Using metapopulation models to assess species conservation–ecosystem restoration trade-offs

Connor M. Wood⁎,⁎⁎, Sheila A. Whitmore⁎, R.J. Gutiérrez⁎, Sarah C. Sawyer⁎, John J. Keane⁎, M. Zachariah Peery⁎

⁎ Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI, USA
⁎⁎ U.S. Forest Service, Pacific Southwest Region, Vallejo, CA, USA
⁎ U.S. Forest Service, Pacific Southwest Research Station, Davis, CA, USA

ABSTRACT

Ecological restoration is needed to counter global-scale ecosystem degradation, but can conflict with endangered species conservation when restoration impacts habitat quality. In such cases, prioritizing long-vacant patches for restoration is an intuitively appealing strategy for minimizing the effects on endangered species. Metapopulation models grounded in empirical data potentially provide a rigorous framework for developing theoretical “patch vacancy thresholds” (i.e., duration of vacancy required before implementing restoration) and assessing the implications of such criteria for restoration objectives. We develop such a model for spotted owls (Strix occidentalis), which embody the species–ecosystem dilemma given their preference for closed-canopy forests that are also susceptible to severe fire and drought and hence the center of debates about forest restoration intended to reduce fire and drought risk. We leveraged a > 20-year territory occupancy dataset to parameterize a Stochastic Patch Occupancy Model (SPOM) to assess relative risk to a metapopulation of owls in California under alternative conservation guidelines, including a range of vacancy thresholds. Territories with greater amounts of owl habitat were more likely to be recolonized and less likely to go extinct. Importantly, the probability of a vacant owl territory becoming recolonized declined as length of vacancy increased; territories vacant for 1 and 10 years had annual recolonization probabilities of 0.34 and 0.06, respectively. Based on our SPOM, projected territory occupancy rates declined as the vacancy threshold decreased and as habitat within territories was impacted by restoration. However, more liberal territory vacancy thresholds were projected to increase the proportion of territories (and thus landscape) that could be restored and that restored conditions could be maintained with repeated treatments. Reintroducing natural disturbance regimes, which eliminated the need for repeated treatments, was projected to reduce risk to owls, particularly with relaxed vacancy thresholds. We provide a simple, yet novel, metapopulation framework for quantifying how alternative conservation guidelines might impact owls occupancy and influence forest restoration guidelines. Similar analyses could facilitate restoration efforts in other systems by more explicitly quantifying tradeoffs between species–ecosystem objectives.

1. Introduction

Human activities have resulted in both biodiversity loss and ecosystem degradation worldwide (Barnosky et al., 2011; Vitousek et al., 1997). Consequently, endangered species conservation and ecosystem restoration have emerged as two important paradigms in natural resource management (Groom et al., 2005). Considerable synergy exists between the two paradigms because habitat restoration has improved the status of many threatened or endangered species (Hogg et al., 2013; Lawson et al., 2014; Rannap et al., 2009; Rinkevich, 2005; Webb and Shine, 2000). However, the trade-offs between species conservation and ecosystem restoration (hereafter species–ecosystem) objectives are increasing in this era of global change (Fraser et al., 2017; Peery et al., 2017). Even when endangered species are expected to benefit from restored ecosystems, restoration practices can produce short-term costs to habitat quality that increases extinction risk before predicted benefits of restoration accrue (Warchola et al., 2018). Therefore, uncertainty exists between the potential short-term costs and long-term benefits of restoration for many species such as prairie and forest birds (Powell, 2008; Wilson et al., 1995), grassland insects (Thomas et al., 1986; Warchola et al., 2018), forest reptiles and marsupials (Cunningham et al., 2007), and freshwater fish (Linternmans, 2000). In such cases,
developing effective ecosystem restoration practices that minimize short-term impacts to endangered species is a key to meeting both objectives. Developing rigorous analytical frameworks that quantify species–ecosystem tradeoffs in the currencies of population viability and restoration accomplishments under alternative management strategies would facilitate such efforts (Fraser et al., 2017).

Metapopulation theory and models have provided conceptual and analytical frameworks for conserving endangered species in fragmented landscapes for over two decades (Hanski, 1998; Levin, 1969; McCullough, 1996) and, we suggest, hold considerable promise for evaluating trade-offs between species and ecosystem conservation objectives. While prioritizing vacant patches for restoration is an intuitively appealing approach for minimizing effects on endangered species, metapopulation theory predicts that reductions in the quality of unoccupied habitat patches resulting from restoration practices reduces population viability (Hanski, 1998). That is, prioritizing patches for restoration based purely on occupancy status is challenging because patches in a metapopulation regularly switch between occupied and unoccupied states. Nevertheless, when targeting long-vacant patches for restoration carries relatively low risk, restoration may lead to metapopulation growth in the long-term (Lawson et al., 2014). A key question is: “how many years of vacancy are necessary before restoration can occur without reducing metapopulation viability?” The question “how do such thresholds influence the ability to meet restoration objectives?” is equally important given that requiring long vacancy periods before implementing restoration actions limits the fraction of a landscape that can be restored. For a vacancy threshold to be informative, a negative relationship must exist between the duration of patch vacancy and the probability that a vacant patch will be re-colonized, otherwise the impacts of restoration to the overall metapopulation are expected to be independent of the time they are vacant.

