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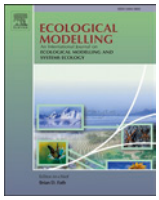

Multiscale habitat suitability modeling for a threatened raptor offers insight into ecological model transferability

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ABSTRACT

Habitat fragmentation and loss are major threats to species conservation worldwide. Studying species-habitat relationships is a crucial first step toward understanding species habitat requirements, which is necessary for conservation and management planning. However, some species inhabit a range of habitat types, potentially making the use of range-wide habitat models inappropriate due to non-stationarity in species-habitat preferences. The Mexican spotted owl (*Strix occidentalis lucida*) (MSO) is a species that inhabits both forests and rocky canyonlands, two habitats with large differences in environmental conditions. It is unclear whether the species uses habitat differently in these two habitat types or if previously-built habitat models for forest-dwelling owls can be used to understand MSO habitat use in rocky canyonlands. To explore this, we developed the first scale-optimized habitat suitability model for this subspecies of spotted owl in rocky canyonlands using an ensemble framework. We then compared our results with a previously-built habitat model for MSO in forested areas. In the rocky canyonland model, slope (800 m scale), cumulative degree days (1200 m scale), insolation (1000 m scale), and monsoon precipitation (100 m scale) were the most important environmental covariates. In contrast, in the forest model, percent canopy cover (100 m scale), percent mixed-conifer (5000 m scale), and slope (500 m scale) were the most important environmental covariates. The rocky canyonland model performed well, while the forest model performed poorly when projected to rocky canyonlands and predicted low suitability across the entire study area, including areas with known nesting locations. These results support the non-stationarity in habitat use for MSOs between rocky canyonland and forest habitats. Hence, when transferring habitat suitability models from one region to another, it is necessary to evaluate the transferability of the model by accounting for non-stationarity in species-habitat preferences.

1. Introduction

Habitat loss and fragmentation are important drivers of the global biodiversity crisis (Cushman, 2006; Mohammadi et al., 2021; Zhu et al., 2021), causing connectivity loss (Mohammadi et al., 2022), weakened genetic structure (Griciuvienė et al., 2021), and decreased demographic viability (Kaszta et al., 2019, 2021; Ash et al., 2022). To address these issues, many management and conservation activities focus on habitat protection and restoration (Miller and Hobbs, 2007). However, geographic location of restoration efforts is a crucial consideration for their effectiveness, requiring scientists to first understand how species use habitat (Elith and Leathwick, 2009; Lewis et al., 2017; Valavi et al., 2022).

To investigate habitat use, researchers are increasingly using habitat suitability models, sometimes interchangeably referred to as species distribution models (Guisan and Thuiller, 2005; Araújo and Guisan 2006; Hirzel et al., 2006). Habitat suitability models are modeling procedures that associate observations of a species (presence-only or presence/absence) with environmental conditions (Guisan and Zimmerman 2000; Guisan et al., 2017). The theory, background, and

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application of habitat suitability models have been extensively studied, and researchers continue to develop new techniques to improve the efficacy of these important tools (Hegel et al., 2010; Naimi and Araújo, 2016; Hysen et al., 2022). Habitat suitability models have been used for a variety of topics including niche characterization and the prediction of a species' response to different factors from climate change to disease dynamics (Guisan and Thuiller, 2005; He et al., 2019; Shabani et al., 2020). While habitat suitability models are powerful tools, inferences should be drawn cautiously due to potential spatial limitations of the models such as the scale of the data and geographic extent of the study area (Araújo et al., 2019).

Across time and space, the impacts of factors on an ecological process and the properties of the covariate of interest can change. This phenomenon is known as non-stationarity (Turner et al., 2001; Osborne et al., 2007; Kaszta et al., 2021; Rollinson et al., 2021). This can pose a problem for habitat suitability models, whereby covariates that have been determined to predict a response at one scale or landscape might incorrectly predict the response when projected to a new environment or geographical area (Turner et al., 2001; Cushman et al., 2011; Shirk et al., 2014). This can happen when the relationship between the predictor and covariates changes both spatially and temporally indicating non-stationarity in species-habitat preferences (Dobrowski et al., 2011; Vergara et al., 2017; Kaszta et al., 2021). For example, the scale of effect (i.e., the scale at which a covariate is most important) could change between two similar habitats in different places (Shirk et al., 2014; McGarigal et al., 2016; Atzeni et al., 2020).

Non-stationarity has been identified as a complex problem in landscape ecology (Cushman, 2010) and recognizing it in a system can enhance inference and prediction for practical management actions (Elith and Leathwick, 2009; Newman et al., 2019; Rollinson et al., 2021). Non-stationarity can be addressed by taking a species' local adaptations and ecology into account when studying their habitat (Pease et al., 2022). This makes it tenuous to generalize a habitat or behavior for a species and all of its subspecies, or even for all populations of a given species or subspecies (Atzeni et al., 2020; Shirk et al., 2023, Jones et al., 2023). Therefore, a species' different habitat associations and ecology in different ecological contexts should be carefully considered before building or applying a habitat suitability model.

Due to limited time and resources, researchers often create habitat suitability models over large spatial extents. While this approach can provide more generalizable species niche estimations by encompassing a wider range of covariate values, for management decisions we often also need to understand more local habitat relationships, which might exhibit non-stationarity. So, there is a trade-off between generalized models and more localized models. We tested this issue of variation across the range with the Mexican spotted owl (*Strix occidentalis lucida*), a federally-threatened subspecies of spotted owl (Willey and Ward, 2004; Willey and Zambon, 2014). Studies have shown that there is non-stationarity in Mexican spotted owl (hereafter MSO) habitat selection in forested environments (Wan et al., 2017; Jones et al., 2023). Mexican spotted owls are unique among the spotted owl subspecies in that they are found across a gradient of ecological conditions, from dense forests to rocky canyonlands (Ganey et al., 2011; Bowden et al., 2015; Wan et al., 2017). Given the differences across this ecological gradient, such as in proportion of forest cover, tree composition, and slope, it is unclear whether MSO in rocky canyonlands could select habitats differently from MSO living in old-growth forests. This opacity makes it difficult for land managers to identify management strategies that would benefit MSO in all portions of their range.

