Landscape Ecol (2019) 34:503–519
https://doi.org/10.1007/s10980-019-00788-w

RESEARCH ARTICLE

Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas

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Received: 22 May 2018 / Accepted: 18 February 2019 / Published online: 4 March 2019

Abstract
Context Habitat loss and fragmentation are the most pressing threats to biodiversity, yet assessing their impacts across broad landscapes is challenging. Information on habitat suitability is sometimes available in the form of a resource selection function model developed from a different geographical area, but its applicability is unknown until tested.
Objectives We used the Mexican spotted owl as a case study to demonstrate how models developed from different geographic areas affect our predictions for habitat suitability, landscape resistance, and connectivity. We identified the most suitable habitats and core areas for dispersal and movement for the species.
Methods We applied two multi-scale habitat selection models—a local model and a non-local model—to a broad study area in northern Arizona. We converted the models into landscape resistance surfaces and used simulations to model connectivity corridors for the species, and created composite habitat and connectivity models by averaging the local and non-local models.
Results While the local and the non-local models both performed well, the local model performed best in the part of the study area where it was built, but performed worse in areas that are beyond the extent of the data used to train it. The composite habitat model improved performances over both models in most cases.
Conclusions With rigorous testing, multi-scale habitat selection models built on empirical data from other geographical areas can be useful. Averaging predictions of multiple models can improve performance, but the effectiveness is subject to the performance of the reference models.

Keywords Connectivity · Corridor · Endangered species · Fragmentation · Habitat loss · Habitat selection · Landscape resistance · Mexican spotted owl · Resource selection function · Scale

Introduction

Species extinction is accelerating exponentially as a consequence of intensified anthropogenic activities

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-019-00788-w) contains supplementary material, which is available to authorized users.

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(Barnosky et al. 2011; Ceballos et al. 2015; De Vos et al. 2015). Habitat loss and fragmentation are considered the most pressing threats to biodiversity and the leading causes of species extinction (Fahrig 2003; Pimm et al. 2014; Newbold et al. 2015). Climate change compounds these threats, exerting further stress on species and exacerbating habitat and biodiversity loss (Thomas et al. 2004; Bellard et al. 2012). Fragmentation diminishes connectivity and dispersal, leading to reduced gene flow, smaller effective population size, and increased genetic drift and inbreeding, all of which accelerate local species extinction (Frankham 1996; Young and Clarke 2000; Stockwell et al. 2003). One of the greatest challenges to assessing the impacts of habitat loss and fragmentation on populations and their connectivity is how to reliably predict and model these effects across broad landscapes. Often the only information available is in the form of a model developed from another geographical area or time period. However, extrapolating research findings and model predictions beyond the spatial or temporal scope of inference suggested by a study is generally scientifically indefensible and may lead to incorrect findings and misdirected management decisions (Burnham and Anderson 1998; Cushman et al. 2013b).

The validity of a model is uncertain when it is applied to a different landscape, because the accuracy and error rates relevant to the original landscape do not necessarily apply to a new landscape, especially when the two landscapes differ in ecological traits, such as biophysical characteristics, climate, and disturbance regimes (Cushman et al. 2013b). If several high-performance models are available from different geographic areas, it is important to take into account all of them. One rigorous approach to this is to conduct a meta-analysis, which is an analytical process that combines the habitat attribute values for all of the models and creates a generalized model (Hedges and Olkin 1985; Gurevitch and Hedges 1993; Gates 2002). Another valuable approach is to quantitatively compare the predictions of the models developed in different places when applied in the same location (Wan et al. 2017). This enables the researcher to formally describe the differences in their predictions.

The Mexican spotted owl (*Strix occidentalis lucida*) is a listed Threatened species under the Endangered Species Act (U.S. Department of the Interior 1993). The main threat to the owl is habitat loss and fragmentation from past timber management activities and increasing uncharacteristically large and severe fires (U.S. Department of the Interior 2012). Landscape-scale restoration and fuels reduction treatments that aim to reduce risk of large and high-severity wildfires and promote forest health and resilience have been planned and implemented, with some treatment areas coinciding with habitats used by the Mexican spotted owl (U.S. Department of Agriculture 2014). Some treatments may aid in reducing habitat loss from wildfires in the long run (Ager et al. 2007; Waltz et al. 2014; Roccaforte et al. 2015; Jones et al. 2016; Chiono et al. 2017; Ziegler et al. 2017). Conversely, because Mexican spotted owls typically nest in areas with high canopy cover, some treatments may degrade owl habitat in the short run (Meiman et al. 2003; Seamans and Gutiérrez 2007; Odion et al. 2014; Tempel et al. 2014; Bond 2016; Stephens et al. 2016). Identifying important movement areas and linkages between core habitats provides critical information for designing treatment plans that can sustain the imperiled species while meeting management objectives in various locations.

In this study, we compared habitat suitability and landscape resistance predictions produced for a common region by two different modeling studies conducted on the Mexican spotted owl in different parts of its range. Both studies used multi-scale resource selection functions to predict and map habitat suitability. We applied both of these models to a wide area in the range of the Mexican spotted owl and used individual-based simulations and resistant kernel connectivity modeling to predict landscape connectivity for the Mexican spotted owl based on each of these two habitat models, and evaluated the similarities and differences in their predictions. We also tested different dispersal distance thresholds in the models to deal with uncertainty regarding the dispersal ability of the Mexican spotted owl. In addition, we created a composite model based on the two resource selection functions to see if it would improve the accuracy of predictions.

We had three goals: (1) to evaluate how models developed from different geographic areas affected our predictions for habitat suitability, landscape resistance, and connectivity; (2) to identify the most suitable habitats for the Mexican spotted owl by comparing predictions from different habitat selection models; and (3) to identify core areas important for

dispersal and movement of the Mexican spotted owl by comparing predictions from different models. We had several a priori hypotheses: First, we expected that the habitat model developed locally would outperform the habitat model developed for a non-local region. Second, we expected that the local model would perform better in the part of the study area where it was built than in parts of the study area that were beyond the extent of the data used to train it. Third, we expected that the model predictions would differ more for predictions of habitat suitability than predictions of connectivity, since connectivity spatially smooths local habitat differences.

