Pairing functional connectivity with population dynamics to prioritize corridors for Southern California spotted owls

Erin Conlisk1 | Emily Haeuser2,3 | Alan Flint4 | Rebecca L. Lewison2 | Megan K. Jennings2

Abstract

Aim: Land use change, climate change, and shifts to disturbance regimes make successful wildlife management challenging, particularly when ongoing urbanization constrains habitat and movement. Preserving and maintaining landscape connectivity is a potential strategy to support wildlife responding to these stressors. Using a novel model framework, we determined the population-level benefit of a set of identified potential corridors for spotted owl population viability.

Location: Southern California, United States.

Methods: Combining habitat suitability and dynamic metapopulation models, we compared the benefit of corridors to the Southern California spotted owl population, measured as the increase in the expected minimum abundance, both now and under a future climate. Our approach considered key corridor characteristics important to conservation decisions, namely corridor irreplaceability and local population network benefit.

Results: We identified two corridors likely to increase Southern California spotted owl expected minimum abundance under current climate conditions. At the regional scale, of the 27 corridors evaluated, one corridor was irreplaceable (i.e., no other corridors in the network could provide a similar increase in abundance when the irreplaceable corridor was removed) and one corridor was identified as redundant (i.e., remaining corridors in the network can provide some of the increases in abundance offered by the removed corridor). Both putative corridors connected two large, populous and similarly sized patches. Additionally, we identified two more corridors at the local scale. We found that, under climate change, population declines may limit the benefit of connectivity for a range-restricted species like the spotted owl.

Main conclusions: Our analytical approach highlights important criteria for corridor identification and prioritization, namely irreplaceability versus redundancy, local versus regional benefit, and corridor impact in a changing landscape. With the capability of incorporating estimated functional connectivity into population dynamics, our modelling framework advances connectivity decision-making for other species of conservation concern and archetypal taxa within ecological communities.
Corridors are a promising conservation strategy because of their potential to limit the negative impacts of fragmentation (e.g., inbreeding), to allow individuals to reorganize after a disturbance, and to promote species’ response to habitat degradation, including degradation due to climatic change (Beier & Gregory, 2012; Heller & Zavaleta, 2009; Hilty et al., 2006; Noss, 1991). Because of the importance of connectivity to metapopulation persistence, corridor modelling is an essential component of reserve design and implementation (Keeley, Ackerly, et al., 2018). Given limited conservation resources (as in Cushman et al., 2018; Torrubia et al., 2014), there is considerable interest in understanding where to establish or protect corridors or linkages, and which provide the most benefit to a population network.

Analytical approaches to specify corridor location have benefited from considerable attention in the literature (Beier et al., 2015). Innovations in least cost path (Cushman et al., 2013), connectivity circuit flow (Littlefield et al., 2017; McRae et al., 2012), centrality (Pinto & Keitt, 2009) and spatial redundancy (Rubio & Saura, 2012) have led to detailed assessments of habitat and corridor quality across a landscape. Once key areas for connectivity have been identified, there is an additional need to prioritize among potential areas often with little information on the actual or potential rate of immigration between habitat patches, termed functional connectivity (in Hodgson et al., 2009). Quantifying functional connectivity can be challenging. Although an ideal test of functional connectivity would be in situ field comparisons of communities in the presence and absence of a given corridor, such empirical testing is rare (Gilbert-Norton et al., 2010, Kool et al., 2013) and unable to address the future impacts of climate change. Thus, an analytical approach is needed to explore the impact of current and future functional connectivity and apply it within a metapopulation network.

Quantifying the population-level benefit of functional connectivity can be even more challenging, where connectivity benefit can be defined as the increase in the abundance of a target population given the presence of a corridor. As an extreme example, a population sink (as described in Furrer & Pasinelli, 2016) would have no connectivity benefit. With a long history in the ecological literature (Hanski, 1998), metapopulation models provide a framework to consider changes in populations due to the addition or removal of a corridor (Kitzes & Merenlender, 2013; Mestre et al., 2017). There are a number of analytical approaches that consider spatial flow and centrality within a metapopulation (Littlefield et al., 2017; McRae et al., 2012; McRae & Kavanagh, 2011), but translating the flow of individuals into increased metapopulation abundance requires a model that explicitly incorporates functional connectivity and population dynamics. Once metapopulation patch and linkage networks have been specified, a corridor’s benefit depends on whether the corridor connects patches that are otherwise functionally isolated from the broader population network. To address this, individual corridors can be removed from a fully connected network, or added to an unconnected network to determine their irreplaceability or redundancy. To date, most redundancy analyses rely primarily on landscape pattern and flow (as in Pinto & Keitt, 2009; Rubio & Saura, 2012).

Because landscape connectivity is scale-dependent (Maciejewski & Cumming, 2016) and conservation objectives are often determined locally (e.g., cactus wren in San Diego; Conlisk et al., 2014), it can be informative to consider a corridor’s benefit to a local network even if the corridor has limited value to the regional metapopulation. In such cases, common reserve design priorities—for example, connecting large, robust habitat patches—may give way to promoting benefits within localized networks. Thus, corridor prioritization techniques need to be able to define a localized network (e.g., graph theory approaches; Pinto & Keitt, 2009) and quantify the benefit of individual corridors to that local network. In the absence of such analysis, the benefit of one corridor to a local population may be obscured by another corridor’s benefit to the larger metapopulation.

