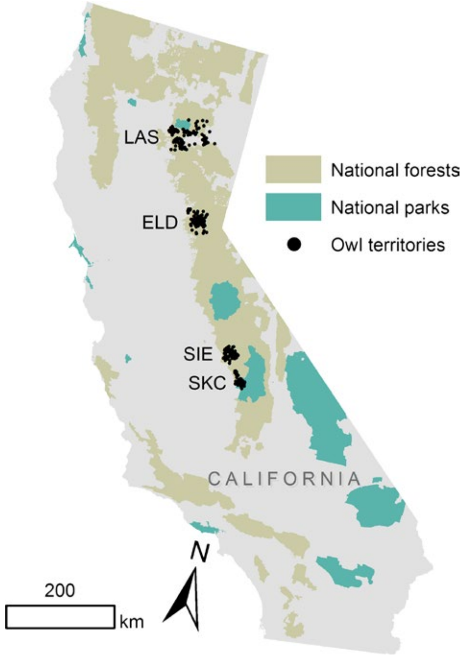

FIGURE 1 Locations of owl territories across the four spotted owl study areas in the Sierra Nevada, California, USA. [Colour figure can be viewed at wileyonlinelibrary.com]

from 300 to 3,050 m across the four study areas, and the climate is Mediterranean (Tempel et al., 2016). LAS, ELD and SIE study areas are primarily located within national forests (with intermixed private land), whereas SKC occurs within two national parks of the same name. While Sierran mixed-conifer montane forest is the primary vegetation type within owl territories across all study areas (Tempel et al., 2016), contemporary structure of these forests has been strongly affected by different management legacies across the two land tenures (i.e., national forests vs. national parks).

Very large (e.g., >125 cm dbh) old trees were not uncommon throughout the Sierra Nevada at the turn of the twentieth century (McKelvey & Johnston, 1992; Safford & Stevens, 2016). Several national parks including Sequoia (of SKC) were established in 1890 (Kings Canyon National Park adjoined in 1940), and the prohibition of logging within park boundaries over the following century largely acted to preserve historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). In contrast, logging activities on what would eventually become Sierra Nevada national forest lands were well underway by 1900 (Beesley, 1996; Thomas, 2008). Commercial logging (i.e., selective removal of very large trees) on Sierra Nevada national forests increased from ~470,000 cubic metres (m^3) $year^{-1}$ in the 1870s to its peak during the 1940s when timber production reached 4.5 million m^3 $year^{-1}$. Timber production remained reasonably high thereafter (generally between 2.8 and 3.8 million m^3 $year^{-1}$) for several decades before a near-historic peak in timber production in 1990 when production again neared 4.5 million m^3 $year^{-1}$ (McKelvey & Johnston, 1992).

Concern about the continued and cumulative loss of large trees required by spotted owls reached a highpoint around the same time and as a result, in 1992, logging of ≥76 cm dbh trees on national forests was restricted (with some allowable exceptions for equipment operability), as was almost all logging within 121 ha areas around known owl nest and roost sites (USFS, 2004; Verner et al., 1992). Our study on spotted owls began in 1993, immediately following near-peak logging activity and subsequent restrictions. Recent work has established that national forest lands indeed contain greater prevalence of younger trees that are smaller in diameter and height (Laudenslayer & Darr, 1990; Stephens et al., 2015) and significantly fewer trees in the largest size classes compared to historical baselines (Collins, Fry, Lydersen, Everett, & Stephens, in press; McIntyre et al., 2015; Safford & Stevens, 2016; Stephens et al., 2015). Given that SKC did not experience the same history of selective logging and forest structural change as the three study areas on national forests, we treated it as a contemporary reference landscape for evaluating differences in forest structure and owl population dynamics between land tenures.

2.2 | Owl surveys

As part of prior work, we have established that temporal changes in occupancy rates of spotted owl territories (i.e., based on detection/non-detection data) can provide inferences regarding overall population trends that are comparably reliable to estimates of overall population trends based on changes in abundance (Conner, Keane, Gallagher, Munton, & Shaklee, 2016; Tempel & Gutiérrez, 2013; Tempel, Peery, & Gutiérrez, 2014). As such, we conducted detection/non-detection surveys for spotted owls at 275 owl territories located during breeding seasons (Apr–Aug on LAS and ELD; Mar-Sept on SIE and SKC) across the four study areas over a 19-year period (1993–2011). All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e., both the areas containing owl territories and all areas not containing known owl territories within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (LAS) or as individual “satellite” territories (i.e., adjacent to, but not part of, the core area) to increase owl sample sizes for demographic analysis (LAS and ELD), and we dropped a portion of SKC in 2006 (Tempel et al., 2016). We surveyed all satellite territories used in our occupancy analyses for a minimum of 3 years; most territories in the core areas were surveyed for ≥15 years.