Methods

Study area

The study spanned the area along and south of the Mogollon Rim in Arizona (latitude 32.6–35.4°N, longitude 108.6–112.1°W; Fig. 1). It covered an area of approximately 9.3 million ha and encompassed the full extent of the Apache-Sitgreaves, Coconino, and Tonto National Forests. The boundary of the study area was defined by the farthest latitude and longtitude of these forests, extended by a 5000-m buffer. Elevation ranged from 300 to 3846 m. Mean annual precipitation ranged from $\sim$ 50 mm to $>$ 5800 mm. A diverse array of vegetation occurred along the elevational climatic gradient (McClaran and Brady 1994). The lowest elevation consisted of desert and semi-desert ecosystems that were populated by arid shrub and grassland species including big sagebrush (*Artemisia tridentata*). Above the desert and semi-

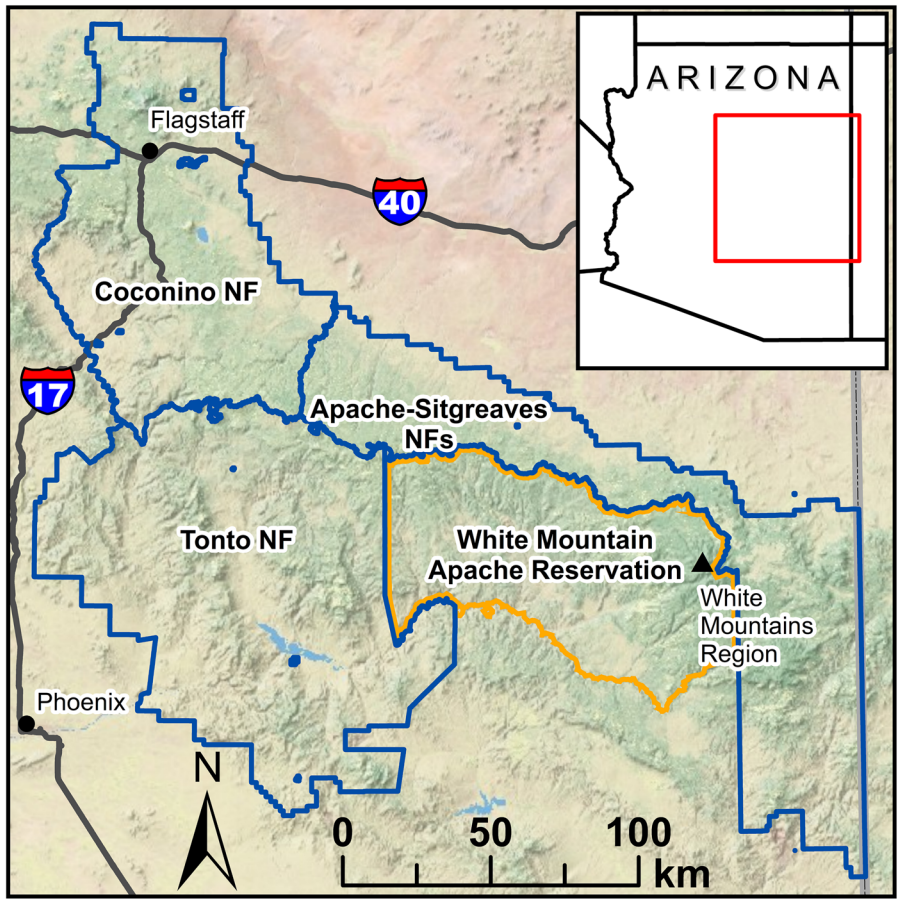

Fig. 1 Map of the study area within Arizona, USA. Blue lines indicate the boundaries of the Apache-Sitgreaves, Coconino, and Tonto National Forests. The Mogollon Rim generally follows the southern border of the Apache-Sitgreaves and Coconino National Forests from interstate highway I-17 to the White Mountains. (Color figure online)

desert, juniper-pinyon woodland dominated and alligator bark juniper (*Juniperus deppeana*), pinyon pine (*Pinus edulis*), and Utah juniper (*Juniperus osteosperma*) were common. At mid-elevation, ponderosa pine (*Pinus ponderosa*) forest dominated, stretching almost continuously from the south rim of the Grand Canyon to the White Mountains in eastern Arizona. A mixture of blue spruce (*Picea pungens*), corkbark fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), southwestern white pine (*Pinus strobiformis*), white fir (*Abies concolor*), and quaking aspen (*Populus tremuloides*) dominated higher elevational forests (> 2800 m).

The Recovery Plan for the Mexican spotted owl (U.S. Department of Interior 2012) recognized five large Ecological Management Units (EMUs) to help focus understanding of spatial variability in distribution and ecology of Mexican spotted owls across their broad and ecologically variable geographic range. Our study area contained most of the Arizona portion of the Upper Gila Mountains (UGM) EMU, as well as the adjacent northern portion of the Basin and Range West (BRW) EMU. The owl population within the UGM EMU represented the core population within the United States (Ganey et al. 2011; U.S. Department of Interior 2012). The UGM EMU is based on the central location within the range of the owl, and has large numbers and widespread distribution of owls. Models suggest that there is high geographic connectivity between the owl population in this EMU and other populations (Keitt et al. 1997; Urban and Keitt 2001). There is also evidence of high gene flow between this and other populations (Barrowclough et al. 2006). Thus, our study area focused on a geographic area of high importance to Mexican spotted owls.

Within this study area, Mexican spotted owls sometimes nest in rocky cliffs or caves in steep canyons with sparse forest cover, but more frequently are associated with forested habitat (Ganey et al. 2011; U.S. Department of Interior 2012). They primarily nest in mixed-conifer forests dominated by Douglas-fir, white fir, and ponderosa pine, but also nest less frequently in pine-oak forests. In both forest types, nesting habitat typically contains large trees and features high canopy cover (Ganey et al. 2011, 2016).

Habitat suitability models

This paper compares the predictions of two resource selection functions developed from previous work (Timm et al. 2016; Wan et al. 2017). Briefly, Timm et al. (2016) and Wan et al. (2017) developed resource selection functions [hereafter local model (Timm et al. 2016) and non-local model (Wan et al. 2017). Both resource selection functions used the same multi-scale optimization modeling approach and habitat variables, but were applied to owl nests and roosts data sets that were collected from two geographic locations, the Mogollon Plateau of Arizona (n = 208; located within our current study area, in the Apache-Sitgreaves and Coconino National Forests) and the Sacramento Mountains within the Lincoln National Forest of New Mexico (n = 2070; located approximately 400 km from our study area) respectively. Terrain in the Mogollon Plateau consisted of high plateaus with incised canyons and volcanic mountains, whereas the Sacramento Mountains consisted of high elevation montane sky islands.

For both models, a set of a priori habitat variables potentially important to the Mexican spotted owl were selected based on existing literature. These variables were classified into three categories: forest composition, topography, and climate. Forest composition variables included percent canopy cover, percent cover of mixed-conifer, percent cover of ponderosa pine, forest edge density, and forest edge proximity. Topographic variables included elevation, slope, topographic roughness index, and topographic position index. Climatic variables included total monsoon-season precipitation, cumulative annual degree days, and solar radiation index. Timm et al. (2016) and Wan et al. (2017) used a univariate logistic regression model to identify the optimal functional form (linear vs. quadratic) and the optimal operative scale for each habitat variable based on a discrete set of a priori scales (100–5000 m radii at 100 m increments for a total of 50 scales), with the best scale and functional form determined using Akaike's Information Criterion corrected for small sample size (AICc). The scale-optimized habitat variables, in the optimal functional forms, were then subjected to all-subsets model averaging based on AICc weights. The main differences between the two models were the optimal scales identified for individual variables and relative importance of habitat variables. For example, percent

canopy cover showed a broad-scale relationship (2700-m radius) relationship in the local model, but had a fine-scale (100-m radius) relationship in the non-local model; additionally, percent cover of ponderosa pine was an important variable in the local model but not in the non-local model (Wan et al. 2017). The differences in optimized spatial scales between the models suggest that habitat selection of the Mexican spotted owl is nonstationary across different landscapes.