Our goal was to uncover potential differences in factors underlying habitat suitability between MSO living in forest versus rocky canyonland environments. We hypothesized that non-stationarity in habitat use exists between the forests and rocky canyonlands inhabited by MSO, and therefore predicted that a habitat suitability model trained in forest environments would not be an effective surrogate for habitat suitability in rocky canyonlands. To test our hypothesis, we created a multiscale habitat suitability model with covariates and scales specific for canyon-dwelling owls and compared it with the predictions of a multiscale model for forest-dwelling MSO developed by Wan et al. (2017). In addition, we sought to address how the MSO might respond to biotic and abiotic covariates, and explored at which scales those covariates were most important.

2. Methods

2.1. Study area

The study area is in southern Utah, spanning a total area of ~139,000 km^2 (Fig. 1). It consists of deeply entrenched rocky canyons rimmed by steep cliffs overlooking rugged canyon bottoms, and often includes terraced slopes dominated by vegetation of desert scrub with scattered Pinyon-juniper (*Pinus edulis - Juniperus osteosperma*) woodland. Desert scrub vegetation is common at arid and exposed mesa tops and south-facing slopes at lower elevations (Willey and van Riper III, 2007). In addition, canyon bottoms may contain small patches of riparian habitat, including box elder (*Acer negundo*), bigtooth maple (*Acer grandidentatum*), various willow species (*Salix* spp.), Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) (Willey and van Riper III, 2007, 2015). Two relatively high elevation sites are dominated by aspen (*Populus tremuloides*), mixed-coniferous forests, subalpine fir (*Abies lasiocarpa*), and Englemans spruce (*Picea englemani*) at the highest elevations (Hood and Miller, 2007). The peak elevation of the area is 3724 m above sea level. The climate of the area can range from warm to cold-temperate, with relatively cold winters and hot summers. Freezing cold temperatures commonly take place in winters, including snow at high elevations (Spence et al., 2011). Precipitation in the study area has a bimodal pattern with a peak in late summer to early fall and rises with elevation from around 150 mm at the lowest elevations to about 250 mm at the highest elevations (Spence, 2001).

2.2. Data collection and preparation

We had a dataset consisting of nest, roost, telemetry and night survey locations for MSO ($n = 1085$). We subset the nest and roost locations of MSO from the dataset (1991–2021) from rocky canyonland and forest habitats in southern Utah, removing duplicates ($n = 362$). The data include roost ($n = 337$), and nest site ($n = 25$) locations based on a telemetry study (Willey, 1998; Willey and van Riper, 2007), and an occupancy survey (Hockenbary, 2011). For the telemetry data, we subsampled to account for independence, where at least 24 h between locations was needed to obtain independence. Roost and nest sites were obtained weekly, both during telemetry, and later during occupancy surveys. To account for the impact of spatial autocorrelation in models, we applied the third filtering and subsampled the presence points based on the average home range size of the species (1.31 km) through spatial rarefaction. This involved filtering the data, to ensure a minimum distance between presence points, allowing us to assume independence of locations. After spatially filtering the training data, we retained 87 nest and roost locations for developing the models. We used 70 % of our presence location data for model training ($n = 61$) and the rest for model testing ($n = 26$). We used the 30 % reserved for model testing to evaluate both the rocky canyonland model and the forest model projected to rocky canyonlands. In addition to the occurrence points, we created 100,000 background points to provide a baseline for comparison with the presence data, using R statistical software (R Core Team, 2022) and randomly placed them across the study area (Barbet-Massin et al., 2012; Hysen et al., 2022). We subset the background points into three categories including 1x (same number of presences and background points), 10x (number of background points being 10 times the presences), and 10k (10,000 background points) following Hysen et al., (2022). Background locations were generated within a 30 km buffer surrounding all nest and roost locations to reflect dispersal ability, and to prevent