Finally, long-term conservation planning requires that the benefit of a corridor be resilient to future landscape change including climate change, landscape development, and habitat restoration (Alagador et al., 2016). While connectivity analyses have historically been designed to connect similar locations in space, rapidly changing landscapes demand resilience assessments across both time and space. New modelling approaches have emerged to combine the strengths of species distribution models (SDMs) and dynamic metapopulation models (Conlisk et al., 2012, 2013), offering a novel way to prioritize potential corridors. Linked species distribution-population models incorporate direct and indirect effects of climate change, disturbance, and species’ population dynamics and dispersal, allowing the benefit of individual corridors to be examined within an evolving network. Approaches that consider multiple global change phenomena are recognized as under-represented in the literature (Beier et al., 2008; Keeley, Basson, et al., 2018).

The need to plan for landscape connectivity is particularly relevant in Southern California, a global biodiversity hotspot (Myers et al., 2000), where the climate is expected to change dramatically (Klausmeyer & Shaw, 2009), a 25% increase in the human population is expected by 2050, and climate and land use changes are projected to alter disturbance regimes (Mann et al., 2016). In this study, we demonstrate how estimated functional connectivity can be used to identify and prioritize corridors that support a metapopulation. In particular, we incorporate ecological processes that determine a corridor’s irreplaceability across local and regional networks under global change. We use the California spotted owl as a model species.
because long-term survival and fecundity data are available and can be used to assess climate change impacts on suitable habitat and population-level connectivity. In particular, we asked which corridors for the Southern California spotted owl metapopulation: (1) are most beneficial; (2) are irreplaceable; (3) are locally versus regionally beneficial; and (4) are beneficial now and in a future climate in 2100. Pairing functional connectivity assessments with population dynamics, we demonstrate a method for identifying and prioritizing the population-level benefit of local and regional corridors under climate change.

2 | METHODS

2.1 | Study system

Our target area was the South Coast ecoregion of Southern California, a geographically and biologically diverse region with a Mediterranean climate. Spotted owls inhabit high-elevation, conifer-dominated sites in these mountain ranges. The area is bounded in the north by the Transverse Mountains and in the east by the Peninsular Range (Figure S1). While already including a broad set of habitats—grasslands, coastal sage and chaparral shrublands, and conifer forests—we further extended our study area to include desert to the east, the north to central coast, and southern Sierra Nevada to describe connectivity in and out of the study region. The study area included elevations below sea level to >3,500 metres at the highest point.

2.2 | Metapopulation and model development

To define the spatial and temporal extent and carrying capacities of metapopulation patches within a demographic model, we used ensemble SDM predictions of habitat suitability for the Southern California portion of the California spotted owl (Strix occidentalis occidentalis) range (Figure 1; see Supporting Information S1). Habitat suitability was modelled as function of variables with demonstrated importance to spotted owls—such as temperature and precipitation (Peery et al., 2012)—that were relatively uncorrelated with...
We used climate data averaged over 1971–2000 from Parameter-Elevation Regressions on Independent Slopes Model (PRISM, Daly et al., 2008) spatially downscaled to a 90-m Digital Elevation Model (Flint & Flint, 2014) to calculate the 19 bioclim variables typically employed in distribution modelling (described in Hijmans et al., 2005). When we found pairs of highly correlated variables, we retained the variable with a stronger influence on suitability in univariate tests. Finally, because non-climate variables can also influence habitat suitability, we included variables describing land use (impervious surface), water resources (distance to perennial and seasonal streams and stream density), and topography (roughness and per cent slope) (see Table S1).

Species presence (n = 1,865) and absence (trimmed to three times the number of presence points, or n = 5,595) points were acquired from eBird (Sullivan et al., 2009) and the California Natural Diversity Database (California Department of Fish & Wildlife, 2017). Absence points were a combination of scientist-collected callback absences in owl habitat (CNDDB data) and of eBird observations in non-owl habitat (see Figure S2), where the utility of eBird absences in non-target habitat has been shown across bird taxa (Robinson et al., 2020). We computed ensemble suitability predictions, weighted by AUC (Area Under the receiver operating characteristic Curve), using generalized linear models, boosted regression trees, and random forest in the biomod2 package (Thuiller et al., 2005, 2016) in R (R Core Team 2017), the mgcv package for generalized additive models (Wood, 2017), and the stand alone MaxEnt software (Phillips et al., 2006). To project the distribution of future suitable habitat, we substituted future climate variables into the ensemble models for two general circulation models: CNRM CM5 and MIROC5 RCP 8.5 (a business as usual emissions pathway) averaged over 2070–2099. Because spotted owls rely on long-lived trees that may persist despite a

**FIGURE 2** Spotted owl metapopulation map, coloured by the fraction of the final population contained in each patch in the (a) no change from historical, (b) CNRM CM5, (c) MIROC5 and (d) vegetation vulnerability full dispersal scenarios. Lines between patches are least cost paths coloured according to the improvement-by-addition benefit provided to the final population. SW = Sierra West, SE = Sierra East, NLP = North Los Padres, CLP = Central Los Padres, ELP = East Los Padres, SG = San Gabriel, SB = San Bernardino, SJ = San Jacinto mountains, PM = Palomar Mountain, and VL = Volcan, Black, Laguna, and Cuyamaca (additional corridor results and patch abbreviations, for all patches, are provided in Table S2 and Figure S4)
changing climate, we included a third, more optimistic, future climate projection focused on forest vulnerability under future climatic conditions. Briefly, our vegetation vulnerability projection is based on the ensemble, across four climate projections, of a statewide vegetation assessment (described in Thorne et al., 2016) that quantifies vulnerability based on the degree to which forests are exposed to marginal climates (defined as extreme quantiles of their existing range).

