COMPARING MEXICAN SPOTTED OWL HABITAT SUITABILITY IN TWO DIFFERENT HABITAT TYPES USING A MULTI-SCALE ENSEMBLE LEARNING FRAMEWORK

By

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ABSTRACT

COMPARING MEXICAN SPOTTED OWL HABITAT SUITABILITY IN TWO DIFFERENT HABITAT TYPES USING A MULTI-SCALE ENSEMBLE LEARNING FRAMEWORK

Danial Nayeri

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. 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 where MSO use habitat 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. I then compared my 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 and predicted low suitability across the entire study area, including areas with known nesting locations. These results confirm the non-stationarity in habitat use for MSOs between rocky canyonland and forest habitats and underscore the importance of accounting for non-stationarity across different geographic regions when modeling habitat. 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.

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provided great feedback. This thesis has been drafted as a manuscript that will soon be in review at Ornithological Applications, as it benefitted from comments from my co-authors, Samuel Cushman, Joseph Ganey, Logan Hysen, Micaela Szykman Gunther, David Willey, and Ho Yi Wan.

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INTRODUCTION

Habitat loss and fragmentation are important drivers of the global biodiversity crisis (Fahrig 2003, Mohammadi et al. 2021, Zhu et al. 2021). When habitat is less available and continuous, many species suffer from connectivity loss (Mohammadi et al. 2022), weakened genetic structure (Griciuvienė et al. 2021), and decreased demographic viability (Kaszta et al. 2019, 2021). To address these issues, many management and conservation activities focus on habitat protection and restoration (Miller and Hobbs 2007). However, location matters for restoration to be effective, requiring scientists to first understand how species use habitat, which might be the most widely studied aspect of applied ecology (Elith and Leathwick 2009, Lewis et al. 2017, Valavi et al. 2022).

To investigate habitat suitability, 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 application of habitat suitability models have been extensively studied, and researchers continue to develop new techniques to improve the efficacy of these important tools (Thuiller et al. 2009, Elith and Leathwick 2009, 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 (Araújo et al. 2019).

Across time and space, the characteristics (e.g., mean, variance) of a covariate will change as the location and scale of measurement changes, which is known as non-stationarity (Turner et al. 2001, Osborne et al. 2007, Newman et al. 2019). 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, Dobrowski et al. 2011, Shirk et al 2014). This can happen when the relationship between the predictor and response covariates changes both spatially and temporally (Dobrowski et al. 2011, Vergara et al. 2017, Kaszta et al. 2021). For example, the scale of effect, or 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, Wan et al. 2017, Atzeni et al. 2020).

Non-stationarity has been identified as one of the complex problems in landscape ecology, 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. 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 (Elith and Leathwick 2009, Wan et al. 2017, Atzeni et al.

2020). Therefore, a species' different habitat types and ecology in varied habitats should be carefully considered before building a habitat suitability model.

Due to limited time and resources, researchers often create habitat suitability models over large spatial extents. However, it is important to test whether this approach is useful for species of conservation concern or if non-stationarity is occurring and limiting the inferences that can be made. I tested this issue 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 occurring in Mexican spotted owl (hereafter MSO) forested habitats (Wan et al. 2017, Jones et al. 2022). Mexican spotted owls are unique among the spotted owl subspecies because they are residents across a gradient of habitat types, from dense forests to rocky canyonlands (Ganey et al. 2011, Bowden et al. 2015, Wan et al. 2017). Given the differences between the habitat types such as their proportion of forest cover, tree composition, and slope, it is unclear whether MSO in rocky canyonlands 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.

My goal was to uncover potential differences in factors underlying habitat suitability between MSO living in forest versus rocky canyonland habitat types. I 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 general enough to accommodate habitat suitability in rocky canyonlands. To test my hypothesis, I created a multiscale habitat suitability model with covariates and scales specific for canyon-dwelling owls and compared it with a model that used coefficients from a multiscale model for forest-dwelling owls developed by Wan et al. (2017). In addition, I sought to address how the MSO might respond to biotic and abiotic covariates, and explored at which scales those covariates were most important.

MATERIALS AND METHODS

Study Site

The study area is in southern Utah, spanning a total area of ~139,000 km^2 (Figure 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*) and mixed-coniferous forests and 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).