We located spotted owls by imitating their vocalizations (vocal lure) for 10 min at a survey station or used vocal lures while walking along a survey route. We then considered sites to be a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting during diurnal hours. Some surveys occurred prior to 1993 but previous analyses have determined that survey coverage and effort required for population analyses (such as ours presented here) became adequate beginning in 1993 (Tempel & Gutiérrez, 2013; Tempel et al., 2016). We did not survey all territories in all years of the study. However, of the 275 owl territories used in the study, ≥205 were surveyed in all but the first year of the study (in 1993, 187 owl territories were surveyed). The average number of owl territories surveyed annually was 239 (87% of all known territories; standard error = 21 territories), with a maximum of 263 territories surveyed in 2008 (95.6% of all known territories). Moreover, while most intervening area between territories was intensively surveyed each year, spotted owls on our study areas rarely established new territories outside of territories located in the early stages of the study. For example, the most recently located territory on the ELD was found in 1997. We included all surveys in our analyses but excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique colour leg-bands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary (see below for information on owl territories) using a Geographic Information System (GIS) to eliminate potential spurious positive detections of owls not occupying the nominal territories. A survey in which no owls were detected needed a total duration of ≥30 min to be included as an absence record. Extensive details about each study area and additional survey details can be found in Tempel et al. (2016).

2.3 | Sampling units and vegetation covariates

We treated owl territories as sampling units, where a territory had at least one owl detection during diurnal hours in ≥3 years. For quantifying habitat covariates within spotted owl territories, we first calculated the geometric centre of each territory as the average spatial coordinates of all nest and roost locations across all years in the territory.

We then calculated the mean nearest neighbour distance among territory centres for each study area as the average distance between each territory centre and the centre of its nearest neighbouring territory. Thus, the location of owl territories was assumed to remain the same throughout the study period, and territories in each study area were assumed to be of equal size based on the nearest neighbour distance. In a recent meta-analysis (Tempel et al., 2016), we defined the spatial extent of a territory as a circle around each territory centre with a radius equal to half of the mean nearest neighbour distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius) and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. In the present study, we defined territories as hexagons instead of circles with areas and geometric centres equal to those determined by Tempel et al. (2016) to facilitate integration into concurrent projects using spatial population models (e.g., HexSim; Schumaker, 2015).

We defined site-specific covariates based on two vegetation variables within owl territories using the "GNN" (Gradient Nearest Neighbour) forest structural maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group (Oregon State University, Corvallis, OR, USA). GNN is an imputation method used by LEMMA that integrates regional forest inventory plots with Landsat imagery to produce fine-scale (30-m resolution) and large-domain (currently the entire land area for the U.S. states of Washington, Oregon and California) vegetation structure and species composition maps. The GNN approach is one variation of nearest neighbour imputation methods that use (1) a neighbourhood value of $k = 1$ as the number of neighbours imputed to each cell and (2) direct gradient analysis as the "distance" metric (see https://lemma.forestry.oregonstate.edu/methods). The first variable was the quadratic mean diameter of dominant and codominant trees in each 30 × 30 m pixel ("QMD_DOM"). Quadratic mean diameter (QMD) is a commonly used metric in forestry that more strongly reflects the influence of large trees on stand tree size classifications than arithmetic mean (Curtis & Marshall, 2000). The second variable was the per cent canopy cover of live trees in each pixel ("CANCOV").

Large trees are a key feature of spotted owl nest sites (Gutiérrez et al., 1992), and owl site occupancy has been positively correlated with large trees (>61 cm dbh) and high canopy cover (>70%) at nest areas (Blakesley, Noon, & Anderson, 2005). However, forests with intermediate canopy cover (40%–70%) can constitute spotted owl nesting or roosting habitat if large, remnant trees are present (Hunter & Bond, 2001; Moen & Gutiérrez, 1997), and recent work found that both medium and high canopy cover were associated with spotted owl occupancy in the Sierra Nevada (Jones, Gutiérrez, Tempel, Zuckerberg, & Peery, 2016; Tempel, Gutiérrez, et al., 2014; Tempel et al., 2016). Thus, we estimated the proportion of each owl territory containing the following five covariates: large trees (QMD > 61 cm) regardless of canopy cover class; high canopy cover (>70% cover) regardless of tree size class; as well as the spatial intersection (∩; see Figure 2) of large trees and high canopy cover, large trees and medium canopy cover (40%–70% cover), and medium trees (QMD = 30–61 cm) and high canopy cover. These proportions were calculated by dividing the number of 30 × 30 m pixels in the territory for a particular variable by the total number of 30 × 30 m pixels in the territory. Several of the predictor variables were highly collinear (e.g., $r = .7–.9$), so we developed