For a given year, we used a habitat suitability map to assign a continuous suitability value (ranging from 0 to 1) to each cell. Annual habitat suitability maps were linearly interpolated across the time horizon. To translate continuous suitability metrics to discrete habitat patches, we used the CoreMap functionality in LinkageMapper (McRae & Kavanagh, 2011) (see Supporting Information S1). The suitable habitat patches we identified (patch map and abbreviations in Figures and Tables of Supporting Information S2) were similar to those identified through field-based monitoring (Table 1 in LaHaye & Gutiérrez, 2005). We then input our core maps into the software package RAMAS GIS® 6.0 (described in Akaçkaya & Root, 2005). RAMAS translates the suitability values within a pixel, summed across a habitat patch, to the carrying capacity of the patch, where patches could grow or shrink through time with concomitant changes to dispersal distances between patches (see Supporting Information S1). In addition to climate-driven changes in carrying capacity, we imposed random fluctuations (15%) in the carrying capacity to reflect environmental stochasticity. We ran all projections for 100 years (discussed here) and 40 years (discussed in Supporting Information S4).

Corridors between patches were identified for each decade using the least cost path analysis in Linkage Mapper (McRae & Kavanagh, 2011), where the cost of moving between patches was defined by the resistance, an inversely proportional function of habitat suitability (Figure 2; additional details in Supporting Information S1). Across decades, no new corridors appeared as a function of changing climate.

We used vital rates across a 12-year time series (LaHaye et al., 2004) and added information from the more recent population model in Peery et al. (2012). Because the goal of our model was to explore the potential of connectivity to influence viability, we adjusted vital rates upward (see equation S1), such that the owl population was at equilibrium when habitat suitability did not change with climate change (no change). Fecundity and survival were drawn each year from a distribution with specified mean and standard deviation. Thus, variability in vital rates represented an additional source of environmental stochasticity. To incorporate demographic stochasticity, vital rates for each individual were drawn from a Poisson distribution (for fecundities) or a binomial distribution (for survival and transition rates). In climate change projections, fecundity was increased 0.75% each year to incorporate existing information showing that Southern California owls may benefit from increasing temperatures (Peery et al., 2012).

We also added a periodic drought event to the model, on average once every 4 years (less than California’s recent drought frequency), because there is evidence that owl fecundity responds poorly to dry conditions prior to the breeding season, especially for younger owls (LaHaye et al., 2004; Peery et al., 2012). Drought occurred randomly in each patch leading to reproductive failure in sub-adults and a 10% decline in adults, where values are based on the lowest 4 years of reproduction in LaHaye et al. (2004). Our motivation for treating owls’ drought sensitivity as a discrete event was to accentuate the year-to-year variability that would require individual owls to reorganize between patches. Note that fire catastrophes, which have become more frequent in Southern California (Safford & Van de Water, 2014) would have a similar influence on the landscape. While there is disagreement in the literature on the effects of fire (Peery et al., 2019), there is evidence that the carrying capacity of a patch decreases after severe fire (Tempel et al., 2014) and thus we included a fire scenario in Supporting Information S3, where the results are similar to those presented here.

We ran 5,000 iterations of the population model and examined the mean and variability in abundance across iterations through time, as well as the expected minimum abundance (average, across time steps, of the minimum abundance across model runs). Given many sources of stochasticity in the model, each set of 5,000 iterations yielded slightly different results. Thus, we ran trials to determine a threshold (1.7% of the expected minimum abundance) above which observed abundance changes were likely due to the influence of a corridor rather than random fluctuations in the stochastic models. We chose the most stringent of thresholds, where threshold calculation and alternate thresholds are described in Supporting Information S1.

### 2.3 Connectivity parameterization and scenarios

We made dispersal between patches inversely proportional to the time-evolving edge-to-edge distances between patches (see Supporting Information S1). Mean and maximum dispersal distance were 25 km and 150 km, respectively, based on Forsman et al. (2002) which measured dispersal within intact forest. In addition, we fixed dispersal between any two patches such that (1) less than 10% of individuals in the giving patch went to any one adjacent receiving patch (although patches could be connected to more than one adjacent patch), (2) the larger the abundance in the giving patch the larger the fraction dispersing, and (3) the larger the carrying capacity of the receiving patch the larger the fraction dispersing. The first condition ensured that no patch lost an excessive proportion of its total abundance; the second and third conditions incorporated realistic density dependence where individuals sought new patches when they were moving from crowded giving patches to resource-rich receiving patches.

We ran the population model in the presence of a given corridor and no other corridors, and in the absence of a given corridor with all other corridors active. To quantify overall connectivity benefit, we compared the expected minimum abundance of models with no dispersal, where there were no active corridors, to full
dispersal, where all corridors were active. To quantify individual corridor benefit, we calculated the per cent increase in the metapopulation when the corridor was added compared to the no dispersal scenario. To quantify redundancy, we looked at the per cent decrease when an individual corridor was taken away from the full dispersal scenario. To examine climate change resilience, we ran a no change from historical climate, a CNRM CM5, a MIROC5 (both RCP 8.5 business as usual CO₂ emissions), and a vegetation vulnerability future projection. In addition to testing individual corridors, we tested local networks of corridors. To identify geographic clusters of patches within the metapopulation—or local networks of more frequently interacting patches within a larger network—we used graph theory implemented in the igraph R package (Csardi & Nepusz, 2006) which converted the patch polygons to a network and identified five clusters in the no change model. We did not include the Sierra cluster in our analysis because it is outside our core study region. Within the remaining four clusters we tested the importance of local corridors using the same tests applied to the regional metapopulation. In future climate projections, there were too few, distantly separated patches to test clusters (see Figure 2b–d). To determine the overall importance of each local cluster, we performed an additional test where we compared the abundances under the full metapopulation, no dispersal scenario to a scenario where all the corridors within the local cluster were activated.