The spotted owl (Strix occidentalis) is an ideal species for using metapopulation principles (particularly vacancy thresholds) to assess tradeoffs between conservation efforts oriented towards short- and medium-term objectives for focal species and those designed for longer-term ecosystem restoration objectives. Spotted owls’ territorial behavior and strong site fidelity result in spatially structured populations whose dynamics are consistent with those of a metapopulation, where individual breeding pairs that occupy the same territories over a long time are analogous to a network of interacting local populations (Gutiérrez and Harrison, 1996). Moreover, populations of this species have been intensively monitored yielding multi-generational territory occupancy histories (Dugger et al., 2015; Franklin et al., 2000; Tempel et al., 2016, 2014). Most importantly, spotted owls reside at the epicenter of regional and national forest management debates that hinge on the tradeoffs between the retention of critical spotted owl habitat and forest restoration treatments. While spotted owl occupancy rates tend to be higher in territories containing greater amounts of the closed-canopy forest (Tempel et al., 2016, 2014), reducing tree densities with fuels reduction treatments in such stands are considered essential for reducing large, severe fires and drought-related tree mortality (Collins et al., 2010; Dow et al., 2016; Hagmann et al., 2017). Developing forest restoration practices that minimize the potential short-term costs of reducing habitat elements important to spotted owls while maximizing the flexibility to achieve forest resilience is imperative for achieving both ecosystem restoration and species conservation objectives (Peery et al., 2017). Moreover, developing criteria for selecting spotted owl territories (i.e., habitat patches) for ecosystem restoration without reducing viability ofowl populations will facilitate this process.

We developed a Stochastic Patch Occupancy Model (SPOM) (Caswell and Etter, 1993; Gyllenberg and Silvestrov, 1994) to explore the potential impacts of treating unoccupied patches under alternative, hypothetical forest restoration strategies on the viability of a spotted owl “metapopulation.” We evaluated forest restoration strategies that varied according to vacancy thresholds prior to restoration and the amount of owl habitat within territories treated. Our specific objectives were to: (1) leverage a 22-year territory occupancy dataset to assess the effects of habitat conditions and duration of territory vacancy on territory extinction and colonization rates, (2) use these statistical relationships to parameterize and implement SPOMs under different forest restoration strategies, and (3) explore trade-offs between projected changes in territory occupancy as a function of treatment frequency and number of territories treated under the different restoration strategies. We predicted that forest restoration involving shorter vacancy thresholds for treatments would result in greater declines in projected occupancy but that shorter vacancy thresholds would increase the frequency that treatments could be implemented within owl territories. This represented a simple yet novel metapopulation framework for explicitly quantifying trade-offs between the implementation of ecosystem restoration and predicted impacts to population viability that also would be applicable to development of species conservation guidelines in a range of ecosystems.

2. Methods

2.1. Territory occupancy surveys

We modeled occupancy histories of 64 spotted owl territories surveyed as part of a long-term demographic study area in the central Sierra Nevada, California (Fig. 1). We used annual territory occupancy histories from 1993 to 2014 based on surveys that followed standardized protocols (Forsman, 1983; Tempel et al., 2014). Briefly, we used vocal lures at established call stations and walking routes covering the entire area. We attempted to capture and band all located owls with unique color-coded combinations to identify owls at individual territories. We considered territories occupied when at least one owl was detected during daylight or twilight hours within or near (< 400 m) the known core area, and reduced false positives as recommended by Berigan et al. (2016). We excluded nocturnal detections from unidentified individuals because they may not be territory holders.

2.2. Modeling patterns in territory extinction and colonization

We included territory occupancy histories in the analysis beginning in the year a territory was first determined to be occupied and that had uninterrupted survey effort through 2014. These two criteria ensured that any recolonization events would occur with a known number of years preceding vacancy. We used the same definitions for extinction and (re)colonization as MacKenzie et al. (2003). We did not use a formal multi-season occupancy modeling approach because detection probabilities for bimonthly survey periods have been estimated to be 0.68 (Tempel et al., 2016), which, over the four-month season, yields an overall detection probability of 0.99. Therefore, we assumed perfect detection and treated the annual survey results as true presence/absence data. We used binomial logistic regression to model associations between extinction and, separately, colonization and predictor variables (described below), which is mathematically equivalent to the process MacKenzie et al. (2003) used to test the influence of covariates on those same probabilities. Our process of estimating extinction and recolonization rates was therefore effectively equivalent to that used to obtain detection-corrected estimates of those rates.