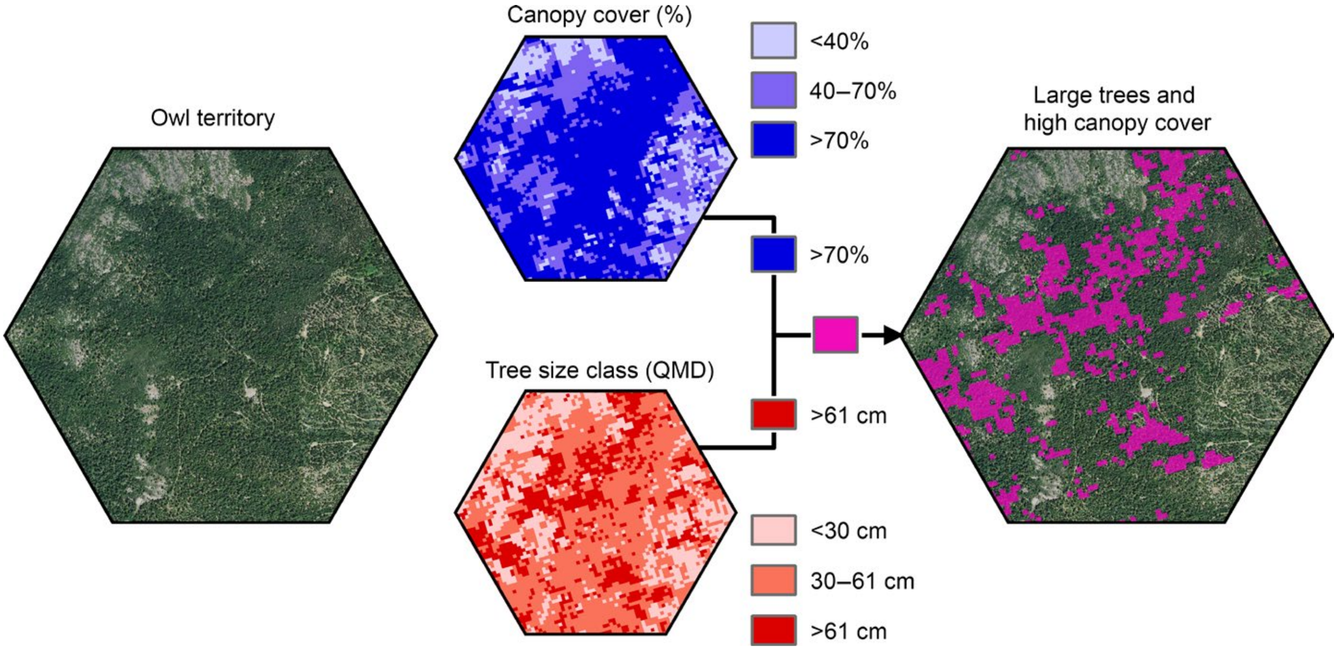

FIGURE 2 An example showing how we produced covariates representing spatial intersections between GNN-derived canopy cover and tree size classes by overlaying classified pixels using a GIS. Here, we see the high canopy cover class (>70% canopy cover) and the large tree size class (>61 cm dbh) combining in a spatial intersection (∩) to produce a covariate called "large trees and high canopy cover" for an example spotted owl territory. [Colour figure can be viewed at wileyonlinelibrary.com]

models that contained a single predictor variable and used AIC to identify which predictor variables best explained owl extinction dynamics (see below).

We adopted the above tree size classes because they are commonly used by foresters (Blakesley et al., 2005; Verner et al., 1992), although the large old trees used by owls for nesting are typically larger than 61 cm dbh (e.g., mean 157 cm dbh; North et al., 2000). Median QMD in the >61 cm dbh size class was 75.5 cm and reached a maximum of 279 cm (Fig. S1). Finally, for each forest structure variable listed above, we averaged the within-territory covariate values across all years (1993–2011) to produce a single, static territory-level covariate that varied across space (but was averaged over time), because nearly all variation in the covariates was spatial rather than temporal (large among-territory differences). Ranges of covariate values for each study area are provided in Table 1.