3 | RESULTS

3.1 | Spotted owl distribution and population trajectories

SDM predictions showed substantially less suitable owl habitat by the year 2100 as compared to historically suitable habitat (Figure 1). Historical ensemble models of habitat suitability achieved high AUC values (0.95–0.96 across ten validation datasets) because of the clear climatic distinction of mountainous owl habitat from lowlands within the study region (see Figure S2). Suitable habitat reduction under future climate projections drove a decline in population abundance (Figure 3) despite parameterizing fecundity to increase by 75% by the end of the century (as modelled by Peery et al., 2012). Under the most optimistic (vegetation vulnerability) future projection, the population was roughly halved; under the CNRM CM5 and MIROC5 future projections the population was reduced by more than 90% (see Figure S3).

3.2 | Corridor benefit under the current climate

Under a no climate change future projection, we saw a maximum increase in the overall metapopulation of 6% in the full dispersal compared to the no dispersal scenario. Two Southern California
corridors and an additional corridor in the Sierras provided a benefit to the owl metapopulation under the no change projection: namely, corridors that linked (1) the San Gabriel to San Bernardino patches, (2) the East Los Padres to San Gabriel patches, and (3) Sierra West to Sierra East patches (see Table S2 for all corridor results, including additional patches labelled in Figure S4). The same corridors were even more beneficial in the fire scenarios (Figure S5). These corridors involved the most populous patches in the model (Figure 2). Despite owls having been observed moving through intact habitat equivalent to the distance between the Transverse Range and Southern Sierra Nevada (Forsman et al., 2002), we did not see any interactions between the Sierra populations and the rest of the metapopulation. Thus, for the purposes of conservation decisions in Southern California, these northern patches are of little interest in our model, consistent with a lack of observed dispersal across the Tehachapi (Tempel et al., 2017). One corridor between the San Bernardino and San Jacinto Mountains decreased the overall population, suggesting that the San Jacinto patch might be a population sink.

### 3.3 Corridor irreplaceability

The value of the three most beneficial corridors is shown in Figure 4 as the per cent difference in expected minimum abundance achieved by subtracting the corridor from an otherwise full dispersal landscape—what we call reduction-by-subtraction—as well as the per cent difference achieved by adding the corridor to an otherwise no dispersal landscape—what we call improvement-by-addition. All corridors were more beneficial in the improvement-by-addition case, where all achieved the threshold (1.7%) above which we assume that change is due to the addition of the corridor as opposed to random chance. In the reduction-by-subtraction case, the Sierra West-Sierra East corridor had slightly lower benefit and the East Los Padres–San Gabriel corridor had much lower benefit. The difference between improvement-by-addition and reduction-by-subtraction suggests that when other corridors are present they can compensate for the loss of the redundant East Los Padres–San Gabriel corridors but not the irreplaceable San Gabriel–San Bernardino corridor. Considering the San Bernardino–San Jacinto corridor, we see that the San Jacinto patch consistently acted as a sink. All corridors not shown in Figure 4 (23 other corridors) were modelled but did not exceed the 1.7% threshold in the owl expected minimum abundance (see Table S2 in Supporting Information S2).

### 3.4 Local versus regional benefits

Some corridors that demonstrated little benefit across the entire population were beneficial within local population clusters. Identifying clusters by graph theory (Figure 5b), we performed local-scale tests that mirrored the tests performed on the entire metapopulation. Assessing a cluster’s regional importance within the metapopulation, we found that patch connectivity within clusters 2 and 4 increased the expected minimum abundance by 5.3% and 2.0%, respectively, over the no dispersal scenario (green bars, Figure 5a). The large, central San Gabriel patch was included in both cluster 2 and 4 (see Figure 2 and 4) because parts of the patch fell in both clusters; however, since the patch’s population is well-mixed, we included the entire population in both clusters. Testing local population networks that included only the patches of a specified cluster, we found that retaining all corridors within the cluster increased the expected minimum abundance of the patches within the cluster by 6.4%–10.2% (grey bars, Figure 5b), more than the 5.1% change in expected minimum abundance between the full dispersal versus no dispersal tested on the entire metapopulation. Within each local network, we found that a single corridor drove the lion’s share of the connectivity benefit for the cluster (blue bars, Figure 5b). The clearest example is cluster 2, where the irreplaceable San Gabriel–San Bernardino corridor led to 10.1% of the overall 10.2% increase in expected minimum abundance for cluster 2 patches (compare blue and grey bar for cluster 2). Cluster 4 had the most connectivity redundancy. While the East Los Padres–San Gabriel corridor increased Cluster 4’s abundance by 4.6% (out of a local full dispersal increase of 6.4%), two additional corridors out of East Los Padres also accounted for a 1.3% increase in overall Cluster 4 abundance. Both the metapopulation and local population tests show that corridors linking two large, yet similarly sized, patches tend to yield the biggest increases in abundance.
3.5 Resilient connectivity benefits

Across climate change future projections, the owl population declined precipitously in both the full dispersal and no dispersal scenarios. Climate change, especially the CNRM CM5 and MIROC5 future projections, was predicted to reduce suitable habitat and increase dispersal distances between patches resulting in lower overall flow of owls among habitat patches. Because of declining populations with increasing dispersal distances, the corridors that provided benefits under the current climate were not able to compensate for the loss of habitat due to climate change (Figure 4). In the MIROC5 future projection, the Sierra West–Sierra East corridor provided some benefit, although still below the 1.7% threshold (Figure 4a,b). Interestingly, the San Bernardino–San Jacinto corridor, between two of the few remaining habitat patches under the CNRM CM5 and MIROC5 future projection, was no longer a pronounced sink. The vegetation vulnerability future projection, while retaining more suitable habitat, still resulted in long dispersal distances that decreased the benefit of connectivity.