We treated the number of years of consecutive preceding vacancy and the amount of owl habitat within 400-ha circular areas (i.e., ~territory size; Tempel et al., 2016) as predictor variables in the colonization logistic regression. Our habitat variable was the proportion of a territory comprised of forests having both ≥70% canopy cover and trees with a quadratic mean diameter-at-breast height (QMD) ≥ 61 cm (hereafter referred to as “owl habitat”). We extracted habitat data from gradient nearest-neighbor (GNN) structure maps, which use Landsat imagery informed by forest measurements taken at Federal Inventory and Analysis (FIA) plots to give 30 m coverage of the
We considered four competing models for recolonization probability: (1) intercept only, (2) years of vacancy, (3) habitat, and (4) years of vacancy and habitat. We modeled extinction probability as a function of habitat (which we log-transformed to improve model fit) and compared this model to an intercept-only structure. We evaluated model support with Akaike information criterion with a correction for small sample size (AICc), and averaged parameters from competitive models (ΔAICc < 2) when appropriate (Burnham and Anderson, 2010). We conducted these analyses using R (R Core Development Team, 2014), and packages MuMIn (Bartoń, 2015), mapplots (Gerritsen, 2013), and popbio (Stubben et al., 2016).

2.3. Modeling the effects of alternative restoration scenarios

We developed forest restoration scenarios that varied by (1) number of years of observed territory vacancy required before a hypothetical restoration treatment was implemented (i.e., vacancy threshold); (2) amount of owl habitat retained within territories following a treatment; and (3) the frequency of restoration treatments. We considered 11 territory vacancy thresholds ranging from 0 to 10 years. Territories eligible for treatment based on observed vacancy history but containing less habitat than the treatment level were not treated. We assumed that managers had no prior knowledge of territory occupancy, so observed vacancy was calculated as the years of vacancy beginning in year one of the simulation.

To represent different effects fuel reduction treatments might have on owl occupancy, we simulated treatments in which owl habitat was reduced to 4 ha ("high-impact"), 12 ha ("low-impact"), or not affected ("no impact"); the range of habitat in a territory was 2.2–91.9 ha (median = 25.5 ha). In practice, fuels reduction treatments may or may not occur in owl habitat as defined in this study. Rather, multiple fuel reduction strategies (e.g., variable-diameter-retention and "thinning from below") could be implemented in multiple forest types with different effects on forest structure, owl habitat quality, and occupancy rates, though it was beyond the scope of this paper to explore the potential impacts of all possible management strategies. Instead, as described above, we treated "owl habitat" as a proxy for the overall quality of an owl territory because it is a strong predictor of occupancy status in our study population (Jones et al., 2018). Changing the area of this forest type allowed us to explore a range of hypothetical treatment effects (from no- to high-impact) that also produced realistic changes in territory occupancy parameters. In our population projections, we assumed that owl habitat in untreated territories increased at a rate of 0.32 ha per year, the approximate growth rate we observed in the GNN data from 1993 to 2012. Research conducted adjacent to our study area suggests that canopy cover and, to a lesser extent, basal area recovered to pre-fuel reduction treatment levels after 30 years (Collins et al., 2011). We set the post-treatment growth rate at 1.5 times the untreated growth rate (0.48 ha/year), such that a territory with a median amount of habitat undergoing a 56% reduction (27.4 to 12 ha) would recover in 30 years, to account for competitive release of remaining trees following treatment. Thirty years after treatment, the increase in owl habitat reverted to the original rate.

We considered two possible scenarios for the timing of additional treatments following the implementation of the initial treatment. First, territories were eligible for treatments after 30 years had elapsed since the previous treatment (i.e., the effective lifespan of fuel treatments; North et al., 2012). This scenario represented a case where desired disturbance regimes were not achieved and periodic treatments were needed to reduce the likelihood of large high-severity fires and high tree-mortality events. The second scenario only allowed for one treatment per territory over the course of the simulation. This scenario represented successful restoration, where management was no longer

![Fig. 1. The Eldorado demographic study area, with territory symbol size proportional to the number of years occupied (1993–2014) and color scaled to the number of times the territory was recolonized.](image-url)
Table 1
Binomial models of territory recolonization and extinction. Vacancy represents the number of consecutive years of territory vacancy preceding year t. Owl habitat represents the proportion of a 400-ha territory containing forests characterized by both ≥70% canopy cover and trees ≥ 61 cm quadratic mean diameter at breast height.