2.4 | Statistical analysis and model selection

We used multi-season occupancy models to assess territory occupancy dynamics on each study area separately (Tempel et al., 2016) using program PRESENCE 11.5. The models contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t) and detection probability ($p_{t,j}$) (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Our primary sampling periods (*t*) were breeding seasons (i.e., years), and our secondary sampling periods (*j*) were bimonthly periods within each breeding season (April 1–15, April 16–30, etc.). No surveys were conducted on SKC in 2005 so we fixed p, ε and γ for that year to zero. We allowed colonization to vary as a year-specific effect rather than a function of covariates because (1) colonization may be related more to site availability than site conditions, and (2) we were interested in factors associated with elevated extinction rates.

We used multi-stage modelling (Tempel et al., 2016). At each stage, we ranked models using AIC (Burnham & Anderson, 2002) to select the base model for the next stage. We first modelled p as a function of the above forest structure covariates and within- and among-year temporal trends (i.e., linear, log-linear or quadratic trends in p) while γ and ε varied by year. We then examined linear, logarithmic and quadratic forms of covariates on ψ_1 while γ and ε varied by year. Finally, we examined the potential effects of covariates on ε while γ varied by year, again considering linear, logarithmic and quadratic covariate forms because previous owl studies showed evidence of non-linear relationships (Dugger, Wagner, Anthony, & Olson, 2005; Forsman et al., 2011). We used analysis of deviance to assess the amount of variation explained by model covariates. This approach compares deviance explained by the covariates in a model with the amount of deviance not explained by these covariates, thus providing an estimate of r^2 for the model (Skalski, Hoffman, & Smith, 1993). The global model for the analysis of deviance consisted of the top-ranked model for the given study area with additional annual effects for ε, and the constant model consisted of the best detection structure with only and intercept for ε (Tempel et al., 2016).

We used the best p model from the first stage with year-specific γ and ε to obtain derived estimates of ψ_t which we used to calculate the geometric mean of the rate of change in occupancy ($\hat{\bar{\lambda}}$) and estimated the realized change in occupancy (Δ_k) for each study area. We calculated variance for $\hat{\bar{\lambda}}$ and Δ_k using the delta method (Powell, 2007).

3 | RESULTS

We found that local extinction rates were higher when owl territories contained less forest characterized by large trees (>61 cm dbh) and high canopy cover (>70%), and extinction rates declined as this forest type increased (Figure 3). Indeed, local extinction was best explained by the proportion of an owl territory containing large tree/high canopy cover forest, as evidenced by the presence of this covariate in the top models on three of the four study areas (ELD, SIE, SKC) having nearly all (88%–97%) of AIC weight (Table S1). The top three models for the fourth study area (LAS) were closely competing (within 1 AIC), containing parameters for large trees only, large trees and high canopy

TABLE 1 Median (*SD*) proportion of a spotted owl territory[a] containing GNN structure variables used to assess local extinction dynamics on four study areas[b] in the Sierra Nevada, CA, USA. The number of spotted owl territories identified on each study area is shown in the bottom row of the table

	Study area			
Variable	LAS	ELD	SIE	SKC
Large trees[c]	0.07 (0.05)	0.11 (0.06)	0.13 (0.11)	0.33 (0.19)
High canopy cover[d]	0.46 (0.16)	0.54 (0.14)	0.25 (0.16)	0.48 (0.16)
Large trees and high canopy cover	0.03 (0.05)	0.06 (0.05)	0.04 (0.08)	0.19 (0.14)
Large trees and medium canopy cover	0.02 (0.02)	0.02 (0.03)	0.05 (0.06)	0.10 (0.08)
Medium trees and high canopy cover	0.28 (0.12)	0.32 (0.09)	0.15 (0.10)	0.18 (0.12)
	$n = 90$	$n = 74$	$n = 66$	$n = 45$

[a] Territory areas (ha) for each study area were as follows: LAS (639.4), ELD (399.5), SIE (301.6) and SKC (254.3) (Tempel et al., 2016).

[b] Study area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon.

[c] Summed across all canopy cover classes.

[d] Summed across all tree size classes.