4 DISCUSSION

Using the Southern California spotted owl as a model species, we described a framework to estimate the benefit of corridors to an overall metapopulation, determining which corridors were irreplaceable, locally versus regionally beneficial, and beneficial now and in a future climate in 2100. Our models allow for the flexible introduction of new disturbances, such as disease, as well as alterations in the timing of these events, to explore uncertainty in potential outcomes. Further, our methodology considers both the regional and local benefits of corridors. Taken together, these approaches offer robust tools for connectivity decision-making, a widely recognized challenge in the literature.

4.1 Beneficial and irreplaceable corridors

We found that a corridor between the large, centrally located San Gabriel and San Bernardino populations was both beneficial in isolation and irreplaceable based on our metrics of improvement-by-addition and reduction-by-subtraction. The ability to distinguish between these two properties is an important benefit of our modelling approach. For example, the most beneficial corridors we identified, the San Gabriel–San Bernardino and East Los Padres–San Gabriel corridors, differed with respect to irreplaceability. When the San Gabriel–San Bernardino corridor was lost from a full dispersal scenario, the overall metapopulation abundance declined; whereas, when the East Los Padres–San Gabriel...
corridor was removed, the overall abundance was unchanged. Examining the metapopulation network, the East Los Padres and San Gabriel populations each retained considerable connectivity in the absence of a corridor between them; making the corridor between them redundant. Depending on conservation goals, redundant networks may be beneficial in vulnerable landscapes or when functional connectivity of a corridor through time is highly variable.

4.2 Local versus regional corridors

By testing local clusters of corridors, we were able to identify redundancy at the local level as well as individual corridors that were uniquely beneficial to local networks. For example, in cluster 4, the East Los Padres–San Gabriel corridor increased the expected minimum abundance by 4.6% when added to the cluster under no dispersal, compared with the full dispersal cluster scenario where expected minimum abundance increased by 6.4%. This difference in relative benefit suggests that there is local redundancy in connectivity where full dispersal provided more benefit than any single corridor. In contrast, a single corridor, the irreplaceable San Bernardino–San Gabriel corridor, increased minimum expected abundance by 10.1% in cluster 2 as compared with 10.2% under full dispersal, suggesting this particular corridor is a conservation priority.

Our local network assessment also revealed two corridors with potential local benefit that were not apparent in the full metapopulation assessment: the North-Central Los Padres and Palomar-Volcan corridors. These corridors did not emerge in the metapopulation scenarios because they connect patches with relatively few individuals: clusters 1 and 3 had less than half as many female owls as clusters 2 and 4. When considering the entire metapopulation, the demographic signal from the biggest clusters obscured the signal in the smallest clusters. The value of this multi-scale approach to evaluating corridors is that we can identify regional priorities based on expected importance to the entire metapopulation (e.g., San Bernardino–San Gabriel corridor) while also recognizing the benefits of conserving local corridors for subpopulations and individuals within those clusters.

These findings provide a quantitative assessment that supports the central premise of Hodgson et al. (2009), that the best course of action is to make conservation decisions focusing on locations of large contiguous habitat. At both the regional and local scales, connecting large, centrally located patches was most beneficial. Further, when we compare our output to more traditional metrics of cost-weighted distance, we see that the two largest populations are within relatively contiguous habitat. The distance between the San Gabriel and San Bernardino patches is relatively short (less than 5.2 km), with a ratio of cost-weighted to Euclidean distance of 24:1 (because of the need to traverse the five-lane interstate I-15 highway), less than the 37:1 cost-weighted to Euclidean distance ratio for the East Los Padres–San Gabriel corridor.

4.3 Global change resilience

Given the modelled decline in owl habitat under climate change, we did not find any corridors that increased metapopulation abundance in 2100. Because owls depend on long-lived trees and SDMs implicitly assume instant climatic equilibration, the CNRM CM5 and MIROC5 projections are likely an extreme, pessimistic future. Instead of seeing rapid declines in adult trees, a more likely scenario is forest decline over hundreds of years due to recruitment failure (Conlisk et al., 2017a, 2017b; Dobrowski et al., 2015). To consider a less dire future projection, we included the vegetation vulnerability future projection where owls might persist in resilient conifer forests (Thorne et al., 2016) which occupy a relatively larger set of climatic conditions than owls. However, even in the vegetation vulnerability future projection, we did not see a benefit of connectivity because of dramatic habitat loss. While it is generally assumed that species with fragmented metapopulations are most likely to need well-designed connectivity networks (Beier et al., 2008), especially under climate change, there are still limitations to the benefit of connectivity given population dynamics and landscape arrangement. For species expected to experience substantial declines in habitat under climate change, like the California spotted owl, connectivity may not be able to compensate for these declines. Nonetheless, methodologies like ours for quantifying the benefit of corridors are critically important to climate-wise conservation planning because they identify beneficial corridors and the limitations of such corridors.

Although there are limits to the benefits of connectivity under climate change, corridors may provide additional impact when paired with conservation measures to enhance and protect areas of core habitat. For example, efforts to improve forest health and reduce fuel loading in closed-canopy forests through understory thinning or other interventions can reduce vulnerability to insect attacks and stand-replacing crown fire, where severe fires can lead to rapid forest loss under the combined stressors of severe fire and hotter, drier climates (Davis et al., 2019). Further, protecting a wider diversity of vegetation types, including high-productivity, low-elevation live oak-Douglas fir forests (LaHaye et al., 1997), can improve owl roosting, nesting, and foraging habitat (Roberts, 2017).