As a first step in the current study, we fitted the two models to our study area, producing two predicted probability maps of suitable habitat for Mexican spotted owls. When fitting the models, we followed Timm et al. (2016) and Wan et al. (2017) and used the earliest LANDFIRE (2001) GIS products to develop forest composition and topographic habitat variables to best match the validation owl location data set temporally (see "Predictive performance assessment" below). Climatic variables were calculated using 30-year normal (1981–2010) PRISM climate data (PRISM Climate Group 2014). We examined the relative performance of the two models, and whether a composite model improved performance over either model (see "Composite habitat suitability model" below). All raster layers used to develop the models and the output prediction raster had a 30 m × 30 m pixel resolution. We expected the local model to perform better than the non-local model in the Apache-Sitgreaves and Coconino National Forests because it was developed with data collected within those areas, but expected poorer performance in the adjacent Tonto National Forest. We expected the non-local model to perform worse because the study area in which the non-local model was developed differed considerably in physiography and vegetation composition from most of the current study area.

Composite habitat suitability model

We created a composite habitat model by averaging the two habitat models to account for uncertainty between the two model predictions. This was done by summing the two raster surfaces of habitat suitability models and then dividing by two. This essentially produced a raster representing the composite prediction that was equally weighted between the local and the non-local models. This composite prediction raster had a range between 0 and 1. High values (i.e., near 1) and low values (near 0) indicated great model agreement with higher or lower habitat suitability, respectively. Intermediate values could result either from lower habitat suitability estimated by both models, or by disagreement between the models. We used this method to create composite prediction models for high and low dispersal ability scenarios (see "Connectivity corridor network simulation" for details on the scenarios).

Predictive performance assessment

We used an independent data set of owl locations to evaluate the predictive performance of the habitat suitability models. This data set was collected in 1993 and consisted of nest and roost locations (n = 442) in the Apache-Sitgreaves (n = 175), Coconino (n = 171), and Tonto National Forests (n = 96). We used the k-fold cross-validation resampling approach (k = 10) and calculated a suite of metrics to evaluate the predictive performance of the habitat models for each of the National Forests, and for all three National Forests combined.

To assess predictive performance, we began by calculating the area-adjusted frequency, which was a predicted-to-expected index suitable for validating presence-only data (Boyce et al. 2002). We partitioned the habitat suitability range into 10 equal-interval classes (i.e., 0–0.1, 0.1–0.2, etc.); and for each class, we calculated the predicted and expected frequencies of points. The predicted frequency was the number of observations in each habitat suitability class divided by the total number of observations among all classes, and the expected frequency was the area covered by each habitat suitability class divided by the total study area. We then divided the predicted frequency by the expected frequency to obtain the area-adjusted frequency for each class. A post hoc evaluation of the results revealed that the higher habitat suitability classes comprised a very small proportion of total study area (e.g., $<$ 1e-10 in some cases). This created erratic results in which the area-adjusted frequency of the higher classes would either be zero or astronomical when only one validation point was within the habitat suitability class. To obtain meaningful results, we reduced the volatility by grouping classes 8–10 (i.e., habitat suitability $\geq$ 0.7) into the same class and recalculated area-adjusted frequency. We used Spearman rank correlation to evaluate the strength of

relationships between area-adjusted frequency and habitat suitability class. A good predictive model would show a monotonically increasing trend and the Spearman correlation coefficient would be near 1 (Boyce et al. 2002).

We calculated five other accuracy metrics, including the percentage of cases correctly classified (PCC), sensitivity (i.e., true positive rate), specificity (i.e., true negative rate), kappa statistics, and area under curve (AUC) using the PresenceAbsence R package (Freeman and Moisen 2008). PCC evaluates model accuracy by identifying the overall percentage of points that have been correctly classified. Sensitivity and specificity calculate the percentage of presences and absences correctly classified respectively. Kappa takes into account the possibility of points being classified correctly by chance, and can be viewed as the percentage improvement over expected accuracy. AUC evaluates model performance at all possible probability thresholds dividing presences and absences. In general, AUC > 0.7 indicates a useful model (Swets 1988). Computing these metrics required samples representing both presence and absence of owls, but our validation data set contained presence-only data. Consequently, we generated a number of pseudo-absence points (Zaniewski et al. 2002; Engler et al. 2004) equal to the number of nest and roost sites in the validation set for each National Forest using the pseudo.absense function in spatialEco R package (Evans 2017). This function generates pseudo-absence samples based on kernel density estimate of known locations, such that pseudo-absence samples are located further away from the occurrence points (Hengl et al. 2009). Because PCC, sensitivity, specificity, and kappa statistics were sensitive to the threshold dividing positive and negative outcomes, instead of selecting a specific threshold, we examined a series of thresholds that spanned from 0–1 at intervals of 0.1, with the optimal threshold determined by the highest kappa statistic.

Landscape resistance

To estimate landscape resistance, we converted the predicted probability maps of suitable habitat into raster surfaces that represented the relative permeability of landscape features to species movement using an exponential decay function:

$$R = 1000^{(-1 \times HS)},$$

where R represented the cost resistance value assigned to each pixel and HS represented the predicted habitat suitability derived from the suitability models described above (Mateo-Sanchez et al. 2015a, b). We used 1000 as the base of our exponential decay function such that areas with > 0.3 habitat suitability would have low cost resistance. We rescaled the resistance values to a range between 1 and 10 by linear interpolation, such that minimum resistance (R_{min}) was 1 when HS was 1, and maximum resistance (R_{max}) was 10 when HS was 0 (Fig. 2). Under the concept of landscape resistance, low resistance values indicate areas through which a species might move easily, whereas high resistance values indicate areas that a species is unlikely to traverse. Because the Mexican spotted owl is a fairly mobile species (e.g., it can fly over structurally disconnected or fragmented habitat patches), an exponential decay function is appropriate for converting habitat suitability to resistance values, such that most habitats have low resistance values and only highly unsuitable habitats have high resistance values. Previous research on other species also supported using negative exponential functions to transform habitat suitability into resistance (e.g., Mateo-Sanchez et al. 2015a, b; Keeley et al. 2016; Fig. 2).