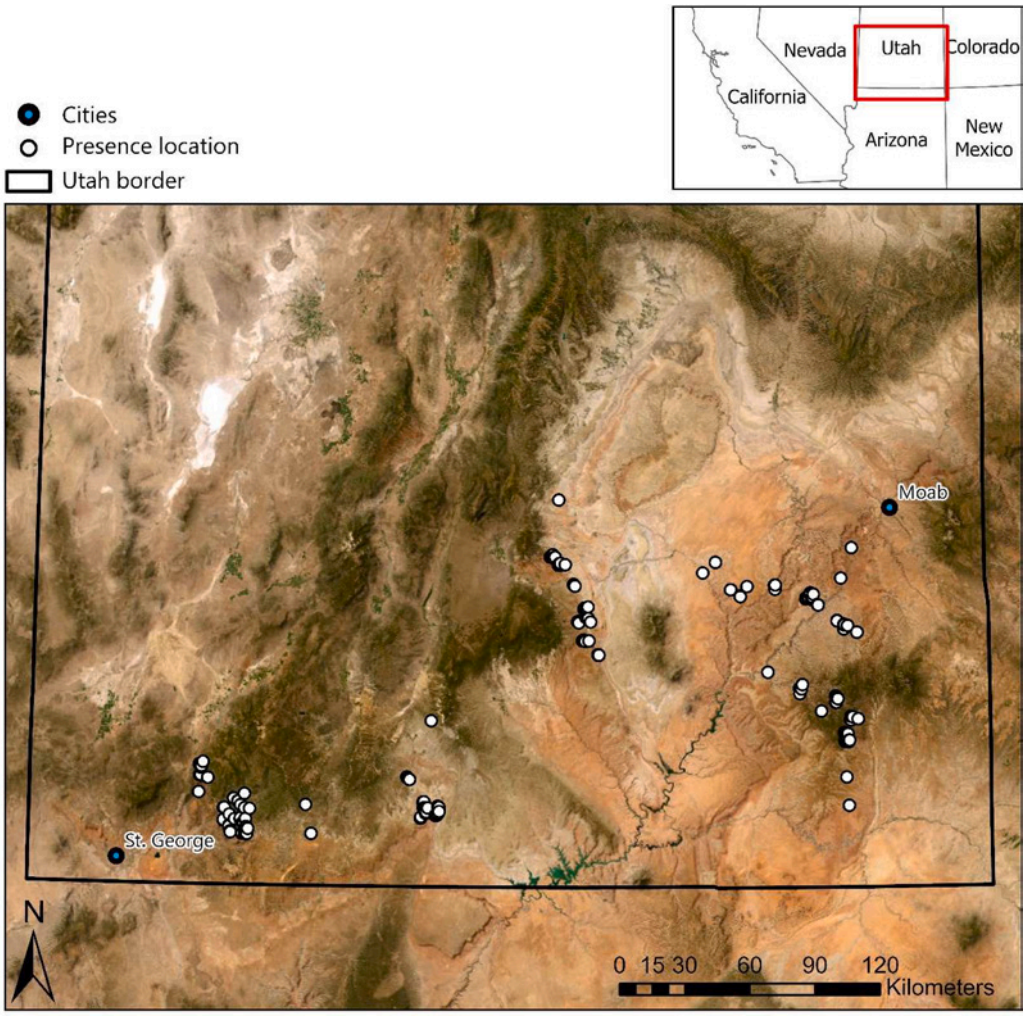

Fig. 1. The study area in southern Utah and nest and roost locations of Mexican spotted owls (1991–2021) prior to spatial filtering and separation into training and testing datasets (all presences before filtering, $n = 362$).

artificial inflation of test statistics due to overdispersion (e.g., Chiaverini et al. 2021). This was also based on our largest spatial scale (5000 m) but not within 1.31 km of nest locations to reflect average home range size of the species (U.S. Fish and Wildlife Service, 2012). Although some studies have identified larger home ranges for MSO in rocky canyonlands (e.g., Willey and van Riper III 2007, Bowden et al. 2015), we used the range-wide averaged home range for the subspecies (U.S. Fish and Wildlife Service, 2012). Defining a region in which to sample background points based on home range size and dispersal ability, with 1.31 km as the minimum and 30 km as the maximum buffer, also plays a role in mitigating the problem of overestimating suitable areas. Thus, background points were never sampled closer than 1.3 km to each presence point but never farther than 30 km. This approach limits the background points to locations that are theoretically available to MSO. It is important that all conditions within a reasonable buffer area around presence points are represented by the background points. This way, we can use a model to compare the conditions that are being used by the species to conditions that are theoretically available to be used (Araujo and New, 2007).

Based on published literature and species ecology, we selected biotic and abiotic covariates from three categories: climatic, vegetation and topographic (Wan et al., 2017). A full list of considered environmental covariates is included in the supplementary materials (Table S1). We obtained environmental covariates from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE, 2017), USA National Phenology Network (NPN; Crimmins et al., 2017), and Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate group (Rupp et al., 2022). We obtained climate data from PRISM, vegetation data from NPN and we derived topographic variables from LANDFIRE. Among the topographic variables we calculated were insolation (amount of solar radiation reaching a given area), curvature (a measurement for understanding to what extent the landscape is curved), and slope position index (the steepness at each cell of a raster surface) and roughness (the degree of irregularity of the surface). Given limitations with available raster data, we obtained all covariates for 2011. We assume that all covariates across our sampling period were stable because environmental conditions change very slowly in arid, rocky canyonlands such as those in our study. For the analyses, we first converted our covariates into raster layers and then projected them into the NAD 1983 / UTM 12N datum, which is geographically appropriate for our study area location. Then, we resampled our layers to 30 m resolution. We used the software FRAGSTATS (McGarigal et al., 2002) to calculate two metrics for the ponderosa pine forest covariates using a moving window: forest edge density and proximity to forest (following Wan et al. 2017).

2.3. *Univariate scaling*

To identify an optimal scale for each covariate, we ran focal statistics on each using a circular moving window of radius equal to each of the 50

scales from 100 m to 5000 m with a 100 m interval (after Wan et al. 2017). To select the optimal scale for each covariate, using two-tailed *t*-tests to assess the difference between values extracted to nesting and roosting locations and background locations for each environmental covariate (after Wasserman et al. 2012). We then selected the scale that had the largest difference in the means (smallest *p*-value) as the best scale.

To account for potential multicollinearity in our models, we compared covariates at their optimal scales using a pairwise Pearson's correlation coefficient. We used a threshold of $|r| > 0.7$ to identify covariates that were highly correlated with each other (Fig. S3). For each pair of highly correlated covariates, we relied on the literature to determine which covariate to remove from the analysis by selecting covariates with more known influence on species ecology specifically in rocky canyonlands (Timm et al., 2016; Wan et al., 2017).