4.4 Population Sink

Our evaluation also identified a corridor that could potentially lead to a population sink for owls, a phenomenon hypothesized in the literature (Tempel et al., 2017). Specifically, we found that the San Bernardino–San Jacinto corridor reduced the expected minimum abundance by roughly 4%—despite our model parameterization to reduce the likelihood of population sinks. To avoid sinks, we increased the likelihood of dispersal to patches with larger carrying capacities and from patches with abundances approaching their carrying capacity. However, there was a large difference in carrying capacity between the San Bernardino and San Jacinto patches. Thus, individuals immigrating to the San Jacinto patch from the San
Bernardino Mountains would experience an increase in cumulative lifetime vulnerability to demographic stochasticity. Further, changing climatic conditions may shift the value of a corridor over time. A corridor could create a temporary sink—as the San Gabriel-San Bernardino linkage did in the 40-year vegetation vulnerability projection (Supporting Information S4)—or a current sink might become a hold-out population in the future. In the latter case, the San Jacinto patch retained much of its suitable habitat by the end of the century under the MIROC5 future projection which translated to a nearly significant (i.e., greater than 1.7%) increase in overall owl population in the reduction-by-subtraction scenario (Figure 4). The ability to identify where corridors are maladaptive or detrimental can be particularly valuable when evaluating conservation investments in connectivity.

4.5 | Model parameterization and generalizability

One limitation of our modelling framework is the difficulty in generalizing the results of our species-specific approach across ecological communities, where single-species analyses are over-represented in the conservation design literature (Reside et al., 2018). Because our goal was to prioritize corridors, we chose a species with a distinct set of habitat patches and high dispersal capacity, parameterizing dispersal rates from intact forest (Forsman et al., 2002). Still, there were few modelled inter-mountain movements through the highly fragmented landscape, similar to the limited observed dispersal from 1987-1998 (LaHaye & Gutiérrez, 2005). Further challenging owls’ dispersal abilities, inter-patch distances increased substantially due to climate change driven habitat loss, in agreement with other studies describing a decline of spotted owls in recent decades, especially in the San Bernardino mountains (LaHaye & Gutiérrez, 2005; LaHaye et al., 2004). Like other high-elevation species, spotted owls are sensitive to climate change because there are limits to migration to higher elevation. If we had instead considered another highly mobile species with broader habitat requirements, we may have found corridors that are beneficial both now and in a future, warmer world.

Similarly, there are many different ways to evaluate and model connectivity. We selected an approach that was readily compatible with the structure of our population models, namely, least cost corridor modelling. However, other approaches, such as those available in Conefor (Saura & Torné, 2009), could provide additional insights, especially in a crossed experiment with additional taxa. A comprehensive regional connectivity design might use our model, other connectivity approaches, and multiple species with different dispersal capabilities and habitat associations (as in Jennings et al., 2020).

Another drawback of our approach is that it is relatively data intensive, lending itself to implementation with species with enough available data to parameterize the model. However, others have found ways around this by defining archetypal species based on dispersal ability (Kitzes & Merenlender, 2013; Littlefield et al., 2017). Our approach could be treated in a similar fashion with the added benefit of considering archetypal regeneration times in addition to different dispersal capabilities. However, this “archetypal species” approach lacks specificity for some conservation and model validation purposes. One advantage of using a well-studied species is there is likely to be additional data—analytic, genetic, and dispersal data—that can be used to validate models.

In addition to our choice of study species, we parameterized the model to provide an upper estimate of the benefit of connectivity. Specifically, we created an initially stable population that minimized the influence of demographic stochasticity, had high inter-annual environmental stochasticity, and emphasized the influences of connectivity. First, we likely overestimated overall metapopulation abundances by rounding vital rates up from the values in (LaHaye et al., 2004), choosing a small territory size for scaling carrying capacities, and, in the climate change future projections, increasing fecundity through time (as seen in Peery et al., 2012). Second, we included the vegetation vulnerability future projection which led to considerably more suitable habitat in 2100 compared to the CNRM CM5 and MIROC5 future projections. Third, we added considerable environmental stochasticity through fluctuating vital rates, fluctuating carrying capacities, and frequent droughts that reduced fecundity in individual patches. The result of this parameterization was that patches were more likely to diverge from one another, making the reorganization of individuals among patches more beneficial. This type of risk spreading has been shown to be beneficial in regions with high fire frequencies and localized damage (Regan et al., 2010). Similarly, in our fire simulations (Figure S5 and Table S3), we found that adding fire increased the benefit of all of the identified corridors. Under the fire scenarios we found an additional corridor, the East to Central Los Padres corridor, increased overall abundance by 4.1%, approaching the threshold above which results were unlikely due to chance. One side effect of introducing considerable environmental stochasticity is that we saw abundances change across multiple sets of 5,000 runs. To account for this between-set variability, we chose the highest threshold (1.7%) from the CNRM CM5 future projection. We could have chosen a threshold based on the no change scenario (1.2%), where variability across individual runs within a given scenario was lower and changes between scenarios could thus be attributed to the effect of connectivity. With the lower threshold, the East to Central Los Padres corridor would have been exceeded in the improvement-by-addition test in the presence of fire.