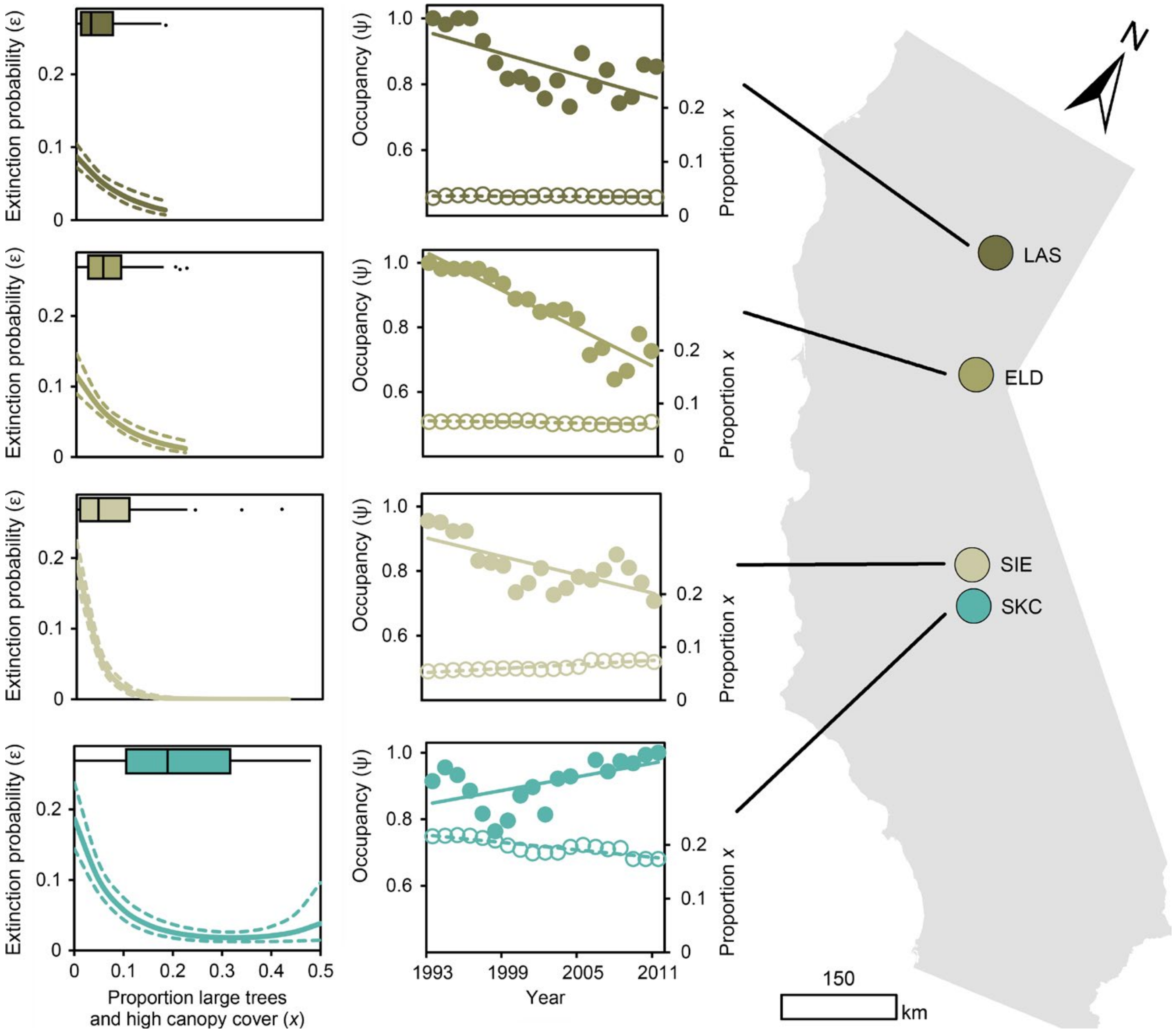

FIGURE 3 The relationship between large tree/high canopy cover forest and spotted owl occupancy dynamics. The left column of panels shows (1) the modelled relationship between spotted owl territory extinction probability and the proportion of an owl territory containing forests with large trees and high canopy cover (*x*), where the solid coloured lines represent the modelled relationship and the dashed lines represent ±1 *SE*, plotted over the range of observed values, and (2) the distribution of values for *x* present on each study area, which are represented by horizontal boxplots (corresponding to the *x*-axis). The right column of panels shows (1) annual estimates of derived occupancy (solid circles) from a fully time-varying model (see Methods) on the primary (left) axis, where the solid line represents a linear trend to emphasize population trajectories (see Table 2) over the 19-year study period, and (2) the median annual proportion of large tree/high canopy cover forest (*x*; open circles) on the secondary (right) axis, where the dashed line represents a linear trend to emphasize that this variable did not decline on national forests (three northernmost study areas, colored brown) over the 1993–2011 study period (also see Fig. S2). [Colour figure can be viewed at wileyonlinelibrary.com]

cover, and high canopy cover only, respectively (Table S1), although the coefficient estimate for the high canopy cover only model was imprecise (Table S2).