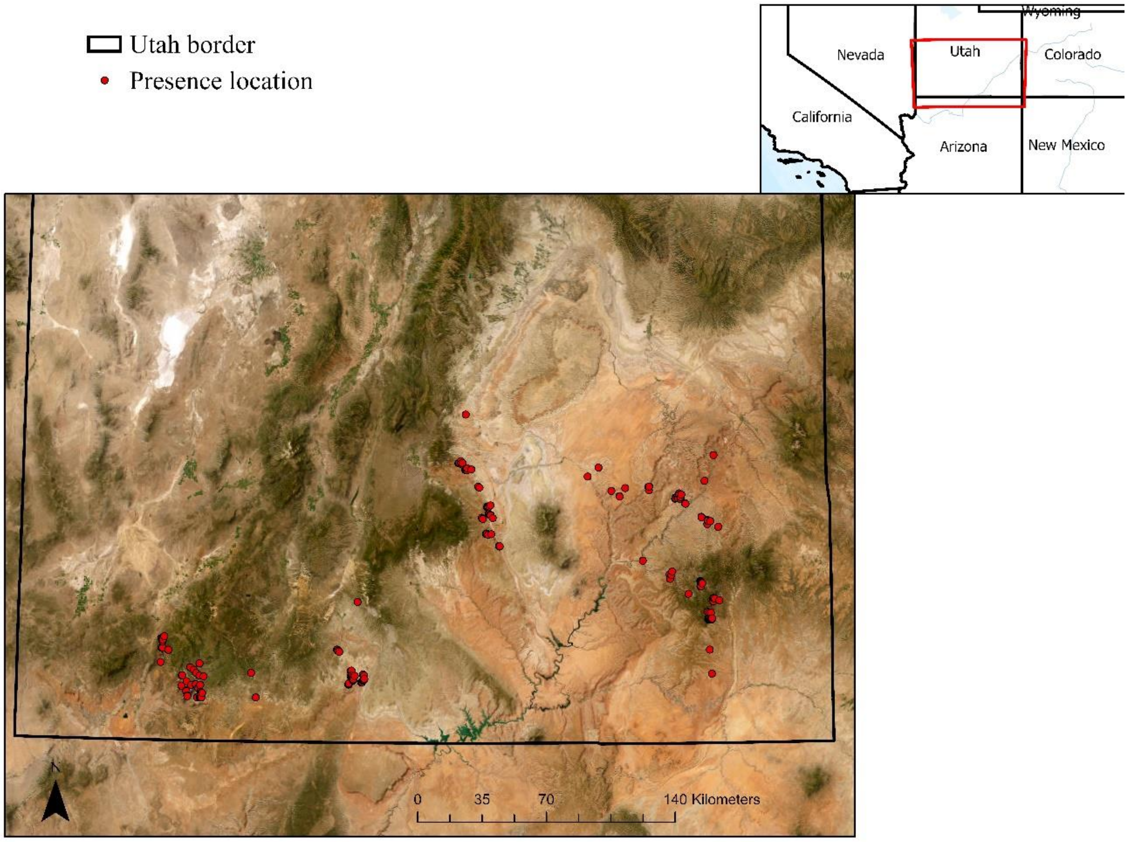

Figure 1. The study area in southern Utah and nest and roost locations of Mexican spotted owls (1991-2021) prior to spatial filtering and separation into training and testing datasets (all presences before filtering, *n* = 362).

Data Collection and Preparation

I had a dataset consisting of nest, roost, telemetry and night survey locations for MSO (*n* = 1085). I subset the nest and roost locations of MSO from the dataset (1991-2021) from rocky canyonland 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 study (Hockenbary 2011). For the telemetry data, I subsampled to account for independence, where at least 24 hours between locations was needed to obtain independence. Roost and nest sites were obtained weekly, both during telemetry, and later during occupancy visits. In addition to the occurrence points, I created 100,000 background points using R statistical software (R Core Team 2022) and randomly placed them across the study area. To account for the impact of spatial autocorrelation on models, I subsampled the presence points based on the average home range size of the species through spatial rarefication. This involves filtering the data, to ensure a minimum distance between presence points, allowing me to assume independence of locations. After spatially filtering the training data, I retained 87 nest and roost locations for developing the models. I used 70% of my presence location data for model training (*n* = 61) and the rest for model testing (*n* = 26). I 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 artificial inflation of test statistics due to overdispersion (e.g., Chiaverini et al. 2021). This was also based on my largest scale but not within 1.31 km of nest locations to reflect average home range size of the species (USFWS 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), I used the range-wide averaged home range for the subspecies (USFWS 2012).