Research addressing corridor efficacy (Resasco, 2019) provides critical implementation prescriptions to complement our analysis. Evidence suggesting the potential efficacy of owl corridors include: frequent inter-mountain dispersal in Mexican spotted owl subspecies (S. occidentalis lucida) (Gutiérrez et al., 2017), Southern California owl movement through non-forested habitat and nesting in live oak stands (LaHaye & Gutiérrez, 2005; LaHaye et al., 1997), and Southern California owl presence observations within 500m of residential development. However, evidence suggesting the difficulty in constructing effective owl corridors include: high stress hormone levels in northern spotted owls (S. occidentalis caurina) when adjacent to roads (Hayward et al., 2011) and limited evidence of inter-mountain dispersal in Southern California owls (Gutiérrez et al., 2017). Regardless, preserving high-quality forested habitat is...
important to spotted owl resilience and would likely benefit additional species, where a 43% overlap in mountain lion and spotted owl least cost corridors has been observed (Beier et al., 2009).

5 | CONCLUSION

Using metapopulation models to estimate functional connectivity of spotted owls, we identified and prioritized redundant and irreplaceable corridors that benefited regional and local population resilience. Both regionally and locally, we found that beneficial corridors were typically between two similarly sized, centrally located, large patches. Although we saw a dramatic decrease in modelled metapopulation abundance and increase in inter-patch distances when we introduced climate change into the model, evaluating connectivity under different scenarios is informative to consider the long-term value of conservation investments. Overall, our approach provides a framework and workflow that can support resilient connectivity planning in changing landscapes.

ACKNOWLEDGEMENTS

This work was funded by the California Wildlife Conservation Board WC-1541SM, Project ID#2015095 and a California State Wildlife Grant F16AF00551; Project G 6198064. Gratitude to Amber Pairis, Dan Cayan, Julie Kalansky, Will Miller, Susan Wynn, Hans Sin, Gail Sevrens, Terri Stewart, Ed Pert, Karen Miner, Ken Devore and Amanda McGarry for helpful discussions as the analysis progressed. This is Point Blue Conservation Science contribution number 2307.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13235.

DATA AVAILABILITY STATEMENT

Models and data are archived with DRYAD: https://doi.org/10.5061/dryad.s4mw6m95s.

ORCID

Erin Conlisk https://orcid.org/0000-0002-4049-4805
Emily Haeuser https://orcid.org/0000-0002-8643-7291
Alan Flint https://orcid.org/0000-0002-5118-751X
Rebecca L. Lewison https://orcid.org/0000-0003-3065-2926
Megan K. Jennings https://orcid.org/0000-0002-3707-851X

REFERENCES

Akçaçayaya, H. R., & Root, W. T. (2005). Linking landscape data with population viability analysis (version 5.0). Applied Biomathematics.
Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2016). Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. Methods in Ecology and Evolution, 7(7), 853–866. https://doi.org/10.1111/2041-210X.12524
Beier, P., & Gregory, A. J. (2012). Desperately seeking stable 50-year-old landscapes with patches and long, wide corridors. PLoS Biology, 10, e1001253. https://doi.org/10.1371/journal.pbio.1001253
Beier, P., Majka, D. R., & Newell, S. L. (2009). Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications, 19(8), 2067–2077. https://doi.org/10.1890/08-1898.1
Beier, P., Majka, D. R., & Spencer, W. D. (2008). Forks in the road: Choices in procedures for designing wildland linkages. Conservation Biology, 22, 836–851. https://doi.org/10.1111/j.1523-1739.2008.00942.x
Beier, P., Sutcliffe, P., Hjort, J., Faith, D. P., Pressey, R. L., & Albuquerque, F. (2015). A review of selection-based tests of abiotic surrogates for species representation. Conservation Biology, 29(3), 668–679. https://doi.org/10.1111/cobi.12509
California Department of Fish and Wildlife. https://www.wildlife.ca.gov/Data/CNDDB
Conlisk, E., Castanha, C., Germino, M. J., Veblen, T. T., Smith, J. M., & Kueppers, L. M. (2017). Declines in low-elevation subalpine tree populations outpace growth in high-elevation populations with warming. Journal of Ecology, 105(5), 1347–1357. https://doi.org/10.1111/1365-2745.12750
Conlisk, E., Castanha, C., Germino, M. J., Veblen, T. T., Smith, J. M., Moyes, A. B., & Kueppers, L. M. (2017). Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of population range shifts. Global Change Biology, 24, 197-211.
Conlisk, E., Lawson, D., Syphard, A. D., Franklin, J., Flint, L., Flint, A., & Regan, H. M. (2012). The roles of dispersal, fecundity, and predation in the population persistence of an oak (Quercus engelmannii) under global change. PLoS One, 7(5), e36391. https://doi.org/10.1371/journal.pone.0036391
Conlisk, E., Motheral, S., Chung, R., Wisinski, C., & Endress, B. (2014). Using spatially-explicit population models to evaluate habitat restoration plans for the San Diego cactus wren (Campylorhynchus brunneicapillus sandiegensis). Biological Conservation, 175, 42–51. https://doi.org/10.1016/j.biocon.2014.04.010
Conlisk, E., Syphard, A. D., Franklin, J., Flint, L., Flint, A., & Regan, H. (2013). Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. Global Change Biology, 19(3), 858–869. https://doi.org/10.1111/gcb.12090
Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. InterJournal Complex Systems.
Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mтare, G., Macdonald, D. W., & Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PLoS One, 13(7), e0196213. https://doi.org/10.1371/journal.pone.0196213
Cushman, S. A., McRae, B. H., Adriaensen, F., Beier, P., Shirley, M., & Zeller, K. (2013). Biological corridors and connectivity. In D. W. Macdonald, & K. J. Willis (Eds.), Key topics in conservation biology 2 (first edition), (384–404). Wiley and Sons.
Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology, 28, 2031–2064. https://doi.org/10.1002/joc.1688
Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., Parks, S. A., Sala, A., & Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences, 116(13), 6193. https://doi.org/10.1073/pnas.1815107116
Dobrowski, S. Z., Swanson, A. K., Abatzoglou, T. J., Holden, Z. A., Safford, H. D., Schwartz, M. K., & Gavin, D. G. (2015). Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography, 24(8), 917–927. https://doi.org/10.1111/geb.12302
Flint, L. E., & Flint, A. L. (2014). California Basin Characterization Model: A Dataset of Historical and Future Hydrologic Response to Climate Change, (ver. 1.1, May 2017).
trade-offs for an obligate seeding shrub. *Ecology*, 91(4), 1114–1123. https://doi.org/10.1890/09-0287.1