2.4. Multi-scale modeling

We used the biomod2 package in R to train and test models (Thuiller et al., 2016). We used seven different modeling algorithms that are common in habitat suitability studies and available in the biomod2 package (Valavi et al., 2022): Generalized Additive Model, Generalized Linear Model, Multivariate Adaptive Regression Splines, Maximum Entropy, Random Forest, Generalized Boosting Model and Artificial Neural Network (Thuiller et al., 2009, 2016). All individual models were built with the optimal background points category reported in Hysen et al. (2022). This means that we did not try to find the optimal number of background points for each model. For example, since MARS performed optimally with 10k background points according to Hysen et al. (2022), we constructed MARS using the 10k background points category (Hysen et al., 2022). We repeated the same procedure for building all our models with the optimal number of background points.

Species presence and background points were used as response covariates in all models for rocky canyonlands, and covariates in Table S1 were used as explanatory covariates. Then we used an ensemble learning approach, which is a method to average single model predictions (Araújo and New 2007). The ensemble model was built with individual models developed with their respective optimal background points category following Hysen et al. (2022). We used the output of the ensemble model for interpreting MSO habitat use in rocky canyonlands. Covariate contributions for each model were calculated following Thuiller et al. (2009). Covariates that had little impact on the models (percent contribution in the model < 0.02) were removed and models were re-run. Response curves were created and visually examined to understand the relationship of each covariate with MSO habitat suitability in rocky canyonlands (Fig. 2). Response curves for the final ensemble model were calculated by changing one covariate and keeping the other covariates constant (Hysen et al., 2023). The model was applied spatially to develop a habitat suitability map across the study area in rocky canyonlands, with values ranging from 0, depicting the lowest habitat suitability, to a value of 1, depicting the highest habitat suitability. We then applied the coefficients from Wan et al. (2017) model (hereafter referred to as the forest model) to the rocky canyonlands, which is our study area, to develop a habitat suitability map in R. The forest model used a binomial GLM framework to understand MSO habitat preferences in a forest ecosystem (Wan et al., 2017). The forest model was trained using nest and roost locations of MSO. The response data used were presence-background locations and the explanatory variables used were also standardized (Wan et al., 2017). The area that Wan et al., model covered was 1500 km^2 which is smaller than our study area (139,000 km^2) and Wan et al., also used nesting and roosting locations as their response variable. Our ensemble model and the binomial GLM used by Wan et al. (2017) are directly comparable due to their underlying theoretical foundation in species distribution modeling and their functionality in capturing complex relationships between response variable and covariates. Similar to the canyonland model, we rescaled the predictions between 0 and 1 so we could compare the predicted suitability values between the two models. We then compared our rocky canyonland habitat model with the forest habitat model (Wan et al., 2017) to identify any differences between the most important covariates and their optimal scales.

2.5. Model evaluation

We calculated the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot, which is one of the most widely used performance metrics in habitat suitability models as well as True Skill Statistic (TSS) to evaluate model performance (Fielding and Bell,

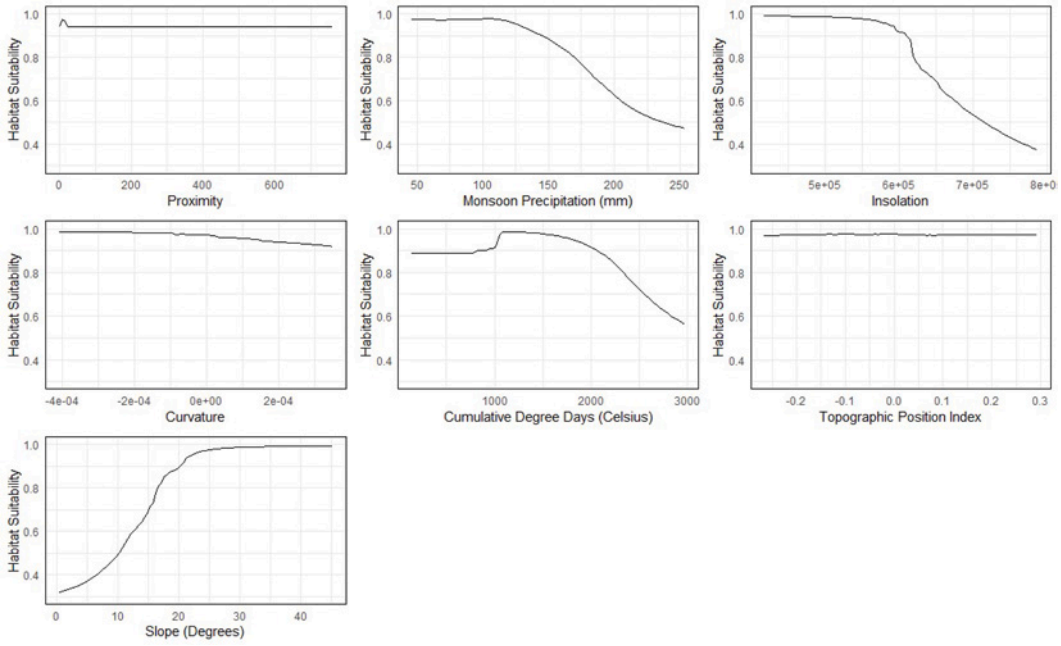

Fig. 2. Covariates derived from the ensemble model for rocky canyonland and their relationships with habitat suitability.