Based on published literature and species ecology, I selected biotic and abiotic covariates from three categories: climate, vegetation and topographic (Wan et al. 2017). A full list of considered environmental covariates is included in the Appendix. I 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). For the analyses, I first converted my covariates into raster layers and then projected them into the NAD 1983 / UTM 12N datum, which is geographically appropriate for my study area location. Then, if necessary, I resampled my layers to 30 m resolution. I used the software FRAGSTATS (McGarigal et al. 2002) to calculate two covariates using a moving window: forest edge density and proximity to forest index using the ponderosa pine forest covariates (following Wan et al. 2017).

Univariate Scaling

To identify an optimal scale for each covariate, I 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). I then performed univariate scaling to select the optimal scale, 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). I 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 my models, I compared covariates at their optimal scales using a pairwise Pearson's correlation coefficient. I used a threshold of $|r| > 0.7$ to identify covariates that were highly correlated with each other. For each pair of highly correlated covariates, I relied on the literature to determine which covariate to remove from the analysis by selecting covariates with more known influence on species ecology or covariate that had little impact on the models ($1-\rho < 0.02$).

Multi-Scale Modeling

I used the biomod2 package in R to train and test models (Thuiller et al. 2016). I 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).

Species presence and background points were used as response covariates in all models for rocky canyonlands, and covariates in Appendix were used as explanatory covariates. Then I used an ensemble learning approach, which is a method to average single model predictions (Araújo and New 2007). I 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), and response curves were created and visually examined to understand the relationship of each covariate with MSO habitat suitability in rocky canyonlands (Fig. 2). 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. I applied the forest model to the rocky canyonlands using the coefficients in Wan et al. (2017) to build a resource selection function in R. I then compared my 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. At the end I averaged both models and tested performance metrics to see if averaging both models would improve the model fit.

Model Evaluation

I calculated the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot (Fielding and Bell, 1997, Scherrer et al. 2019), which is one of the most widely used performance metrics in habitat suitability models, to evaluate the models (Scherrer et al. 2019) as well as True Skill Statistics (TSS; Allouche et al. 2006, Shabani et al. 2016). True Skill Statistics is a threshold-dependent metric, although the selection of a threshold is often done arbitrarily. Therefore, I chose a threshold that maximized the sum of the specificity and sensitivity metrics for my models (Liu et al. 2013, 2016). I also assessed 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).

RESULTS

I used the eight remaining 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 degree Celsius, while insolation showed a negative relationship with habitat suitability with very low habitat suitability at high insolation values (Table 1, Figure 2). Habitat suitability increased with increasing monsoon precipitation up to ~100 mm and then decreased. The resulting ensemble model performed well, with a TSS of 0.5 and an AUC value of 0.851. The rest of the covariates in both models had low importance ($1-\rho < 0.01$). Response curves for all environmental covariates are provided in Figure 2. Based on the Continuous Boyce Index, the rocky canyonland model outperformed the forest model (Figure 3, 4). The predictive nesting/roosting habitat map produced by the rocky canyonland model shows that suitable habitats are patchily distributed within my study area and largely follow areas with steep slopes and low solar exposure (Figure 5A). This model also predicts areas of highly suitable habitat in central Utah and southwestern Utah with little suitable habitats in southeastern Utah (Figure 5A).

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 whereas. ** the covariate was not examined in the model.

		Rocky Canyonland Scale (m)	Rocky Canyonland Contribution	Forest Scale (m)	Forest Contribution
Climatic	Cumulative Degree Days	1200	0.13	5000	Excluded*
Climatic	Monsoon Precipitation	100	0.09	5000	Excluded*
Vegetation	Forest Edge Density	5000	Excluded*	3700	0.04
Vegetation	Percent Canopy Cover	1800	Excluded*	100	0.26
Vegetation	Percent Mixed Conifer	200	<0.01	5000	0.22
Vegetation	Percent Ponderosa Pine	200	Excluded*	3600	Excluded*