<table>
<thead>
<tr>
<th>Terms</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recolonization</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vacancy</td>
<td>346.70</td>
<td>0.00</td>
<td>0.55</td>
<td>1</td>
</tr>
<tr>
<td>Vacancy + owl habitat</td>
<td>347.13</td>
<td>0.43</td>
<td>0.45</td>
<td>2</td>
</tr>
<tr>
<td>Null</td>
<td>365.57</td>
<td>18.87</td>
<td>0.00</td>
<td>0</td>
</tr>
<tr>
<td>Owl habitat</td>
<td>366.00</td>
<td>19.30</td>
<td>0.00</td>
<td>1</td>
</tr>
<tr>
<td>Extinction</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(owl habitat)</td>
<td>623.30</td>
<td>0.00</td>
<td>0.71</td>
<td>1</td>
</tr>
<tr>
<td>Null</td>
<td>625.04</td>
<td>1.74</td>
<td>0.29</td>
<td>0</td>
</tr>
</tbody>
</table>

needed to maintain desired forest conditions (i.e., natural disturbance regimes returned). For simplicity, we only considered single-entries involving reductions in owl habitat to 12 ha. Thus, we developed four hypothetical scenarios for each of the 11 vacancy thresholds: (1) owl habitat reduced to 4 ha and repeated treatments allowed (“high-impact”); (2) owl habitat reduced to 12 ha and repeated treatments allowed (“low-impact”); (3) owl habitat not reduced and repeated treatments allowed (“no-impact”); and (4) owl habitat reduced to 12 ha in a single treatment (“true restoration”).

To project owl occupancy at the 64 territories forward in time under different restoration strategies, we use the statistical relationships between colonization/extinction and their supported covariates identified by the logistic regression models to parameterize a SPOM. Future occupancy was projected forward 75 years by simulating annual colonization and extinction events according to the following framework: territories became colonized (or went extinct) if a randomly generated patch of territory became colonized (or went extinct) if a randomly generated occupancy was projected forward 75 years by simulating annual colonization occurred as follows:

\[
\begin{align*}
0, & \text{ if } \psi_{t} - \psi_{t-1} < 0, \\
1, & \text{ if } \psi_{t} - \psi_{t-1} \geq 0
\end{align*}
\]

where \( \psi \) represented the simulated binary occupancy state for territory \( s \) in year \( t \), \( \beta_0 \) and \( \beta_0 \) represented the intercept for either colonization or extinction, \( x_{t,i} \) and \( x_{t,j} \) (where \( i = 1, 2, ..., 11 \) and \( j \) is a temporal variable) represented spatio-temporal variables \( (i) \) colonization or \( (j) \) extinction) for territory \( s \) in year \( t \), and \( \beta_i \) and \( \beta_j \) represented regression coefficients that scaled colonization or extinction probabilities to \( x_{t,i} \) and \( x_{t,j} \), respectively. This process was repeated recursively 75 years into the future for each of the restoration scenarios (see below). We used the occupancy status and true years of vacancy for (unoccupied territories) on our study area in 2014 to initialize occupancy projections with the SPOM. True vacancy was the number of years of vacancy observed prior to 2014. We used owl habitat values derived from 2012 GNN data as starting points for the model, as these were the most recently available estimates, where the median amount of owl habitat in the 64 territories was 27.4 ha (range: 2.2–91.9 ha).

We ran 1000 simulations of the SPOM at each treatment level (“high-impact”, “low-impact”, “true restoration”, and “no impact”) and each vacancy threshold (0 through 10 years of vacancy before treatment) plus a no-treatment scenario (45 total scenarios). For each scenario, we recorded (1) the mean proportion of occupied territories at year 75, (2) the mean number of times territories were treated, and (3) the proportion of territories treated at least once. Thus, the first output provided a measure of the potential detrimental impacts of forest management on owl occupancy, whereas the second and third outputs quantified the degree to which these management strategies might reduce fuel loadings across the landscape and thus achieve forest restoration objectives. The second output, the mean number of times territories were treated, provides a measure of the frequency at which restoration practices could be implemented and thus an indication of how consistently the landscape might remain in a desired state over time. The third output, the proportion of territories treated, measured the spatial extent of restoration at a landscape scale, an important metric given that the cumulative area within spotted owl territories encompassed approximately half of our study landscape. We conducted these analyses with Microsoft Excel and @Risk (Palisade Software, 2016).

3. Results

3.1. Patterns in territory recolonization and extinction

The most supported logistic regression model of territory recolonization (\( w = 0.55 \)) indicated that the probability of recolonization declined with the number of years of preceding vacancy (Table 1; Fig. 2a). The probability of territory colonization was 0.34 after a single year of vacancy and declined to 0.06 after 10 years of vacancy. Considerable support existed for the second-ranked model (\( w = 0.45; \Delta \text{AICc} = 0.43 \)), which indicated that recolonization probability was greater in territories containing a relatively high proportion of owl habitat (Table 1, Fig. 2b) and declined as a function of years of vacancy. These top two models outperformed the null and owl-habitat-only recolonization models substantially (\( \Delta \text{AICc} = 18.87 \) and 19.30, respectively). Although the owl habitat parameter was statistically uninformative in the second-ranked model, it added an element of ecological realism and was supported by previous studies that have detected a link between territory recolonization and owl habitat quality (Tempel et al., 2016, 2014). Therefore, we model averaged parameter estimates from the top two recolonization models for the purposes of developing the SPOM, which yielded:

\[
\logit(\text{colonization}) = -0.54 + 1.5X_1 - 0.23X_2
\]

where \( X_1 \) was ha of owl habitat in the territory and \( X_2 \) is years of vacancy.