No other models were competitive with the large tree/high canopy cover model for any study area (all >5 AIC from top model; Tables S1 and S3). However, models containing other forest structural covariates such as high canopy cover, medium trees and high canopy cover, and large trees and medium canopy cover sometimes outperformed the null model and yielded coefficient estimates with 95% confidence intervals that did not overlap zero (Table S2), suggesting they may be biologically meaningful. Analysis of deviance showed that the covariate for large tree/high canopy cover forest explained 28%, 26%, 77% and 53% of the variation in local extinction rates on LAS, ELD, SIE and SKC, respectively.

The median proportion of an owl site containing large tree/high canopy cover forest on national forests (LAS, ELD, SIE) was similar, ranging from 0.03 to 0.06 (Table 1). These values corresponded with higher predicted rates of local extinction (ε = 0.06–0.074) and ongoing

TABLE 2 Estimates[a] of model parameters[b] and occupancy trends[c] for California spotted owls on four study areas in the Sierra Nevada, CA, USA

Study area	α	β_x	$\beta_x{}^2$	$\hat{\hat{\lambda}}$	Δ_k
LAS	−2.35 [−2.74, −1.96]	−10.58 [−18.68, −2.48]	—	0.991 [0.9827, 0.9997]	0.853 [0.720, 0.987]†
ELD	−2.04 [−2.58, −1.50]	−11.84 [−20.25, −3.43][d]	—	0.983 [0.9733, 0.9918]	0.728 [0.601, 0.855]†
SIE	−1.45 [−1.82, −1.08]	−26.24 [−36.28, −16.19]	—	0.981 [0.9717, 0.9904]	0.709 [0.583, 0.834]†
SKC	−1.47 [−2.08, −0.87]	−15.66 [−24.85, −6.47]	24.30 [1.86, 46.74]	1.005 [0.9997, 1.0105]	1.096 [0.990, 1.202]*

[a] Numbers in square brackets represent the lower and upper boundaries of 95% confidence intervals for the point estimate, which precedes the square brackets.

[b] α = intercept, β_x = model coefficients for the variable (x) representing the proportion of a spotted owl territory containing large trees and high canopy cover.

[c] $\hat{\hat{\lambda}}$ = geometric mean of the annual rate of change in occupancy, Δ_k = realized change in occupancy (ψ_k/ψ_1) where k is the number of years in the study. Symbols († and *) following estimates and confidence intervals for Δ_k indicate groups resulting from pairwise comparisons where estimates that share the same symbol had Δ_k estimates that were not statistically different from one another at the α = 0.05 level.

[d] $\beta_{\ln(x)}$.

occupancy declines according to estimates of the geometric mean rate of change in occupancy ($\hat{\hat{\lambda}} < 1$) and realized change in occupancy ($\Delta_k < 1$) over the period 1993–2011 (Table 2). By contrast, the median proportion of large tree/high canopy cover forest within owl territories on national parks (SKC) was 0.19 (Table 1), which was associated with much lower predicted extinction rates (ε = 0.027) and stable occupancy ($\hat{\hat{\lambda}} = 1$, $\Delta_k = 1$) (Figure 3, Table 2). Thus, extinction probability at a "typical" owl territory was ~2.5 higher on average in national forests (LAS, ELD, SIE) than national parks (SKC). A post-hoc comparison showed that estimates of realized change in occupancy (Δ_k) for LAS, ELD and SIE were not statistically different from one another, but all were significantly lower than SKC (Table 2).

The extent of large trees/high canopy cover forest within owl territories differed among study areas ($F_{3,271} = 38.3$, $p < .01$) and was ~4 times greater in national parks than in national forests on average (Table 1). Furthermore, this forest type did not appear to decline within owl territories on national forests over the study period (Figures 3 and S2), suggesting the considerable deficit of large tree/high canopy cover forest on national forests may have resulted from historical (as opposed to more recent) logging activities that selectively removed very large old trees (Collins et al., in press; Laudenslayer & Darr, 1990; McKelvey & Johnston, 1992; Stephens et al., 2015).