		Rocky Canyonland Scale (m)	Rocky Canyonland Contribution	Forest Scale (m)	Forest Contribution
Vegetation	Proximity to Forest	1300	0.01	4000	0.05
Topographic	Curvature	800	0.01	Excluded**	Excluded**
Topographic	Elevation	100	Excluded*	5000	Excluded*
Topographic	Insolation	1000	0.12	100	0.08
Topographic	Roughness	3000	Excluded*	Excluded**	Excluded**
Topographic	Slope	800	0.52	500	0.21
Topographic	Slope Position Index	900	Excluded*	Excluded**	Excluded**
Topographic	Topographic Position Index	900	<0.01	300	0.14
Topographic	Topographic Roughness Index	900	Excluded*	Excluded**	Excluded**

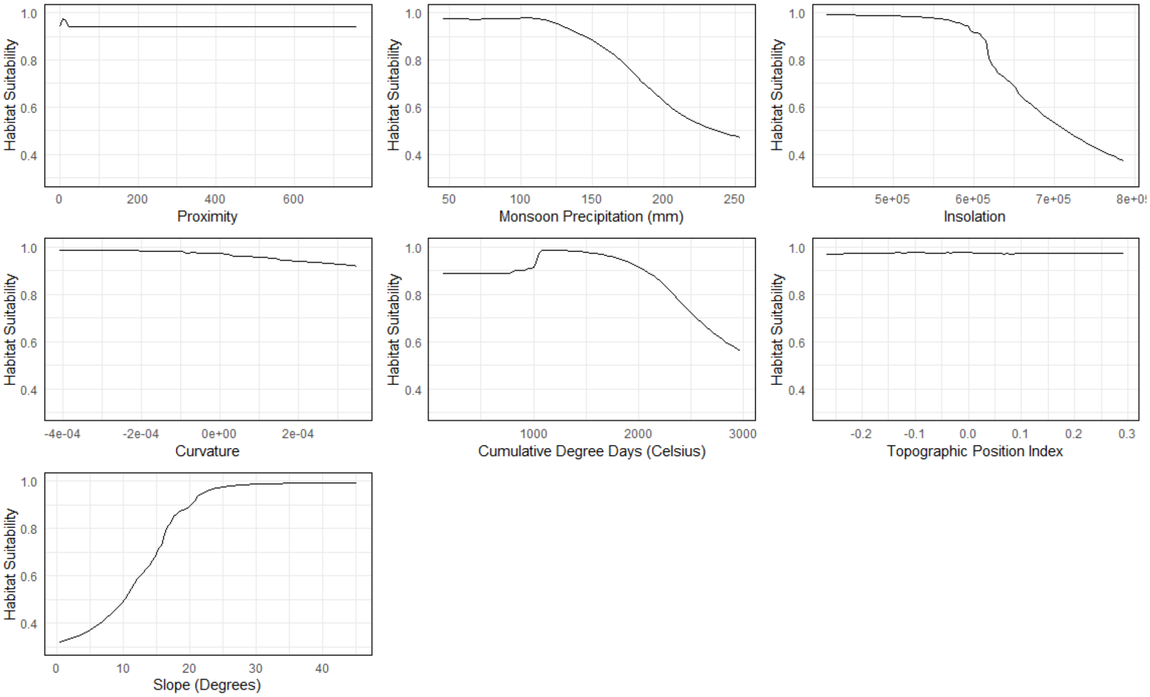

Figure 2. Covariates derived from the ensemble model for rocky canyonland and their relationship with habitat suitability.