1997; Allouche et al., 2006; Shabani et al., 2016; Scherrer et al., 2019). True Skill Statistic is a threshold-dependent metric, although the selection of a threshold is often done arbitrarily. Therefore, we chose a threshold that maximized the sum of the specificity and sensitivity metrics for our models (Liu et al., 2013, 2016). We also assessed the Continuous Boyce Index for both forest and rocky canyonland models using enmSdmX package in R (Hirzel et al., 2006; Smith et al., 2023). This metric can be used for presence/background data and assesses the correlation between the proportion of sites and the expected proportion of predictions in each prediction class based on the proportion of the landscape in the class (Hirzel et al., 2006). Continuous Boyce Index values range from -1 to 1, where a value closer to 1 indicates that the distributions of model predictions and observed data are consistent, a value closer to zero indicates model predictions are randomly distributed relative to the observed data, and a value closer to −1 indicates that model predictions are opposite the observed data.

3. Results

We used eight environmental covariates at their optimal spatial scales for training the models (Table 1). The most important environmental covariates in the final ensemble rocky canyonland model were slope (800 m scale), cumulative degree days (1200 m scale), insolation (1000 m scale), and monsoon precipitation (100 m scale). Slope generally had a positive relationship with nesting/roosting suitability and contributed the most to model accuracy. Cumulative degree days had a unimodal response, with a predicted optimum of 1141 cumulated degrees Celsius. Insolation showed a negative relationship with habitat suitability, with very low habitat suitability at high insolation values (Table 1, Fig. 2). Monsoon precipitation also had a unimodal relationship with habitat suitability, increasing up to ~100 mm and then decreasing. The resulting rocky canyonland ensemble model performed well, with a TSS of 0.50 and an AUC value of 0.85. The rest of the covariates in both models had low importance (contribution <0.01). We provided response curves for all environmental covariates in Fig. 2. Based on the Continuous Boyce Index, the rocky canyonland model outperformed the forest model in predicting nest and roost locations in rocky canyonlands (CBI = 0.8) (Figs. S1, S2, individual model performance metrics are provided in Table S2).

The predictive nesting/roosting habitat map produced by the rocky canyonland model shows that suitable habitats are patchily distributed within our study area and largely follow areas with steep slopes and low solar exposure (Fig. 3A). This model also predicts areas of highly suitable habitat in central Utah and southwestern Utah with little suitable habitats in southeastern Utah (Fig. 3A).

The forest model performed poorly in the rocky canyonland environment and only had a TSS of 0.03. It also failed to identify any part of the study area as highly suitable habitat, and classified most of the study area as low suitability (Fig. 3B). The forest model showed a fairly high AUC (0.84), suggesting a discrepancy between apparent model accuracy and the actual habitat suitability, which is a known bias of AUC (Smith 2013). We also assessed the Continuous Boyce Index for the forest model (CBI = 0.7), which showed a lower accuracy compared to the rocky canyonland model (Figs. S1, S2).

4. Discussion

Non-stationarity can bias inferences made from spatial models and make it difficult to implement management actions effectively (Peterson et al., 2007; Cushman, 2010; Yates et al., 2018). To help managers craft species- and region-specific actions for at-risk species, non-stationarity should be addressed in species-habitat relationships (Kaszta et al., 2019). Given the high contrast between forest and rocky canyonland ecosystems of the U.S. Southwest, it is important to understand different limiting factors like precipitation that vary spatially and influence species within these distinct habitats (e.g., Cushman et al. 2011, Short Bull et al. 2011, Vergara et al. 2017). Mexican spotted owls exhibit different habitat use by selecting different covariates in forests and rocky canyonlands, thus necessitating distinct management strategies. This paper provides information for how to manage MSOs better in rocky canyonlands and is the first study to explicitly model the multi-scale habitat suitability of MSO in rocky canyonlands. Our results suggest that there is non-stationarity in the factors that drive habitat use of MSO in forests in Arizona and New Mexico versus rocky canyonland habitats in southern Utah (Wan et al., 2017).

4.1. Non-stationarity in habitat use

Mexican spotted owls live in a gradient from rocky canyonlands to various forest communities, such as wet mixed-conifer and dry pine-oak forests, across the subspecies' range (U.S. Fish and Wildlife Service, 2012, Ganey et al., 2011). For MSO living in rocky canyonlands, our model identified slope, cumulative degree days, insolation, and monsoon precipitation as the most important covariates related to habitat suitability. In contrast, within the forested environment, percent canopy cover, percent mixed-conifer, and slope were identified as the most important covariates (Wan et al., 2017). The presence of slope in the top three most important covariates for each model suggests that this is an important environmental condition across the two systems. Slope has been identified as an important factor governing habitat suitability of MSO both in forests and rocky canyonlands (Willey and Zambon 2014, Willey and van Riper III, 2015, Wan et al., 2017). This might

Table 1
Covariates included in the rocky canyonland model built in this study and the forest model that was built previously (Wan et al., 2017), and scales at which they performed best. *the covariate was excluded from the model due to correlation with another covariate (Fig. S3). ** the covariate was not examined in the model.

		Rocky Canyonland Model (this study)		Forest (Wan et al., 2017)	
		Scale (m)	Contribution	Scale (m)	Contribution
Climatic	Cumulative Degree Days	1200	0.13	5000	Excluded*
	Monsoon Precipitation	100	0.09	5000	Excluded*
Vegetation	Forest Edge Density	5000	Excluded*	3700	0.04
	Percent Canopy Cover	1800	Excluded*	100	0.26
	Percent Mixed Conifer	200	<0.01	5000	0.22
	Percent Ponderosa Pine	200	Excluded*	3600	Excluded*
	Proximity to Forest	1300	0.01	4000	0.05
Topographic	Curvature	800	0.01	Excluded**	Excluded**
	Elevation	100	Excluded*	5000	Excluded*
	Insolation	1000	0.12	100	0.08
	Roughness	3000	Excluded*	Excluded**	Excluded**
	Slope	800	0.52	500	0.21
	Slope Position Index	900	Excluded*	Excluded**	Excluded**
	Topographic Position Index	900	<0.01	300	0.14
	Topographic Roughness Index	900	Excluded*	Excluded**	Excluded**