The most supported logistic regression model for territory extinction indicated that the probability of extinction decreased as the amount of owl habitat increased (Table 1, Fig. 2c). The probability that occupied territories with a first- and third-quartile amount of habitat (14.7 and 36.9 ha, respectively) went extinct was 0.13 and 0.10, respectively. While the null model was competitive (\( \Delta \text{AICc} = 1.74 \)), the 85% confidence intervals (−0.62, −0.09) associated with the parameter estimate for owl habitat in the top model did not overlap zero (Arnold, 2010). Consequently, we used the top-ranked logistic regression model to model extinction dynamics in the SPOM, which was expressed as:

\[
\logit(\text{extinction}) = -3.03 - 0.35\log X_1
\]

where \( X_1 \) was the ha of owl habitat in the territory.

3.2. Projected changes in territory occupancy

Projections of the SPOM indicated that, in the absence of forest restoration treatments (“reference scenario”), spotted owl occupancy rates would decline from \( \psi = 0.56 \) in 2014 to 0.40 (SD = 0.06) over 75 years. Hereafter, we refer to \( \psi = 0.40 \) at year 75 as the “reference level” to evaluate the impacts of different restoration scenarios on owl occupancy. When multiple treatments were allowed in a...
territory over the projection period, ending occupancy did not decline below the reference level under the most conservative restoration scenario (no-impact treatment, vacancy threshold = 10 years) \((\psi = 0.40, \text{SD} = 0.06)\). Under this scenario, 58% of territories were expected to be treated and territories were expected to be treated an average of 1.1 times over the projection period. Projected ending occupancy rates decreased as the vacancy threshold was relaxed (fewer years of vacancy required before treatment) under both the low- and high-impact scenarios (Fig. 3). The expected number of treatments per territory (Fig. 3a) and the proportion of territories treated (Fig. 3b) both increased as the vacancy threshold was relaxed. In the most aggressive restoration scenario (high-impact treatment, vacancy threshold = 0 years), occupancy rates declined 0.18 below the reference level \((\psi = 0.22, \text{SD} = 0.05)\). Under this scenario, every territory was treated and territories were treated an average of three times (the maximum possible).

Expected declines in occupancy were relatively small when only one treatment per territory was allowed and low-impact treatments were implemented (i.e., true restoration scenario; Fig. 4). When the vacancy threshold was between 0 and 4 years, true restoration scenarios resulted in greater ending occupancy rates than multiple-entry scenarios; with a threshold of 5 or more years, there was essentially no difference in ending occupancy presumably because the number of treatments in the multiple-entry scenario was generally low (Fig. 4). Under the true restoration scenario, a 10-year vacancy threshold resulted in a 0.01 decline in occupancy below the reference level \((\psi = 0.39 \text{ SD} = 0.05)\), whereas a 0-year vacancy threshold resulted in a 0.06 decline in occupancy \((\psi = 0.34 \text{ SD} = 0.06; \text{Fig. 4})\). These scenarios resulted in 57% and 100% of territories being treated over the projection period (Fig. 4a), respectively (the mean number of treatments and the number of treatments were identical in the true restoration scenarios because the number of treatments was capped at one). The proportion of territories treated was nonetheless almost identical between the true restoration and multiple-entry scenarios when low-intensity treatments were implemented (Fig. 4b).

The mean number of treatments per territory and the proportion of territories treated responded differently to changes in vacancy threshold. The mean number of treatments per territory steadily decreased as the vacancy threshold was relaxed (fewer years of vacancy required before treatment) under both the low- and high-impact scenarios (Fig. 3). The expected number of treatments per territory (Fig. 3a) and the proportion of territories treated (Fig. 3b) both increased as the vacancy threshold was relaxed. In the most aggressive restoration scenario (high-impact treatment, vacancy threshold = 0 years), occupancy rates declined 0.18 below the reference level \((\psi = 0.22, \text{SD} = 0.05)\). Under this scenario, every territory was treated and territories were treated an average of three times (the maximum possible).

Expected declines in occupancy were relatively small when only one treatment per territory was allowed and low-impact treatments were implemented (i.e., true restoration scenario; Fig. 4). When the vacancy threshold was between 0 and 4 years, true restoration scenarios resulted in greater ending occupancy rates than multiple-entry scenarios; with a threshold of 5 or more years, there was essentially no difference in ending occupancy presumably because the number of treatments in the multiple-entry scenario was generally low (Fig. 4). Under the true restoration scenario, a 10-year vacancy threshold resulted in a 0.01 decline in occupancy below the reference level \((\psi = 0.39 \text{ SD} = 0.05)\), whereas a 0-year vacancy threshold resulted in a 0.06 decline in occupancy \((\psi = 0.34 \text{ SD} = 0.06; \text{Fig. 4})\). These scenarios resulted in 57% and 100% of territories being treated over the projection period (Fig. 4a), respectively (the mean number of treatments and the number of treatments were identical in the true restoration scenarios because the number of treatments was capped at one). The proportion of territories treated was nonetheless almost identical between the true restoration and multiple-entry scenarios when low-intensity treatments were implemented (Fig. 4b).