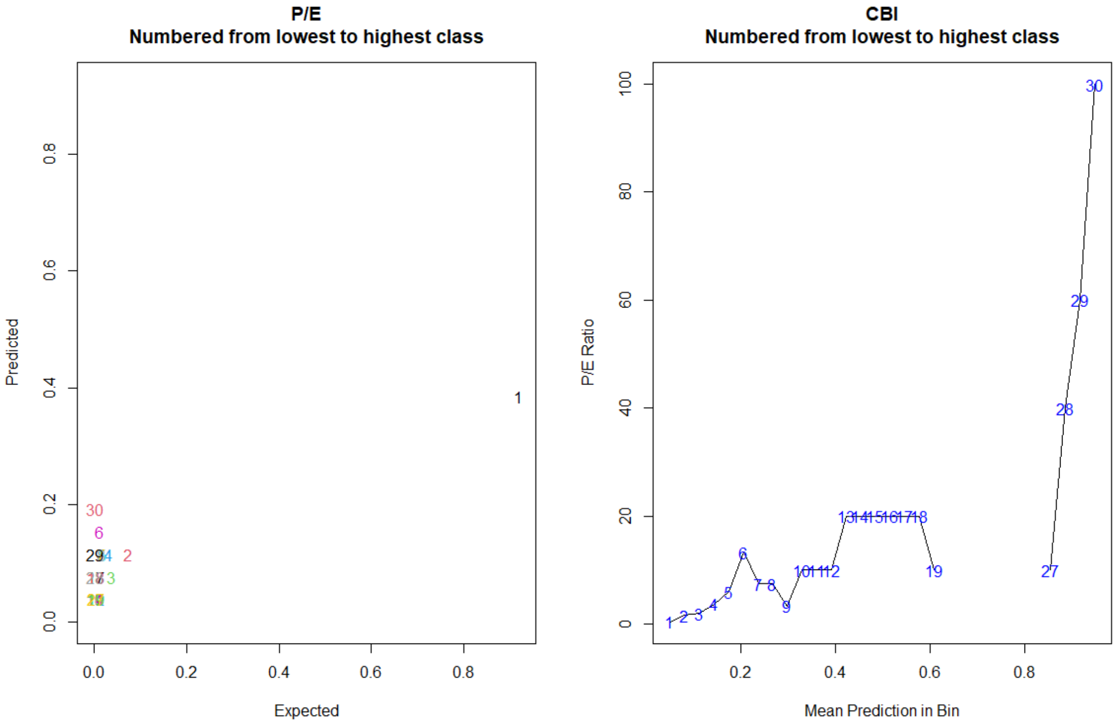

Figure 3. Continuous Boyce Index curves for the rocky canyonland model.

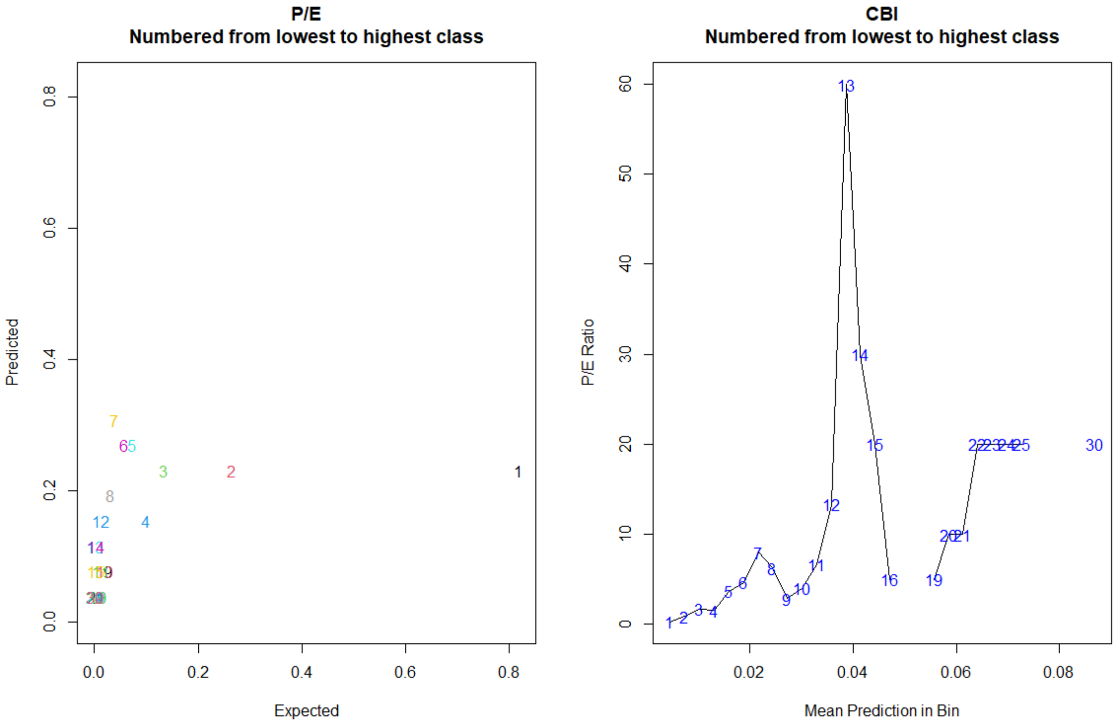
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Figure 4. Continuous Boyce Index curves for the forest model.