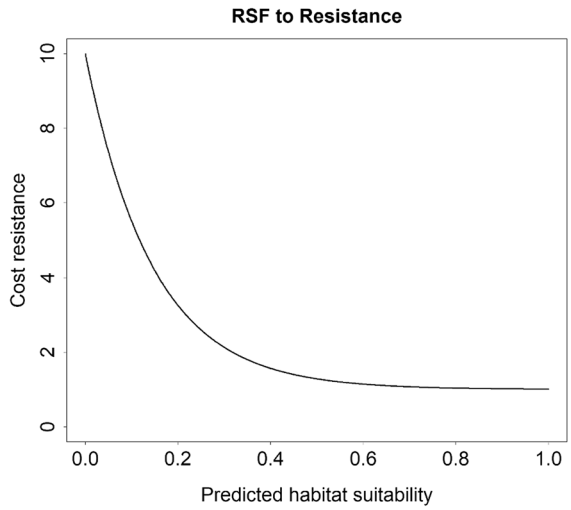

Fig. 2 Exponential decay functional curve used to transform habitat suitability to landscape resistance. The function used the formula: $R = 1000^{(-1 \times HS)}$ where R represented the cost resistance value assigned to each pixel and HS represented the predicted habitat suitability from a resource selection function (RSF) model

Two resistance surfaces were created in this step (i.e., converted from the local and non-local models respectively), which were used as inputs in simulations for evaluating connectivity and gene flow of Mexican spotted owl.

Connectivity corridor network simulation

We used landscape connectivity simulation software UNICOR (Landguth et al. 2012) to model patterns of connectivity corridors for Mexican spotted owls. We used the predicted probability maps of suitable habitat described above to randomly generate 1000 habitat-suitability weighted nodes on the landscape (i.e., higher predicted habitat suitability had more random nodes). These nodes represented the starting locations of individual owls on the landscape. We applied a spatial filter such that each node was at least 2 km from its nearest node to approximate nearest neighborhood distances from demography studies (Peery et al. 1999; May and Gutiérrez 2002). We used the cumulative resistant kernel approach in UNICOR for mapping connectivity corridors. This approach calculates the least-cost dispersal Gaussian kernel around each source node up to a cost distance threshold, and then sums all kernels to produce a density map predicting connectivity strength at each location on the landscape (Compton et al. 2007). Simulations were conducted separately on resistance surfaces derived from the local model and non-local models.

In addition, because of the uncertainty regarding the maximum dispersal distance of the Mexican spotted owl, we tested two cost distance thresholds 200 km (low dispersal ability) and 300 km (high dispersal ability), which corresponded to 200,000 and 300,000 cost units, respectively, on a uniform landscape of minimum resistance value of 1. These distances reflected our best estimates of the range of uncertainty based on known Mexican spotted owl ecology. During natal dispersal, radio-marked juvenile owls moved distances up to 92 km from their natal sites, and moved through highly variable terrain (Ganey et al. 1998). These observed distances were considered minimum estimates of natal dispersal capacity, however, because most radio-marked juveniles disappeared during tracking or died before settling on a territory (Ganey et al. 1998; Willey and van Riper 2000). Although observed movements of adult owls between breeding territories (i.e., breeding dispersal) were relatively short (< 15 km) for most banded owls (Ganey et al. 2014), such owls at least occasionally move long distances, with documented movements of two banded owls covering approximately 187 km (Gutiérrez et al. 1996) and 462 km (Ganey and Jenness 2013). Collectively, these data suggest that Mexican spotted owls are able to move long distances through highly variable terrain. The edge-to-edge distance of the study area was 301 km, and therefore, we restricted the dispersal limit of the high dispersal scenario to 300 km in the simulation.

Correlation analysis

To compare predictions in habitat suitability, resistance surfaces, and connectivity between the local and the non-local models, we performed a moving window correlation analysis (30×30 pixel window) and calculated pixel-by-pixel Pearson coefficients among model predictions using the rasterCorrelation function in the spatialEco R package (Evans 2017). This produced a raster of correlation coefficients with a range between 1 and -1 at any given pixel, with a correlation coefficient near 1 indicating higher agreement, and a value near -1 indicating higher disagreement between predictions of the two models. We also calculated the mean correlation coefficient for the whole raster.

Composite connectivity model

We created a composite connectivity model by averaging the predictions of the local and non-local connectivity models to account for uncertainty between the two model predictions. This was produced the same way as the composite habitat suitability model, except connectivity surfaces were used instead of habitat suitability surfaces. Composite models were created for the high and low dispersal ability scenarios described above.

Results

Predicted habitat suitability

The local and non-local models predicted different patterns of potential suitable habitat for the Mexican spotted owl. Suitable habitats predicted by the local

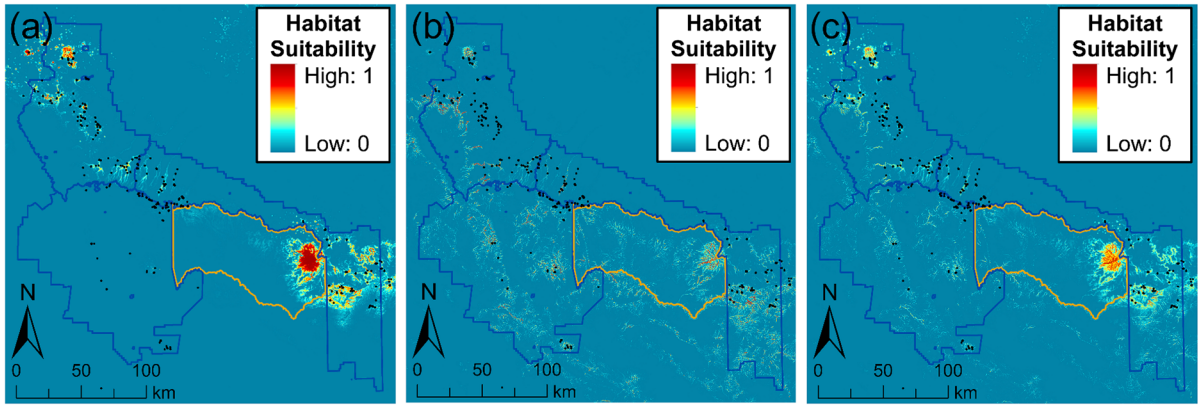

Fig. 3 Habitat suitability predicted across the study area based on predictive habitat models: **a** a locally-developed predictive model (AUC = 0.91, Timm et al. 2016), **b** a non-local predictive model developed in the Sacramento Mountains, New Mexico (AUC = 0.88; Wan et al. 2017), and **c** a composite model based on averaging the two individual models (AUC = 0.92). Blue lines indicate the boundaries of the Apache-Sitgreaves, Coconino, and Tonto National Forests. The orange line is the boundary of the White Mountain Apache Reservation. Black markers represent nest locations used to evaluate model performance. (Color figure online)

model were concentrated in the White Mountains region in the southeastern portion of Apache-Sitgreaves National Forests, and in the northern portion of the Coconino National Forest (Fig. 3a). While the non-local model also predicted suitable habitat in those general areas, predicted habitat under this model was less concentrated and more widely dispersed (Fig. 3b), as opposed to the more aggregated patches predicted by the local model. The non-local model also predicted many of the forested mountains and canyons in the Tonto National Forest as potential habitats, whereas the local model did not (Fig. 3a, b). The composite habitat suitability map predicted that the White Mountains region contains some of the most concentrated habitats for the Mexican spotted owl in the study area (Fig. 3c). Topography also appeared to be an important feature as predicted habitat often was associated with linear canyon systems (Fig. 3c).