The mean number of treatments per territory and the proportion of territories treated responded differently to changes in vacancy threshold. The mean number of treatments per territory steadily decreased as the vacancy threshold was relaxed (fewer years of vacancy required before treatment) under both the low- and high-impact scenarios (Fig. 3). The expected number of treatments per territory (Fig. 3a) and the proportion of territories treated (Fig. 3b) both increased as the vacancy threshold was relaxed. In the most aggressive restoration scenario (high-impact treatment, vacancy threshold = 0 years), occupancy rates declined 0.18 below the reference level \((\psi = 0.22, \text{SD} = 0.05)\). Under this scenario, every territory was treated and territories were treated an average of three times (the maximum possible).

### Fig. 2. Logistic regression showing the probability of recolonization as a function of the years of vacancy (a) and habitat (b), and extinction as a function of habitat (c). These were the top models of each process \((\Delta AICc < 2.00; \text{Table 1})\). Owl habitat is the amount (ha) of a territory (400 ha) that had high canopy cover \((\geq 70\%)\) and large trees \((QMD \geq 61 \text{ cm})\). The histograms along the top and bottom of each panel represent the number of territories that were recolonized (top, a and b), remained vacant (bottom, a and b), went extinct (top, c), or remained occupied (bottom, c). Vacancies > 10 years were combined for clarity.
increased as the vacancy threshold was relaxed when multiple entries were allowed, reaching a maximum at a 0-year vacancy threshold (Fig. 3a). In contrast, all 95 to 100% of territories were expected to be treated with a vacancy threshold of \( \leq 3 \) years, with impacts to population-level occupancy depending on how much habitat was modified at territories (Figs. 3b, 4b); shorter vacancy thresholds resulted in further declines in owl occupancy without substantial increases in the proportion of territories that were treated.

4. Discussion

Spotted owl territories that were vacant for long periods of time were less likely to be recolonized on an annual basis than territories that were vacant for shorter time periods. The mechanism(s) behind this pattern is uncertain, but long-vacant territories may not contain adequate amounts of some habitat elements such as large trees (Jones et al., 2018; North et al., 2017), or a population process such as an Allee Effect where individuals might serve as cues to settling responses could hinder recolonization (Seamans and Gutiérrez, 2006). Consequently, projections of our metapopulation model indicated that adopting a stringent territory vacancy threshold before restoration was allowed had a relatively small impact on projections of future occupancy rates but limited the frequency and spatial extent of treatments. Territories were often not vacant long enough to be treated when stringent vacancy criteria were adopted. Such a strategy, then, is expected to constrain forest restoration (Stephens and Moghaddas, 2005). Alternatively, a liberal territory vacancy threshold allowed greater frequency and spatial extent of restoration treatments but was projected to incur greater direct impacts to owl territory occupancy unless “no-impact” treatments were implemented. While these findings underscore existing conservation conflicts between forest managers and owl conservationists (Collins et al., 2010; Dow et al., 2016; Tempel et al., 2018).
2014), our modeling framework provides explicit estimates of how alternative conservation guidelines (i.e., territory vacancy thresholds), given assumptions, might impact both future population status and the implementation of forest restoration treatments over space and time. The quantification of species–ecosystem tradeoffs provides forest managers with a scientific basis for considering restoration strategies that would be most likely to meet both objectives or, alternatively, a basis for prioritizing objectives.

While the adoption of a liberal vacancy threshold was projected to increase both the frequency and spatial extent of treatments, we observed a notable difference in the response of these two restoration measures. The projected frequency of treatments in spotted owl territories steadily increased as the vacancy threshold was reduced from 10 to 0 years (Fig. 3a), whereas the projected proportion of territories treated was effectively maximized (95% treated) with a vacancy threshold of 3 years (Fig. 3b). Yet, territory occupancy rates were projected to continue declining with vacancy thresholds < 3 years, suggesting little gain in the spatial extent to which landscapes can be restored relative to stricter criteria. While the frequency at which territories can be treated is expected to increase below 3-year vacancy thresholds, which potentially increases the ability to meet ecosystem restoration objectives, such a strategy comes at a cost to projected occupancy rates. Identifying points at which the benefits to one objective–restoration or species conservation–cease to accrue, while the costs to the other objective continue increasing (e.g., 3-year vacancy threshold) are important to bracketing the range of acceptable management actions.