4 | DISCUSSION

4.1 | Extinction debt and restoration opportunities

Our work presents several key inferences suggesting ongoing declines in spotted owl populations on national forests are consistent with an extinction debt, or a legacy effect, resulting from logging of large trees prior to the initiation of our study. First, we found that local extinction rates were consistently higher across a large bioregion (the Sierra Nevada) when large tree/high canopy cover forest was less common in owl territories. Second, large tree/high canopy cover forest was far more common in owl territories on national parks (SKC), where large trees have not been logged. Third, owl populations are declining on all national forest study areas, which contain far less large tree/high canopy cover forest in owl territories than national parks where the owl population is stable. Fourth, although logging activities prior to our study led to a deficit of large tree/high canopy forest on national forests, no further declines in this forest type were observed from 1993 to 2011 (Fig. S2) while owl populations experienced long-term declines over the same period. Together, these inferences suggest that past large tree logging on national forests, which removed key habitat elements for spotted owls, may have created an extinction debt that led to contemporary owl declines long after policies were enacted to protect large trees (Figure 3).

We note that other emerging threats to the spotted owl, such as large, severe wildfires (Jones, Gutiérrez, Tempel, Whitmore et al., 2016) and invasive barred owls (*S. varia*) (Wiens, Anthony, & Forsman, 2014) did not contribute to observed declines given that our study areas did not experience significant severe fire or appreciable numbers of barred owls during the study period (Keane, 2017). Secondary ingestion of anticoagulant rodenticides used to kill rodents on illegal marijuana (*Cannabis* sp.) cultivations has been documented in fishers (*Pekania pennanti*) and barred owls in the Sierra Nevada and northwestern California (Gabriel et al., 2012; Keane, 2017). However, we know of no documented cases of exposure in spotted owls, and it is currently unknown to what extent this stressor has contributed to observed changes in spotted owl populations.

The concept of extinction debt is defined by the idea that individuals, populations or species can initially survive habitat change but later become locally extirpated or experience declines without any further habitat modification (Kuussaari et al., 2009). As such, it is important to note that by identifying the potential presence of an extinction debt in owl populations on national forests, our inferences do not suggest that total population extinction is a foregone conclusion. On the contrary, it is possible (or even likely) that spotted owl occupancy on national forests will eventually reach a new, lower equilibrium once the extinction debt is paid (Hylander & Ehrlén, 2013). In the present study, we did not explore when the extinction debt might be paid off (i.e., when the population will stop declining and persist at its new lower equilibrium level), nor did we attempt to identify an empirical extinction threshold (i.e., the minimum amount of habitat required in a territory for individuals to persist). Rather, we focused on identifying potential mechanisms of extinction debt to guide more targeted conservation action (Hylander & Ehrlén, 2013).

An emerging conservation paradigm for degraded old-forest ecosystems, and the many endangered species that inhabit them, centres on restoring forest structure and function (Chazdon, 2008) thereby increasing forest resilience to disturbance from fire, disease, and drought (Millar & Stephenson, 2015) and conserving wildlife habitat over the long term (Tempel et al., 2015). The consistent relationship we identified between spotted owl extinction rates and large tree/high canopy cover forest across the latitudinal range of the Sierra Nevada has significant implications for developing meaningful ecosystem restoration targets at bioregional scales (Peery et al., 2017). In particular, high canopy cover is thought to increase severe fire risk and spread by creating fuel continuity, yet appears to be relatively more prevalent (when co-occurring with large trees) within owl territories in national parks (SKC) that have been subjected to restored, lower-severity frequent-fire regimes for nearly half a century (van Wagtendonk, 2007). This indicates the potential that increased prevalence of large tree/high canopy cover forest types within owl territories in national forests may not be incompatible with fire resistance/resilience while at the same time providing conservation benefits to spotted owls.

The potential direct benefits to owls of increasing this forest type may be considerable. Employing our models, increasing large tree/high canopy cover forest from the median within-territory value of 0.03–0.06 to 0.10 (30–64 ha) on national forests reduced predicted local extinction rates by 36%–79%. Increasing the median within-territory value further to 0.20 (60–127 ha), similar to the median value at SKC (0.19), reduced predicted extinction rates by 80%–98%. Furthermore, because they are cornerstones of old-forest ecosystem stability, greater prevalence of large trees within owl territories and across the broader landscape probably would provide direct benefits to both spotted owls and increase resilience of old-forest ecosystems to emerging stressors.

Forests in national parks representing contemporary reference landscapes generally contain less canopy cover and lower tree densities than fire-suppressed forests on average (Lydersen & North, 2012). Why then do owl territories on national parks appear to contain considerably more large tree/high canopy cover forest than their counterparts on national forests? First, although national forests may contain higher densities of trees of all sizes, they contain significantly lower densities of trees in the largest diameter (i.e., >91 cm dbh) (Collins et al., in press) and height classes (>48 m) (North et al., 2017). Second, forest patches characterized by both large trees and higher canopy cover are not a product of fire suppression, but occurred historically throughout Sierra Nevada forests within a diverse mosaic of forest types in systems maintained by mixed-severity fire regimes (Hessburg et al., 2016). Spotted owl territories likely contained disproportionately more large trees and higher canopy cover than the broader forested landscape because owls are known to select for these specific features (Lahaye, Gutiérrez, & Call, 1997; Moen & Gutiérrez, 1997; North et al., 2017).