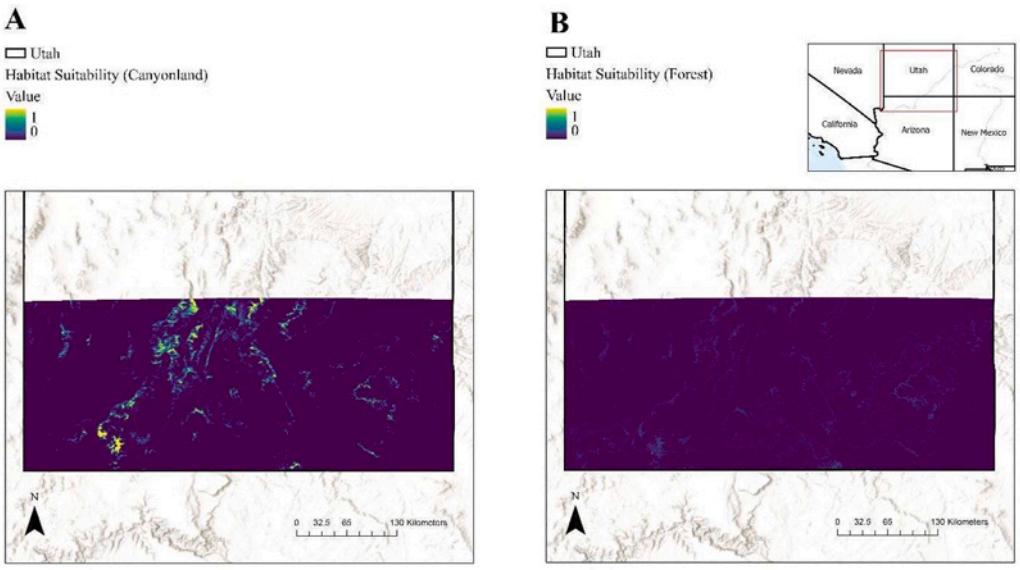

Fig. 3. The habitat suitability maps produced by applying the rocky canyonland model to the rocky canyonland region and (B) applying the forest model to the rocky canyonland region, both developed using nest/roost data. Values closer to one indicate more highly suitable nesting/roosting habitat, while values closer to zero indicate less suitable nesting/roosting habitat.

reflect the fact that steeper slopes offer a refugia for avoiding predators, provide topographical and edaphic conditions favorable to moderate microclimates, and the occurrence of preferred large tree vegetation conditions in forests. Large steep vertical cliffs provide an abundance of caves and ledges for both nest sites and roost sites in the rocky canyonland region, where no nests have ever been detected in trees (Willey and van Riper III, 2015). High exposure to intense solar radiation causes high temperatures that are not tolerated well by MSO and drive patterns of vegetation (e.g., small trees or non-tree habitat) that are not preferable to MSO occurrence. In treeless habitats in Utah, steep and complex cliffs apparently substitute for forest structure (Willey and Zambon, 2014). Insolation plays an important role in determining their habitat, particularly in arid rocky canyonland habitats. Overall, topography plays an important role in habitat use across different habitat types.

Canopy cover was not included in the final model in rocky canyonlands while the contribution of the vegetation indices (ponderosa pine and proximity to forest) that were included in the rocky canyonland model were low. This indicates that the vegetative conditions in rocky canyonlands are not important predictors of MSO nesting/roosting habitat use. Meanwhile, the proportion of canopy cover and mixed-conifer were included and identified as significant predictors in the forest model. This is consistent with other studies of MSO habitat use. For example, MSO in forest environments nest in large trees in areas of high canopy cover and large extents of mixed-conifer forests (Ganey et al., 2016; Timm et al., 2016; Wan et al., 2017). The same pattern of selecting for greater proportions of forest cover and canopy cover has been observed in the other two subspecies of spotted owls (Carrol 2010; Wan et al., 2017).

In contrast, MSO in rocky canyonlands select caves and ledge sites in rocky canyons with high topographic complexity, where soaring cliffs provide complete overhead cover in areas characterized by low or no canopy cover provided by trees (Willey and van Riper, 2007; Jones et al., 2023). Furthermore, cumulative degree days had a unimodal relationship with MSO habitat suitability, and habitat suitability was maximized when cumulative degree days and monsoon precipitation were moderate and insolation was low. This unimodal relationship with cumulative degree days and monsoon precipitation suggests that environments can be suboptimally cool and rainy, even in rocky canyonlands. However, if insolation is high, even when cumulative degree days are moderate, the habitat is also suboptimal for MSO. In Arizona and New Mexico, MSO in different subregions selected for lower cumulative degree days in general (Jones et al., 2023). Mexican spotted owls probably avoid high temperatures, especially in more xeric locations, which may be accomplished by selecting higher elevations or for complex topographic features (Jones et al., 2023). In dry rocky canyonlands, high temperatures, exacerbated by a warming climate, might lead to challenges for MSO or their prey such as woodrats (*Neotoma spp*) and white-footed mice (*Peromyscus spp*) (Willey, 2013; Ganey et al., 2020). Although currently little evidence suggests that climate change is causing reductions in MSO population size (U.S. Fish and Wildlife Service, 2012), with increasing temperature, cumulative degree days and monsoon precipitations, conditions might become more limiting to MSO habitat suitability.