The effects of adopting a liberal vacancy threshold of ≤3 years on spotted owl occupancy rates could be reduced – potentially considerably so – by (i) developing and implementing restoration treatments with reduced impacts to owl habitat and (ii) the restoration of natural disturbance regimes after a single treatment. Notably, projected

![a) Treatment frequency](image)

**Fig. 4.** Simulated changes in occupancy (displayed relative to no treatment) in the true restoration and low-impact scenarios as the vacancy threshold changes. Treatments affected owl habitat equally in both scenarios, but eligible territories were only treated once in the true restoration scenarios, and up to three times in the low-impact scenarios. Occupancy decreases and treatment frequency (average number of treatments per territory) increases as the vacancy threshold decreases; point size is proportional to treatment frequency (a). Occupancy decreases and the extent of treatment across the landscape (proportion of territories treated at least once) increases as the vacancy threshold decreases (b). Point fill is proportional to the extent of the landscape (proportion of territories) subject to treatment.
differences in the change in occupancy between no-, low-, and high-impact treatments were greatest when the vacancy threshold was shortest. This finding highlights the importance of developing treatments that do not result in significant impacts to owl habitat, particularly the loss of large trees, and thus occupancy, if short vacancy thresholds are adopted (Jones et al., 2018; North et al., 2017). Restoration treatments in habitat dominated by medium and small trees, rather than the large-tree-dominated areas seemingly important to owls, are more likely to reflect a low- or no-impact scenario. Yet, to date, it has proven challenging to empirically ascertain the effects of restoration on spotted owls and their habitat for multiple reasons (Tempel et al., 2016, 2014). For example, treatments in the large-tree, closed canopy habitat are likely to decrease canopy cover while increasing average tree size, leading to mixed, rather than directional, change in the attributes that we used to define owl habitat. Clearly, additional empirical information on the effects of restoration treatments on spotted owls at the territory scale would provide opportunities to refine the modeling of potential species–ecosystem tradeoffs, as well as the design of restoration treatments that minimize negative impacts to this species. Moreover, the restoration of natural disturbance regimes following initial treatments could eliminate the need for additional treatments that have potentially adverse effects on spotted owls (North et al., 2012). Our results support this hypothesis because the “true restoration” scenario we modeled was projected to lead to occupancy rates that were 0.062 and 0.044 greater than when multiple treatments were allowed using 0- and 1-year vacancy criteria, respectively. It also underscores the need to restore natural disturbance regimes under which owls evolved, rather than relying on repeated restoration treatments (Gutiérrez et al., 2017).

As is the case with all population projection models, our metapopulation analysis involved several simplifying assumptions that could impact inferences regarding the effects of adopting a given vacancy criterion. First, our modeling approach did not allow us to quantify either: (i) the potential long-term benefits that ecosystem restoration could provide to owls by reducing risk of severe fire; or (ii) the risk of not conducting restoration, namely that habitat loss resulting from severe fire could effectively remove territories from the metapopulation (Jones et al., 2016a,b). Either or both of these factors would incentivize shorter vacancy thresholds, but incorporating them into our modeling would have required linking specific restoration treatments to changes in fire behavior and vegetation change. Existing fire behavior models cannot replicate megafires known to impact spotted owls or be simulated with enough replications to link them to population modeling projections (S. Stephens pers. comm.). As a consequence, inferences of effects on owls in our study were limited to comparing the potential direct impacts of different vacancy thresholds on owl territory occupancy among alternative forest restoration scenarios. Second, we assumed that factors responsible for relatively low annual recolonization rates at long-vacant territories on our study area would remain unchanged following vacancies in our simulated model projections resulting from, for example, the implementation of treatments. Third, extended periods of vacancy at some territories in our study may have reflected the absence of potential recruits resulting from a declining population (Tempel et al., 2016; Tempel and Gutiérrez, 2013). If recruits are lacking, the recolonization of territories – and ultimately population-level occupancy – may be less sensitive to a given vacancy threshold than estimated. Indeed, a large-tree deficit resulting from the selective removal of such trees may have contributed to recent declines in population-level occupancy on our study (Jones et al., 2018). This suggests that lost habitat elements at a landscape scale could contribute to long vacancy at some territories by driving population declines, while their absence at a local scale could make the recolonization of particular territories unlikely. These interrelated factors could contribute to a negative feedback loop where low-occupancy areas are more likely to be treated and thus less likely to become occupied in the future. Fourth, we made several potentially important assumptions about temporal changes in forest conditions including: (i) projected rates of habitat regeneration reflected recently published rates; (ii) over the 75-year projection those regeneration rates would remain constant; and (iii) the matrix outside the habitat patches had and would continue to have no value to the owls. However, the complex effects of climate-driven changes in temperature, precipitation, and fire on the quantity, quality, and distribution of owl habitat are uncertain. High-elevation territories could become key refugia for spotted owls, and thus benefit from a more cautious management approach (Jones et al., 2016a,b). The value of the matrix could increase if woodrats, a key prey item, colonize higher elevations as the climate warms (Moritz et al., 2008). Finally, habitat conditions were the only exogenous condition in the model that influenced site occupancy. Competition, particularly from barred owls (S. vario), could lead to substantial declines in spotted owl occupancy independent of restoration activities (Dugger et al., 2015). Despite these caveats, our metapopulation approach provided a simple analytic framework with explicit assumptions that could facilitate managers’ ability to quantify species–ecosystems tradeoffs associated with alternative conservation guidelines and restoration strategies (i.e., Fig. 3) rather than relying on, for example, expert opinion.