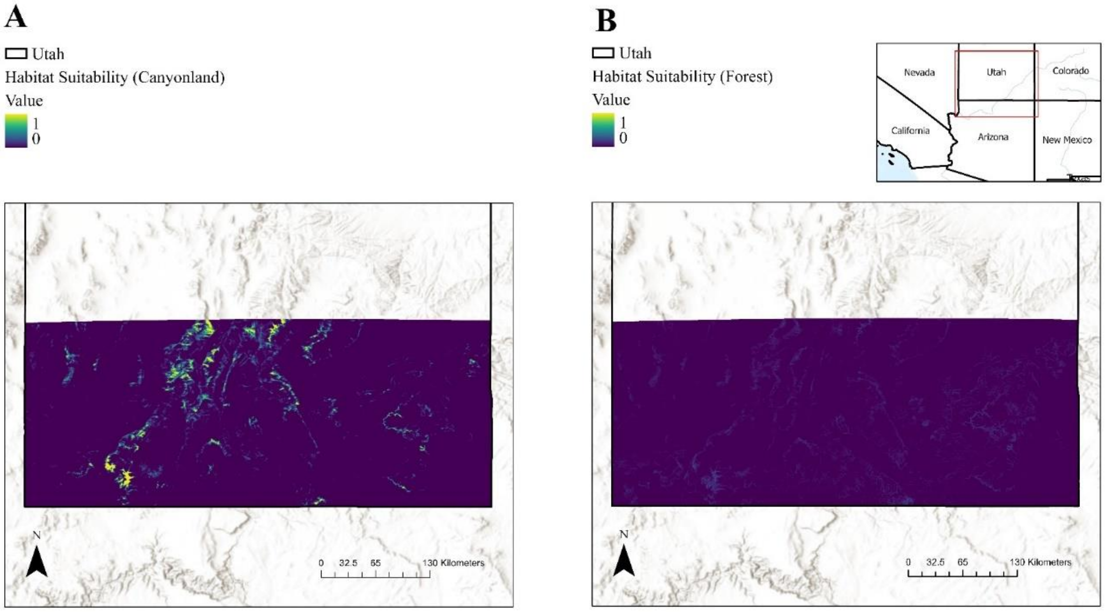

Figure 5. The habitat suitability maps produced by applying the rocky canyonland model (A), and applying the forest model (B), both developed using nest/roost data. Values closer to one indicate more highly suitable nesting/roosting habitat, while values closer to zero indicate less suitable nesting/roosting habitat.

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 (Figure 5B). The forest model showed a fairly high AUC (0.848), suggesting a discrepancy between apparent model accuracy and the actual habitat suitability, which is a known bias of AUC (Smith 2013).

DISCUSSION

Non-stationarity can bias inferences made from spatial models and make it difficult to implement management actions effectively (Peterson et al. 2007, Cushman et al. 2011, Shirk et al. 2014, 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 the spatially varying limiting factors that influence the species within its different habitats (e.g., Cushman et al. 2011, Short Bull et al. 2011; Shirk et al. 2014, 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 as it is the first study to explicitly model the multi-scale habitat suitability of MSO in rocky canyonlands. My results suggest that there is non-stationarity in the factors that drive habitat use of MSO in forests in Arizona and New Mexico (Wan et al. 2017) versus rocky canyonland habitats in southern Utah.

Mexican spotted owls live in a gradient from rocky canyonlands to various forest habitats such as wet mixed-conifer and dry pine-oak forests across the subspecies’ range (USFWS, 2012, Ganey et al. 2011). However, in southern Utah, they are only found in rocky canyonlands, despite the presence of forests. For MSOs living in rocky canyonlands, my model identified slope, cumulative degree days, insolation, and monsoon precipitation as the most important covariates related to habitat suitability. In the forest habitat, percent canopy cover, percent mixed-conifer, and slope were identified as the most important covariates respectively (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, Timm et al. 2016, Wan et al. 2017). This might 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. In rocky canyonlands, large steep vertical cliffs provide an abundance of caves and ledges for both nest 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. Insolation plays an important role in determining their habitat, particularly in arid rocky canyonland habitats. In treeless habitats in Utah, steep and complex cliffs apparently substitute for forest structure (Willey and Zambon 2014).