Habitat model predictive performance assessment

For all three National Forests combined, the composite model was the best overall model in terms of highest PCC (0.76), sensitivity (0.58), kappa statistic (0.51), and AUC (0.92; Fig. S1a) among all models. It also ranked second in area-adjusted frequency analysis (r_s = 0.62; Fig. 4a). Although the non-local model performed better in area-adjusted frequency (r_s = 0.79; Fig. 4a), it had lower PCC (0.66), sensitivity (0.38), kappa statistic (0.32), and AUC (0.88; Fig. S1a). The local model performed the worst based on area-adjusted frequency (r_s = 0.48; Fig. 4a), but had better PCC (0.75), sensitivity (0.55), kappa statistic (0.49), and AUC (0.91; Fig. S1a) than the non-local model. Specificity was high and similar among the models (0.93–0.94).

For the Apache-Sitgreaves National Forest, the composite model also appeared to be the best model. It had high AUC (0.90; Fig. S1b) and PCC (0.76), and fairly high sensitivity (0.63) and kappa statistics (0.51). It also performed well in area-adjusted frequency (r_s = 0.81; Fig. 4b). Although the local model performed slightly better than the composite model in terms of PCC (0.79), sensitivity (0.69), kappa statistic (0.58), and AUC (0.92; Fig. S1b), it did not perform well in area-adjusted frequency because of poor predictions in areas with high suitability (r_s = 0.57; Fig. 4b). The non-local model had the lowest PCC (0.67), sensitivity (0.43), kappa statistic (0.34), and AUC (0.87; Fig. S1b), but performed better than the local model on area-adjusted frequency (r_s = 0.69; Fig. 4b). Specificity was high and similar among the models (0.89–0.91).

For the Coconino National Forest, the local model outperformed other models and had the highest PCC (0.84), sensitivity (0.73), kappa statistic (0.67), and AUC (0.95; Fig. S1c). The composite model also performed well and had identical AUC (0.95; Fig. S1c) but slightly lower PCC (0.78), sensitivity (0.61), and kappa statistic (0.57) compared to the local

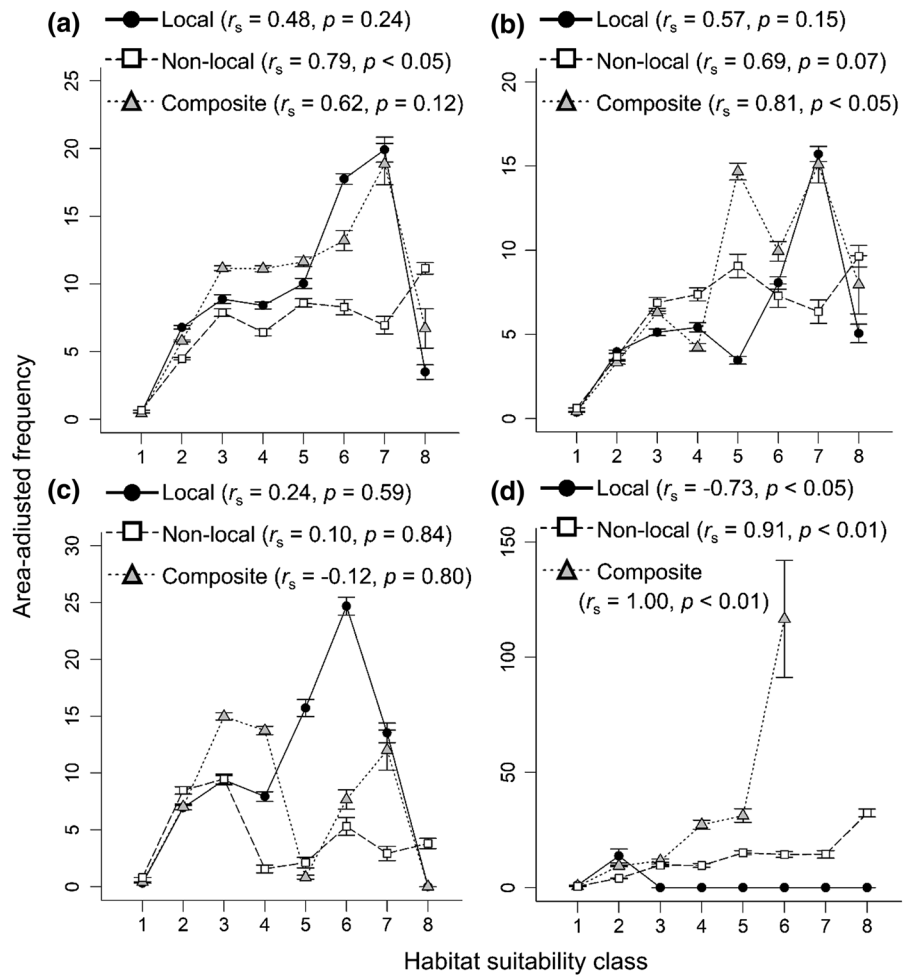

Fig. 4 Area-adjusted frequencies of the local model, the non-local model, and the composite model by habitat suitability classes over **a** the three National Forests (Apache-Sitgreaves, Coconino, and Tonto) within the study area, **b** the Apache Sitgreaves National Forest, **c** the Coconino National Forest, and **d** the Tonto National Forest. Error bars represent 95% confidence interval. Spearman's correlation (r_s) and p values (p) are shown in parentheses in the legend

model. The non-local model ranked last, with lowest PCC (0.60), sensitivity (0.23), kappa statistic (0.20), and AUC (0.89; Fig. S1c). None of the models performed well in area-adjusted frequency, but the local model still ranked first (r_s = 0.24; Fig. 4c). Specificity was high and similar among the models (0.95–0.98).

For the Tonto National Forest, the non-local model and the composite model both performed well, with the former showing slightly better performance. The non-local model had the highest PCC (0.74), sensitivity (0.55), and kappa statistic (0.48) among the models. It also had high AUC (0.91; Fig. S1d) and performed well in area-adjusted frequency (r_s = 0.91; Fig. 4d). The composite model performed slightly better in AUC (0.93; Fig. S1d) and area-adjusted frequency (r_s = 1.00; Fig. 4d), but had lower PCC (0.70), sensitivity (0.44), and kappa statistic (0.41). Performance of the composite model was impacted by poor prediction by the local model, in this area, which resulted in no area predicted to have high suitability and both upper classes of predicted suitability being missing in the area-adjusted frequency plot (Fig. 4d). The local model performed poorly. It predicted nearly no Mexican spotted owl habitat in the Tonto National Forest (Fig. 3a), which contributed to poor PCC (0.50), sensitivity (0.00), kappa statistic (0.00), and AUC (0.61; Fig. S1d). Specificity was high and similar among the models (0.97–1.00). See Table S1 for complete results for PCC, sensitivity, specificity, kappa, and AUC.