The overlap of factors governing MSO habitat suitability in rocky canyonlands and forests suggests that some universal predictors (e.g., availability of cool, shady microsites with suitable nest structures) limit MSO nesting site suitability in the two systems, but that the proximate habitat factors differ (e.g., shaded cliffs with caves and potholes versus forests with large trees and high canopy cover) (Willey and van Riper, 2007; Willey and Zambon, 2014; Ganey et al., 2011). In both systems, topography is highly important. Indeed, in the Timm et al. (2016) and Wan et al. (2017) forest system MSO models, topographical covariates overall had stronger predictive ability of MSO nest and roost site selection than vegetation composition or structure (based on variance explained by covariate sub-groups). This suggests that MSO habitat use in both forest and rocky canyonland systems is highly dependent on topographical features that provide shade to moderate microclimate, and edaphic conditions for preferred vegetation structure for both MSOs and key prey species (Willey 2013). It also suggests that vegetation covariates are not as important in rocky canyonlands as they are in forests. However, a conclusion should be drawn with caution, as the canopy cover, a forest covariate, was dropped due to correlation with monsoon precipitation. Therefore, forest covariates could be important still for rocky canyonlands, however the high covariate importance of topographic covariates is still apparent, suggesting that topographical covariates are highly important for habitat use in rocky canyonlands (U.S. Fish and Wildlife Service, 2012). For example, wildfire is probably less of a threat to MSO populations in rocky canyonlands compared to forests due to a lack of flammable material (Wan et al., 2019).

4.2. Non-stationarity in scales of effect

Although habitat use is an inherently multi-scale and hierarchical process, many habitat studies evaluate species-habitat relationships at a single scale (McGarigal et al., 2016; Fletcher and Fortin, 2018; Scherrer et al., 2019). The MSO is a unique study species because there are multiple studies that have evaluated habitat suitability at multiple scales. However, previous studies have primarily focused on forest habitats (Timm et al., 2016; Wan et al., 2017). Rocky canyonlands also provide important habitat for MSO in some regions (Lewis 2014; Willey and Zambon, 2014; Willey and van Riper III, 2015), and our study allowed us to compare the optimal scales for each covariate between our model and the previously developed forest model. In the rocky canyonlands model, slope had the greatest contribution to habitat use at coarser spatial scales (800 m), while in the forest model it was more important at slightly finer spatial scales (500 m). In comparison, a previous study in forest habitat also found that slope had the greatest contribution to habitat use at fine spatial scales (400 m, Timm et al., 2016). One reason for this difference could be that MSO selects the overall characteristics of a canyon, such as how steep the canyon walls are and how continuous the canyon reach is rather than simply the slope at a particular point within a canyon.

Cumulative degree days, the second most important covariate in the rocky canyonland model, was most important at a moderately-coarse spatial scale (1200 m), while it was most important at a very coarse spatial scale (5000 m) in the forest model. One reason for this pattern could be the presence of microclimates in rocky canyonlands that will vary more over finer spatial scales than climatic conditions in less topographically diverse areas. However, the scales could also be coarse due to the limitations with interpolated climate data, which often have low confidence at fine scales.

Insolation was the third most important covariate in the rocky canyonland model at a moderately-coarse spatial scale (1000 m), while it was most important at a very fine spatial scale (100 m) in the forest model. This could suggest that owls in forests find topographic microsites that minimize insolation, versus larger canyon stretches to accomplish that in rocky canyonlands.

In the forest model, percent canopy cover contributed most to the model at a relatively fine spatial scale (200 m). While we ultimately did not include percent canopy cover in the rocky canyonland model due to high correlation with monsoon precipitation, its optimal scale was much coarser (1800 m). In rocky canyonlands, tree cover tends to be more limited and more intermittent along canyon bottoms than in forests, likely requiring MSO to consider canopy cover across broader areas, if they consider it at all. In canyon environments, it is likely that cliffs provide overhead cover for MSO. Finally, percentage of ponderosa pine forest was included in the forest model at a coarse optimal spatial scale (3600 m), while it was included in the rocky canyonlands model at a very fine optimal spatial scale (200 m). The reason might be due to the sparsely distributed patches of forests in rocky canyonlands, whereas the proportion of ponderosa pine forests appears to be more abundant and visible from coarser scales in forests. It has also been found that small, isolated stands of large old trees were remarkably important roost sites, and likely promote prey species (Willey and Willey, 2010). Hence, the responses of MSO to percent canopy cover at a coarser scale and ponderosa pine at a finer scale complement each other, underscoring the significance of ponderosa pine as a potential roosting site in rocky canyonlands.

4.3. Local model outperforms the non-local model

Our rocky canyonland model, although built with a low number of presence points ($n = 61$), performed well and outperformed the forest model in predicting nest and roost locations in rocky canyonlands. The forest model performed poorly as suggested by the lower TSS and Continuous Boyce Index when compared with the canyonland model, and more importantly, by the fact that none of the study area was predicted as suitable habitat on the map. Continuous Boyce Index is a better index for presence-only data as, unlike most measures of model goodness of fit, it evaluates the model's ability to forecast multiple levels of suitability (Hirzel et al., 2006). Area Under the Curve has been shown to be a biased performance metric when using presence-background data because it is threshold-independent, which can lead to discrepancies between apparent model accuracy and the actual suitability (Lobo, 2008; Smith, 2013). This is further supported by the fact that while both of our models showed similar AUC values, the other metrics we used indicated more of a difference in model performance. Therefore, the high AUC values obtained for both models should be considered with extreme caution. Our Continuous Boyce Index results also showed that the rocky canyonland model's output had a higher positive correlation with the true probability of presences, indicating better predictive performance. However, while the canyonland model produced a higher CBI (0.8) than the forest model (0.7), both are considered to indicate acceptable model performance. This could be due to the fact that few presences were used to validate the model, which caused the CBI for the forest model to be artificially high. This could also have happened because the forest model was still able to identify presences in a single bin at a very low habitat suitability value (see Fig. S2). When CBI is assessed in tandem with the spatial predictions in Fig. 3, we can see that the predictions do not make ecological sense. Still, a CBI of 0.8 indicates that the predictions for the canyonland model were more consistent with observed presences than the forest model and thus better performance.