Uncertainty in model projections resulting from the aforementioned assumptions could be reduced within an adaptive management context by monitoring how the adoption of a particular vacancy criterion affects both the frequency and spatial extent of treatments and spotted owl site occupancy. If restoration targets are not achieved, the model could be refined using additional information on spotted owl recolonization patterns and treatment impacts on site occupancy rates. Characterizing how restoration treatments affect spotted owl site occupancy has proven remarkably challenging in part because a large sample size of territories needed to detect modest effect sizes (Popescu et al., 2012); however, a recently-developed bioregional-scale site occupancy monitoring program (based on passive acoustic surveys) in the Sierra Nevada may provide a novel and potentially statistically powerful means for quantifying the effects of treatments on this species (Authors’ unpublished data). Moreover, as our understanding of this ecosystem grows, relaxing some of our modeling assumptions and incorporating greater ecological realism will become increasingly possible. In particular, emerging research provides opportunities for linking treatments to fire occurrence, severity, and size at bioregional scale (Keyser et al., 2017). Predictions of the spatial distribution of intense fire could then be linked to projected changes in spotted owl site occupancy using well-defined statistical relationships describing the negative impacts of severe fire on owls (Jones et al., 2016a,b). Such an approach would have the advantage of considering both the potential direct adverse effects of restoration treatments on spotted owls and the potential benefits that treatments confer to owls by reducing severe fire risk. Regardless of the focal species, spatially extensive monitoring programs can provide the foundation for (i) developing more nuanced management criteria based on site conditions or classes, (ii) introducing a spatial dimension into subsequent models (e.g., Yackulic et al., 2012), and (iii) a more responsive adaptive management approach (e.g., Martin et al., 2009).

4.1. Conclusions

The increase of large, severe fires and drought-related forest mortality events in dry forest ecosystems has had a range of undesirable ecological and social consequences. While restoration practices that reduce tree densities are generally believed necessary to restore the resilience of these ecosystems (Stephens et al., 2016), managers are also confronted with the need to conserve sensitive species that depend on some vegetation conditions believed to promote high fire risk. Our analysis indicates that prioritizing vacant spotted owl sites for forest restoration treatments based on the duration of vacancy, with appropriate assumptions and caveats about implementation of treatments (e.g., removing large trees reduces owl habitat quality), could help
reconcile these two seemingly incompatable objectives and facilitate progress in a long-standing conservation conflict. The restoration of natural disturbance regimes, for example, via managed and prescribed fire following initial treatments that eliminate the need for additional treatments, could be a key to meeting ecosystem restoration objectives without increasing risk to sensitive species as ovals — particularly if relatively short vacancy thresholds are adopted. A greater empirical understanding of the duration and nature of treatment impacts on focal species would improve the defensibility of adopting a particular vacancy threshold (Mutz et al., 2017).

The need to quantify ecosystem–species tradeoffs will intensify as ecosystems become increasingly degraded and more species become imperiled (Cunningham et al., 2007; Lintermans, 2000; Powell, 2008; Thomas et al., 1986; Wilson et al., 1995). Moreover, with ecosystems and their constituent species facing complex and interacting threats, management actions may conflict and be difficult to prioritize (Fraser et al., 2017), particularly when restoration induces short-term costs to species of conservation concern (Warchola et al., 2018). We expanded the application of metapopulation biology to address the tension between ecosystem and species conservation objectives by using patch occupancy histories to develop empirical basis for prioritizing habitat patches for restoration efforts. In doing so, we demonstrated that simple metapopulation models can be employed to make tradeoffs between these two objectives explicit and quantifiable. Thus, our approach can be a valuable way to balance apparently conflicting objectives, particularly when they potentially lead to dramatically different outcomes. However, we caution that modeling efforts such as ours should be viewed as hypotheses rather than definitive inferences or recommendations because implementing widespread restoration activities without proper evaluation (i.e., monitoring) can lead to a shifting baseline of deteriorating habitat conditions (Soga et al., 2018). Therefore, the value of this approach lies in its capacity to quantify the possible outcomes of different management actions, make assumptions explicit, and provide testable predictions in the face of high uncertainty.

Authors’ contributions
Authors RJG and MZP managed the long-term study and sequenced funding for it. Authors MZP and JJK conceived the ideas and approach; author SCS helped refine the approach; authors SAW, RJG, MZP, and CMW contributed to field data collection; author SAW managed data collection; and author CMW led the analyses and writing of the manuscript. All authors contributed to the analyses and writing.

Acknowledgements
We thank Doug Tempel, William Berigan, dozens of field technicians, and several anonymous reviewers. This work was supported by the USDA Forest Service Region 5, USFS Pacific Southwest Research Station, US Fish and Wildlife Service, California Department of Fish and Wildlife, and the University of Wisconsin-Madison.

References
Barrett, K., 2015. Multi-model Inference. CRAN.