Landscape resistance

Resistance surfaces produced by the local model and the non-local model showed similar patterns as habitat

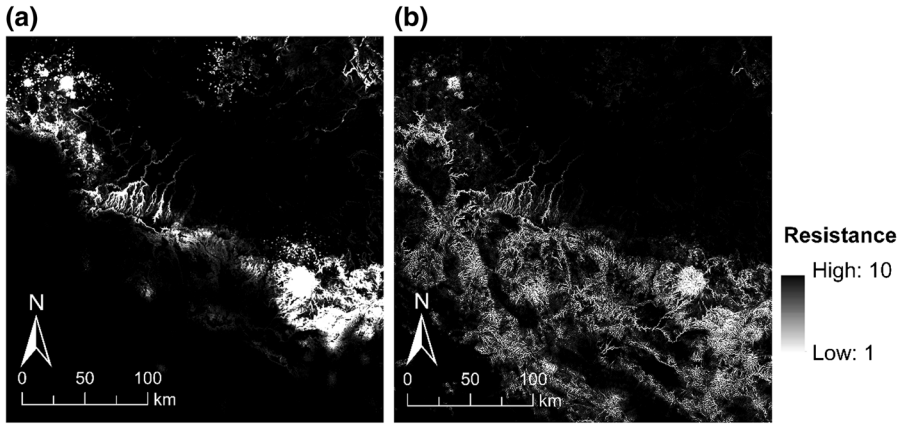

Fig. 5 Landscape resistance surfaces used in connectivity corridor network simulations. **a** Landscape resistance estimated with the local model. **b** Landscape resistance estimated with the non-local model. Higher resistance values indicate less likelihood of species traversing that area

suitability predictions. Areas of low resistance were confined mostly to the Apache-Sitgreaves National Forests and the Coconino National Forest in the local model (Fig. 5a), whereas areas of low resistance were patchier but more broadly distributed in the non-local model (Fig. 5b).

Connectivity corridor network

Resistant kernel analyses predicted patterns of synoptic connectivity for the Mexican spotted owl across the study area. Both models identified extensive connectivity in the White Mountains region, but the local model predicted higher and more highly concentrated connectivity in that area (Fig. 6). Patterns of connectivity in the local model were similar between both high and low dispersal ability scenarios, with slightly broader extent of cumulative resistant kernel for the high dispersal scenario (Fig. 6a, c). In contrast, dispersal ability showed a stronger effect on connectivity strength under the non-local model, with the high dispersal ability scenario producing a broader and more connected network than the low dispersal ability scenario (Fig. 6b, d). The most noticeable difference between the two models occurred within the Tonto National Forest and White Mountain Apache Reservations south of the Mogollon Rim. This region was predicted to provide important connectivity for the Mexican spotted owl under the non-local model but not under the local model. The composite connectivity map showed high connectivity strength in the White Mountains region under both high and low dispersal ability scenarios (Fig. 7). The map also identified a network of multiple corridors (more obvious in the low dispersal ability scenario) that provided linkages across the study area (Fig. 7), although those linkages were relatively weak.

Correlation analysis

Agreement between the two predictive habitat models varied spatially (mean correlation = 0.37), but generally appeared negative in the southern half and positive in the northern half of the study area (Fig. 8a). Correlation between the landscape resistance surfaces also varied (mean correlation = 0.46) and had a large cluster of positive correlation pixels in the upper portion and many small patches of negative correlation pixels scattered across the study area (Fig. 8b). For the connectivity models, under both high and low dispersal ability scenarios, correlation was generally high and positive (mean correlation = 0.80 and 0.86 respectively). As expected, we generally observed high positive correlation in areas where connectivity strength was predicted to be either very high or very low (Fig. 8c, d).

Discussion

Given the urgency of habitat loss and fragmentation it is critical to obtain reliable knowledge about patterns of habitat suitability and population connectivity for species of conservation concern so conservation

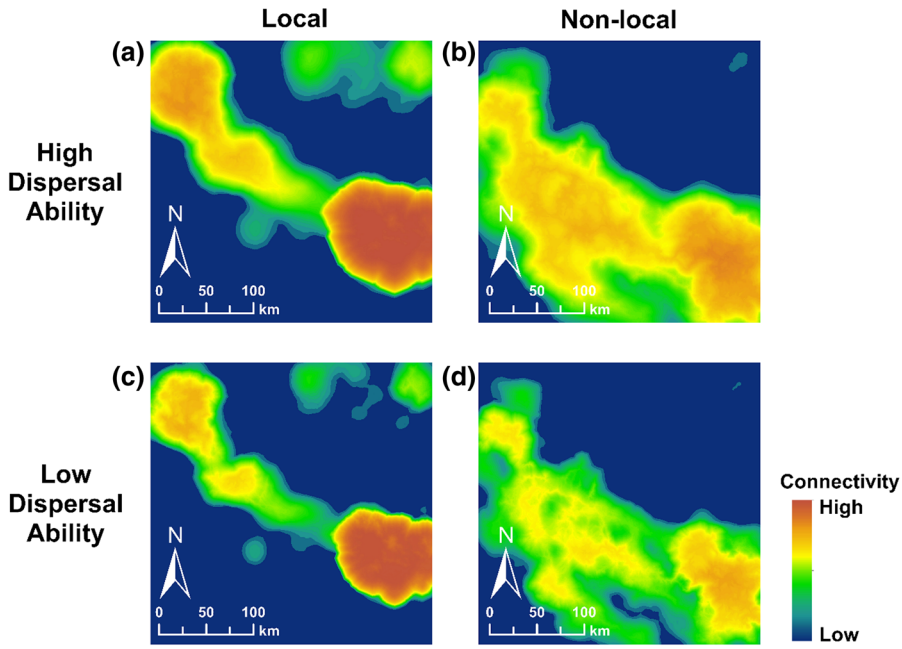

Fig. 6 Resistant kernel connectivity models calculated using individual-based simulations. Simulations were conducted on the landscape resistance surfaces of the local (left) and the non-local (right) models under high (top) and low (bottom) dispersal ability scenarios