Taking all of these metrics into account, it is clear that the canyonland-specific model performed better in the rocky canyonland habitat than the forest model, despite being based on a much smaller sample of owl locations (Forest model, $n = 2070$, Wan et al., 2017; Rocky canyonlands model, $n = 61$). We recognize that the difference in sample sizes used to train each model and likely sampling variance could contribute to the differences observed between the two models. This is a limitation of our study, given that MSO sampling efforts in rocky canyonlands have been limited relative to sampling efforts in forest habitats. However, our finding that the local model outperformed the non-local model is consistent with the results of previous studies (Torres et al., 2015; Wan et al., 2017, 2019). These studies have shown that models tend to perform poorly when projected outside of the geographic range for which they were originally fitted (Charney et al., 2021). Specifically, Wan et al. (2019) found that non-local models performed worse in areas that were outside of the range of the trained data for MSOs in two different geographical regions. Another study also revealed the decreased transferability of non-local models for grey petrel (*Procellaria cinerea*) in different islands (Torres et al., 2015). Similarly, Péron et al. (2018) demonstrated limited model transferability and non-stationarity between habitats for Scopoli's shearwater (*Calonectris diomedea*), in two contrasted regions of the Northwestern Mediterranean Sea. These previous findings combined with our results serve as a cautionary tale for researchers considering using habitat suitability models across areas with diverse environmental conditions.

4.4. Challenges to model transferability

In line with our expectation, high levels of non-stationarity in species-habitat preferences were observed both in environmental covariates and scales concerning MSO habitat use between the two regions. Such non-stationarity offers insight into model transferability. High levels of non-stationarity in species-habitat preferences are not uncommon for other species in other systems (e.g., Short Bull et al. 2011, Vergara et al. 2016, 2017, Atzeni et al. 2020). For example, Short Bull et al. (2011), in a case study of American black bear (*Ursus americanus*), showed that inability to explore multiple study areas with variable landscape features might lead to erroneous interpretation of models based on varying limiting factors at different spatial scales. Another study also showed that covariates explaining stone marten (*Martes foina*)

distribution differed among areas and generalizing one model to multiple areas is misleading (Vergara et al., 2017). Non-stationarity can exist among similar habitat types, too. For example, it was reported that MSO in northern Arizona uses habitat differently from those in New Mexico despite both dwelling in forests (Wan et al., 2017). We suspect that the same case might be true for MSO habitats that are collectively labeled as rocky canyonland. For example, the topography, climate, and vegetation of our southern Utah study area is quite different from the conditions in Grand Canyon National Park, but both areas are typically classified as rocky canyonland habitat for the MSO. Therefore, we speculate that our model will not perform well for predicting MSO habitat in the Grand Canyon, and we call for future research to confirm our speculation.

5. Conclusion

Our study is particularly important for the conservation of MSO that inhabits rocky canyonlands, a unique habitat that contrasts with more explored forests (Willey and van Riper III, 2007; U.S. Fish and Wildlife Service, 2012). Our study demonstrates that there is likely non-stationarity in MSO habitat use between rocky canyonlands and forested habitats. Given that most MSO studies are conducted in forest habitat, with only a handful conducted in rocky canyonlands, we call for more MSO research efforts across rocky canyonland ecosystems. Despite the valuable insights our study provides into the habitat suitability of MSO in this landscape, it is important to acknowledge certain limitations that may affect the generalizability of our findings. Given the unavailability of raster layers for each year and the extensive timespan of our research (1990–2021), we primarily relied on layers from 2011. As a result, certain covariates, particularly climatic data, should be interpreted with caution. Furthermore, our model provides spatially-explicit information for managers to make informed decisions, such as to prioritize areas for monitoring and management. Our study of the MSO in two different habitat types highlights the potential problems that can arise from neglecting non-stationarity in species-habitat preferences. Understanding local habitat peculiarities and limiting factors is crucial for accurately predicting region-specific habitat models. Our findings confirm that model transferability cannot be taken for granted and requires careful assessment. Failing to do so may lead to misinformed conservation decisions resulting from the casual use of habitat models with poor transferability (Péron et al., 2018).

From a broader perspective, this study underscores the importance of considering non-stationarity in habitat modeling and the potential problem of over-extrapolating model results for any species (Osborne et al., 2007; Cushman, 2010; Wan et al., 2017). Model transferability is a critical concept in ecological modeling, as it enables researchers to expand their models and improve their predictive power (Randin et al., 2006; Yates et al., 2018). Transferring models to novel conditions can provide predictions in situations with limited data, leading to better-informed management decisions (Péron et al., 2018). However, ignoring non-stationarity, an important driver of model transferability, can introduce biases and impair prediction accuracy (Yates et al., 2018). When possible, we recommend habitat models be made with local data to achieve the most reliable information for conservation and management.

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CRediT authorship contribution statement

Danial Nayeri: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Samuel Cushman:** Writing – review & editing, Writing – original draft, Conceptualization. **Joseph Ganey:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition. **Logan Hysen:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Micaela Szykman Gunther:** Writing – review & editing, Writing – original draft, Supervision. **David Willey:** Writing – review & editing, Writing – original draft, Investigation, Data curation, Conceptualization. **Ho Yi Wan:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Supplementary materials

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