While areas managed for multiple uses including resource extraction (i.e., national forests) and protected areas serve different societal purposes and, for this reason and others, are unlikely to have convergent forest structure and function, we can still learn important lessons when protected areas contain stable populations of species of conservation concern. For example, protected areas often form refuges for ecosystems containing distinctive biological features such as large old trees (Miller et al., 2016) and, therefore, they can act as blueprints for ecological restoration (Boisramé, Thompson, Collins, & Stephens, 2017). Furthermore, protected areas may contain tree sizes, age structure and intact disturbance regimes (Lydersen & North, 2012) characteristic of ecologically resilient landscapes (i.e., landscapes that have the capacity to recover their ecological functioning following a disturbance) and that more closely reflect species' evolutionary environments (Moore, Covington, & Fulé, 1999). Thus, in certain cases, protected areas might act as contemporary reference landscapes (Collins et al., 2016; Meyer, 2015) to provide a frame of reference for the goals of ecological restoration (White & Walker, 1997) for large old trees and recovery of old-forest-associated species across different land tenures.

Care should be taken, however, to acknowledge the potential limitations of using national parks and other protected areas as contemporary reference landscapes to inform conservation action at broader spatial scales. For example, protected areas do not necessarily represent a random sampling of area on the landscape, but instead are often biased towards places that are less likely to face land conversion pressures—areas characterized by higher elevations, steeper slopes and greater distances to roads and cities (Joppa & Pfaff, 2009). In our study, we treat Sequoia and Kings Canyon national parks (SKC) as a contemporary reference landscape, yet it is also most southerly of all study areas examined (Figure 3). This raises the question of whether SKC can truly act as a reference, or if other fundamental differences related to differences in latitude (e.g., climate or vegetation types) could play a stronger role than past forest management on observed dynamics of spotted owls.

While this is a possibility, we present several lines of evidence to support our use of SKC as a contemporary reference landscape. First, average temperatures and annual precipitation in SKC fell within the range experienced by the other three more northerly studies (Franklin et al., 2004). Second, mixed-conifer forests characterized primarily by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*) and incense cedar (*Calocedrus decurrens*) were the dominant vegetation type on all four study areas. While SKC did contain ten groves of giant sequoia (*Sequoiadendron giganteum*), these covered only 7% of the study area (Tempel et al., 2016). Third, the two most southerly study areas, SIE and SKC, occur immediately adjacent to one another in the southern Sierra Nevada in a paired study design. Yet these two study areas exhibit the largest differences in population trends according to estimates of $\hat{\hat{\lambda}}$ and Δ_k (Table 2), suggesting differences in trajectory may be unrelated to underlying differences in climate or potential vegetation type.

4.2 | Global conservation of large trees and forest policy

The case study presented here demonstrates globally informative principles for old-forest species and large tree conservation. Notably, our results are consistent with an extinction debt resulting from historical logging of large trees that yielded long-term declines in old-forest species populations even after policies protecting large trees were enacted, highlighting an urgent need to protect existing old-forest habitat and potential large tree refugia (Lindenmayer et al., 2014). Indeed, national and international environmental legislation often do not emphasize the protection of large trees and old-forest ecosystems (e.g., the European Union Habitats Directive; EU, 1992).

Regional-scale plans to protect and restore old-forest ecosystems allow exceptions to rules limiting removal of large old trees to meet needs for equipment operability in forest restoration projects (e.g., USFS, 2004), and the sale of larger trees is necessary to offset operational costs of ecological restoration activities in heavily managed or degraded forests ecosystems (North et al., 2015). Therefore, alternative approaches for funding restoration may be required to prevent further large tree loss, which may lead to ecosystem collapse in landscapes with significant legacies of exploitive land use (Burns et al., 2015; Lindenmayer, Messier, & Sato, 2016). Despite these global challenges and conservation gaps, an emerging paradigm is to emphasize highly targeted and fine-scale conservation of large old trees as small (or sometimes individual) natural features (Lindenmayer, 2017). Policies that emphasize the protection as well as the social and ecological value of individual large old trees will offer a new hope for the perpetuity of old-forest ecosystems and the increasingly rare biodiversity that depends on them.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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