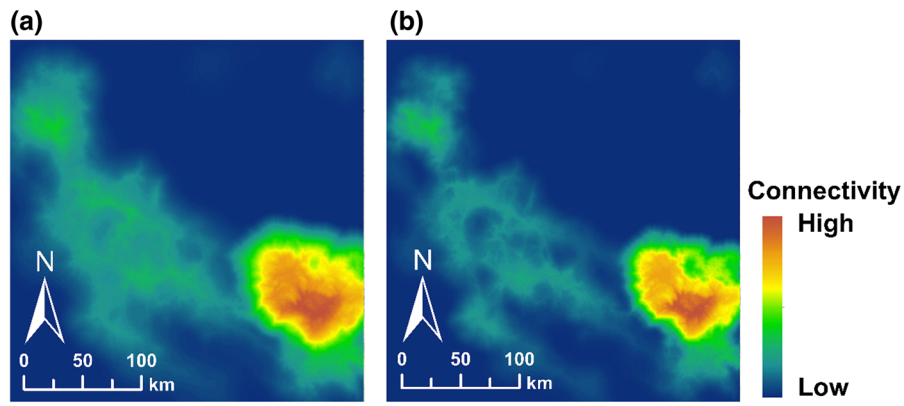

Fig. 7 Composite connectivity map under **a** high dispersal ability scenario and **b** low dispersal ability scenario. Connectivity was calculated with the local and the non-local connectivity models both having equal weights

planning can be undertaken. However, there is a severe shortage of quantitative research on habitat quality and connectivity for most species. For many species in many areas there are no locally developed quantitative habitat or connectivity models available. Thus, it is important to consider how well models that are produced in different locations or different times perform in predicting habitat suitability and connectivity (Cushman et al. 2013b), in order to determine whether the knowledge gained from existing models can be extrapolated to new areas. If several models are available from different geographic areas, it is important to compare them and their predictions. In this paper we quantitatively compared the predictions of two models of habitat suitability and connectivity for Mexican spotted owl. One of these models was locally derived and the other was developed several hundred kilometers from the focal study area. The two areas differed considerably in topography and vegetation composition (Timm et al. 2016; Wan et al. 2017).

Each of our a priori hypotheses received some support from the results. Consistent with our first

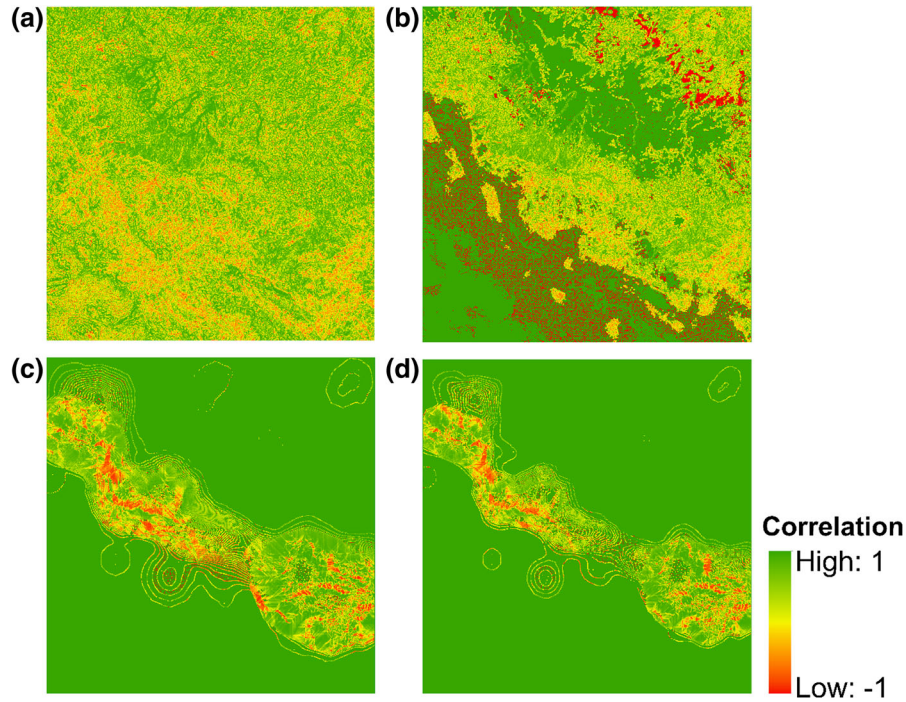

Fig. 8 Correlation of **a** predicted habitat suitability, **b** landscape resistance surfaces, **c** connectivity under high dispersal scenario, and **d** connectivity under low dispersal scenario between the local and the non-local models. Positive correlation indicates agreement, and negative correlation indicates disagreement between the two models

hypothesis we found that the local model had generally higher performance in predicting an independent spotted owl occurrence data set than the non-local model for most of the study landscape when AUC was the performance criterion (Table S1). When area-adjusted frequency was considered, however, the non-local model often outperformed the local model. Area-adjusted frequency predicts conditional probability of presence, evaluates presence-only locations, and is sensitive to the number of bins and their boundaries. The area-adjusted frequency performance of the local model was by disparaged by the fact that few presence data were in areas belonging in the upper bins (i.e., predicted highly suitable habitat). But if we look at bin 1–6, the local model performs mostly better than the non-local model (Fig. 4). Therefore, the differences between area-adjusted frequency and AUC results were at least partly due to the sensitivity of bins in area-adjusted frequency. Additionally, because AUC measures discrimination and considers both presence and absence locations, this also contributes to the differences between area-adjusted frequency and AUC results. Remarkably, our composite model that combined the two predictions had somewhat higher overall performance. Consistent with our second hypothesis we found that the local model performed best in the parts of the study area where it was parameterized (e.g., Coconino and Apache-Sitgreaves National Forest) and worse in areas where it was not (e.g., Tonto National Forest). Importantly, the local model performed extremely poorly in the Tonto National Forest, where it predicted an absence of suitable spotted owl habitat. In contrast, the non-local model performed very well in that part of the study area. There were some similarities in topography between this region and the landscape where the non-local model was developed, as the Tonto National Forest contained numerous mountain ranges. However, the Tonto National Forest was generally lower in elevation, drier, and far less dominated by mixed-conifer forest than the area where the non-local model was developed. Thus, the relatively strong predictive power shown by the non-local model in this area was somewhat surprising, but may indicate convergence in habitat selection between owls in these different landscapes.

Consistent with our third hypothesis, we found that there was much higher agreement between the connectivity models produced by the two habitat models than between the habitat suitability models themselves. We expected this to be the case because habitat quality is a multi-scale function of local

conditions, and models that include different variables or different scales for the same variables will produce divergent predictions of habitat quality. In contrast, connectivity predictions are based on habitat quality but also are influenced by spatial contagious spread processes, which smooth the differences between models. Indeed, we found dramatically higher similarity between the predicted connectivity models than between the habitat suitability models. There has been much debate and discussion around the topic of how to best estimate and optimize landscape resistance (e.g., Rudnick et al. 2012; Zeller et al. 2012; Cushman et al. 2013a). The observation made here that differences in resistance surface have relatively modest effects on predictions of connectivity for a highly mobile species, at least in comparison to how the differences in models affect predictions of habitat suitability itself, is encouraging and suggests that connectivity modeling may be more robust to uncertainty in resistance surfaces than has previously been assumed. It remains to be tested whether our results apply to less mobile species.