Resasco, J. (2019). Meta-analysis on a decade of testing corridor efficacy. *Current Landscape Ecology Reports*, 4(3), 61–69. https://doi.org/10.1007/s40823-019-00041-9

Reside, A. E., Butt, N., & Adams, V. M. (2018). Adapting systematic conservation planning for climate change. *Biodiversity and Conservation*, 27(1), 1–29. https://doi.org/10.1007/s10531-017-1442-5

Roberts, S. (2017). California spotted owl use and characteristics. In R. J. Gutierrez, P. N. Manley, & P. A. Stine (Eds.), *The California spotted owl: Current state of knowledge* (pp. 49–74). Ch 3. Gen. Tech. Rep. PSW-GTR-254. : Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.

Robinson, O. J., Ruiz- Gutierrez, V., Reynolds, M. D., Golet, G. H., Strimas-Roberts, S. (2017). California spotted owl use and characteristics. In R. J. Reside, A. E., Butt, N., & Adams, V. M. (Eds.), *Adapting systematic conservation planning for climate change*. *Biodiversity and Conservation*, 27(1), 1–29. https://doi.org/10.1007/s10531-017-1442-5

Rubio, L., & Saura, S. (2012). Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data. *Ecological Complexity*, 11, 28–37. https://doi.org/10.1016/j.ecocom.2012.01.003

Rudolfsen, R., & Saura, S. (2012). Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data. *Ecological Complexity*, 11, 28–37. https://doi.org/10.1016/j.ecocom.2012.01.003

Safford, H. D., & Van de Water, K. (2014). Using *Fire Return Interval Departure (FRID)* analysis to map spatial and temporal changes in fire frequency on national forest lands in California. United States Department of Agriculture, Pacific Southwest Research Station, Research Paper PSW-RP-266.

Saura, S., & Torné, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, 24(1), 135–139. https://doi.org/10.1016/j.envsoft.2008.05.005

Sullivan, B. L., Wood, M. J., Illiff, R. E., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142, 2282–2292. https://doi.org/10.1016/j.biocon.2009.05.006

Tempel, D. J., Gutierrez, R. J., & Peery, M. Z. (2017). Population distribution and trends of California spotted owls. In R. J. Gutierrez, P. N. Manley, & P. A. Stine (Eds.), *The California spotted owl: Current state of knowledge* (pp. 75–108). Ch 4. Gen. Tech. Rep. PSW-GTR-254. : Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.

Tempel, D. J., Gutierrez, R. J., Whitmore, S. A., Reetz, M. J., Stoebling, R. E., Bergin, W. J., Seamans, M. E., & Peery, M. Z. (2014). Effects of forest management on California Spotted Owls: Implications for reducing wildfire risk in fire-prone forests. *Ecological Applications*, 24(8), 2089–2106. https://doi.org/10.1890/13-2192.1

Thorne, J., Boynton, R., Holguin, A., Stewart, J., & Bjorkman, J. (2016). *A climate change vulnerability assessment of California's terrestrial vegetation*. California Department of Fish and Wildlife (CDFW).

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2016). *Biomod2: Ensemble platform for species distribution modeling*. R-Project, 3.3-7. 856

Thuiller, W., Lavoro, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102(23), 8245. https://doi.org/10.1073/pnas.0409902102

Torrubia, S., McRae, B. H., Lawler, J. J., Hall, S. A., Halabisky, M., Langdon, J., & Case, M. (2014). Getting the most connectivity per conservation dollar. *Frontiers in Ecology and the Environment*, 12(9), 491–497. https://doi.org/10.1890/130136

Wood, S. (2017). *Generalized additive models*. Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279

**BIOSKETCH**

Erin Conlisk is interested in quantitative techniques to aid management of California plants and wildlife threatened by global change. Her work spans bird conservation in the Central Valley of California, climate manipulations in high-elevation alpine meadows and forests, and fire ecology in California shrublands. Co-authors Rebecca Lewison and Megan Jennings share these interests, integrating conservation, ecology, policy and resource management for Southern California wildlife. Currently at the University of Washington's Institute for Health Metrics and Evaluation, Emily Haeuser has worked on high-elevation conifer encroachment and climate-driven shifts in the invasion potential of common European plants. Alan Flint applies the Basin Characterization Model to add hydrologic response to climate change and downscales, high-resolution climate data.

Author contributions: EC and MJ conceived the ideas; AF provided climate data; EC and EH ran models; EC, EH, RL and MJ analysed the data; and EC led and all co-authors contributed to writing.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Conlisk E, Haeuser E, Flint A, Lewison RL, Jennings MK. Pairing functional connectivity with population dynamics to prioritize corridors for Southern California spotted owls. *Divers Distrib.* 2021;27:844–856. https://doi.org/10.1111/ddi.13235