Resource selection functions developed with data sets collected from different geographic locations lead to differences in predicted habitat suitability and landscape resistance patterns (Figs. 3, 5, 8). Conversely, connectivity model predictions showed high correlation and agreement even when they were derived from different source nodes and resistance surfaces (Fig. 7, 8). This suggested that, in our case, the individual-based resistant-kernel models were relatively insensitive to differences in resource selection functions. Uneven sensitivity of habitat suitability, landscape resistance, and connectivity to resource selection functions could be related to differences in specificity and precision in nesting versus dispersal habitats. Spotted owls have more specific and localized requirements for selecting nesting habitat but can use more general and diverse habitats for dispersal (Forsman et al. 2002).

Our composite habitat model was able to calibrate prediction uncertainty arising from sensitivity to different resource selection functions and improved performance over the two habitat models in the Apache-Sitgreaves National Forest and in the combined area of the three National Forests. The improvements were likely a result of reduction in overprojection from either model. The composite model did not, however, improve performances in the Coconino National Forest and the Tonto National Forest, where the best models were the local model and the non-local model respectively. The inability to provide improvement was a result of poor performance by one or both models. For example, the local model showed extremely poor performance in the Tonto National Forest, and the composite model suffered from such poor performance. Based on our results, we think that when the reference models perform reasonably well, the composite modeling approach can create an even better model that provides greater precision in predicting suitable habitats. On the other hand, when one (or more, in the case of > 2 models) of the reference models is bad, the composite modeling approach is not as useful.

White Mountains region

The local, non-local, and composite models all predicted the White Mountains region as important to the Mexican spotted owl. Because of the agreement among all models, we have high confidence that this region is a core area that provides critical habitat and connectivity for the owl. Two recent large fires, Rodeo-Chediski Fire in 2002 and Wallow Fire in 2011, burned over 189,600 ha and 211,500 ha of land respectively near this region. Some early assessments suggest that numbers of Mexican spotted owls have decreased in at least some areas burned at high severity within these fires (M. Lommler, Personal Communication, 2018). The effects of fire on the Mexican spotted owl are understudied and currently subject to debate (Bond 2016; Ganey et al. 2017; Wan et al. 2018). The GIS layers used to develop the models predated the two fires, and therefore, the models did not evaluate the effects of the fires on habitat and connectivity. If these large fires have, indeed, had a negative influence on the populations of the Mexican spotted owl in this region, then the repercussions could extend to other areas as well because of the important role of the White Mountains as a core area.

Comparison to past work

Two decades ago, Keitt et al. (1997) conducted a quantitative landscape-level assessment of habitat connectivity of the Mexican spotted owl using a graph theory approach. This groundbreaking study was useful in identifying both critical thresholds for

connectivity based on straight-line dispersal distance between habitat patches, and the importance of individual patches in maintaining connectivity. However, in the absence of habitat suitability models, the study relied on an underlying map that identified habitat patches based on forest cover type maps and assumed equal resistance for all areas traversed. Thus, the graph theory framework (Keitt et al. 1997; Urban and Keitt 2001) simplified the landscape and reduced habitat patches and connections between them to dots and lines (called nodes and edges) respectively. Our study complements and extends this work by analyzing spatially explicit connectivity using a resistant kernel approach based on predictive habitat models grounded in empirical data. This approach provided high-resolution (30-m pixel) information that better pinpoints core areas and corridors most likely to be used by the species although in a smaller study area. Our model predictions thus have the potential to provide practical guidance for identifying the most critical habitats for maintaining connectivity among Mexican spotted owl populations. The approach underlying the model can be extended across the range of the owl to better inform management decisions in prioritizing areas for the protection of the species.

Future research opportunities

Although the Mexican spotted owl typically nests in forested habitats with high canopy cover, it also nests and roosts in high cliffs, caves, and rock ledges in rocky environments with relatively low tree cover (Willey and van Riper 2007). The resource selection functions tested in our study were developed exclusively for predicting habitat suitability of the Mexican spotted owl in forested environments (Timm et al. 2016; Wan et al. 2017). We see an opportunity to employ the same methodology with owl location data collected from rocky canyonland to develop habitat and connectivity models for these unique environments. Combining models developed for specific geographic areas or habitat types based on empirical data on habitat use by Mexican spotted owls in those areas or habitats will provide a better understanding of connectivity across the range of the Mexican spotted owl.

In addition, although using detection data to infer resistance to movement is a common approach (Zeller et al. 2012), several studies suggest that detection-based habitat models may not accurately reflect movement behavior or landscape resistance (Spear et al. 2010; Mateo-Sánchez et al. 2015a; Keeley et al. 2017; Zeller et al. 2017). Resource selection functions tested in this study were based on habitat suitability models and were developed with nest and roost site detection data, which were the best data available to us. Improvement on predictions will be possible when data sources that are more connected with species dispersal and mating movement become available. Currently, movement data (e.g., GPS telemetry) on the Mexican spotted owl is too limited for conducting this type of connectivity analysis. Therefore, although the connectivity models provided here are currently the most quantitatively rigorous, we advocate the collection of movement data in future Mexican spotted owl studies to improve the accuracy of connectivity assessment. The combination of movement data and connectivity models illustrated here will also be useful in discerning differences in habitats used by the spotted owl between natal and breeding dispersal of spotted owls (Forsman et al. 2002). Furthermore, we envision that future assessments will be able to incorporate genetic data to evaluate gene flow and genetic connectivity of the threatened species. Additional movement and genetic data will also be useful for validating the connectivity models in this study.

Uncharacteristically large and severe wildfires (e.g., Rodeo-Chedeski Fire and Wallow Fire mentioned above) and climate change in the southwestern U.S. are driving landscape changes and emerging as threats to potentially aggravate the decline of the Mexican spotted owl (Wan et al. 2018). Under these emerging threats, and especially under climate change, plant communities will likely be reassembled, which will influence the configuration and connectivity of habitats in the future (Beier et al. 2011). Our research serves as a baseline assessment of habitat suitability and connectivity for the Mexican spotted owl under current landscape conditions, providing high-resolution and spatially explicit information for developing hypotheses on evaluating the potential influences of climate change, disturbance, and treatment effects on the species in future landscapes. For example, projected climate data from general circulation models can be used with the multi-scale modeling techniques shown in this study, and the resulting model can be compared against predictions from this

study to understand climate effects on the Mexican spotted owl. In addition, as mentioned above, the GIS layers used in this study predated some large fires within the study area. Research repeating the same methods in this study along with post-fire GIS and remotely sensed data to analyze potential fire effects on the habitat and connectivity of the Mexican spotted owl is underway (Wan 2018). This research will provide much needed information for the management and conservation of the Mexican spotted owl (Ganey et al. 2017; Wan et al. 2018).

Acknowledgements This project was funded by Joint Fire Sciences Project and the National Fire Plan. We thank C. Vojta, C. Aslan, and P. Fulé for their constructive comments and feedback on this project. We also thank J. Evans for his speedy response and exceptional assistance on troubleshooting and debugging spatialEco R package.

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