No composition or forest-related covariate turned out to be significant for MSOs in rocky canyonlands, whereas proportions of canopy cover and mixed-conifer were significant predictors in forested habitats. 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 two other 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 geo-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. 2022). 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 suggests that environments can be suboptimally cool and suboptimally rainy, even in rocky canyonlands. Rocky canyonlands, especially the south-facing slopes of them, can become hot and inhospitable for MSOs, but they offer ledges, crevices, and caves that provide contrasting temperatures. MSOs can use these microhabitats as refuges against the warming climate. 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. 2022). 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. 2022). In dry rocky canyonlands, high temperatures, exacerbated by a warming climate, might lead to challenges for MSO, or their prey’s water sources (Willey 2013, Ganey et al. 2020). Although currently, little evidence suggests that climate change is causing reductions in MSO population size (USFWS 2012) with increasing temperature, cumulative degree days and monsoons 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 variable 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 the 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 cold be important still for rocky canyonlands, however the high variable importance of topographic covariates is still apparent, suggesting that topographical covariates are highly important for habitat use in rocky canyonlands (USFWS 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).

Although habitat use is an inherently multi-scale 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 my study allowed me to compare the optimal scales for each covariate between my 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 it was more important at slightly finer spatial scales (500 m) in the forest model. In comparison, a previous study in forest habitat also found that slope had the greatest contribution to habitat use at fine (400 m) spatial scales (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 (200 m) spatial scale. While I 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 limited and intermittent along canyon bottoms than in forests, likely requiring MSO to consider canopy cover across broader areas, if they consider it at all, where instead it is likely that cliffs provide overhead cover for MSO. Finally, the 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).

My rocky canyonland model, although built with a low number of presence points (*n* = 61), performed well and outperformed the forest model. The forest model performed poorly as suggested by low TSS and Continuous Boyce Index, 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 that assess if models are good at predicting presences and absences, it evaluates the model ability to forecast multiple levels of suitability (Hirzel et al. 2006). My results also suggest that AUC can be a biased performance metric because the forest model shows a high AUC value. This was probably due to AUC being threshold-independent, which can lead to discrepancies between apparent model accuracy and the actual suitability (Smith 2013). TSS is threshold-dependent and showed poor prediction of forest model, meaning that the forest model failed to discern non-habitat from habitat and identified almost no suitable habitat. My Continuous Boyce index results also showed that the rocky canyonland model's output had a higher positive correlation with the true probability of presences and performed better.

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). My 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. (2017) 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 my results serve as a cautionary tale for researchers considering using habitat suitability models across areas with diverse environmental conditions.

In line with my expectation, high levels of non-stationarity were observed both in environmental covariates and scales concerning MSO habitat selection between the two regions. Such non-stationarity offers insight into model transferability. High levels of non-stationarity are not uncommon for other species in other systems (e.g., Short Bull et al. 2011, Cushman et al. 2011, Vergara et al. 2016, 2017, Atzeni et al. 2020, Kaszta et al. 2021). For example, Short Bull et al. (2021) with 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. 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 selects habitat differently from those in New Mexico despite both dwelling in forests (Wan et al. 2017). I 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 my southern Utah study area is quite different from the conditions in Grand Canyon, but both areas are typically classified as rocky canyonland habitat for the MSO. Therefore, I speculate that my model will not perform well for predicting MSO habitat in the Grand Canyon, and I call for future research to confirm my speculation.

CONCLUSIONS

My study is particularly important for the conservation of MSO that inhabit rocky canyonlands, a unique habitat that contrasts with more explored forests (Willey and van Riper III 2007, USFWS 2012). My study demonstrates that using a forest model to infer MSO habitat use in rocky canyonland is inappropriate. Given that most MSO studies are conducted in forest habitat with only a handful conducted in rocky canyonland, we call for more MSO research efforts in the rocky canyonland. Furthermore, my model provides spatially-explicit information for managers to make informed decisions, such as to prioritize areas for monitoring and management. My study of the MSO in two different habitat types highlights the potential problems that can arise from neglecting non-stationarity. Understanding local habitat peculiarities and limiting factors is crucial for accurately predicting region-specific habitat models. My 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. 2017). 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, 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. 2017, Yates 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, I recommend habitat models be made with local data to achieve the most reliable information for conservation and management.

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APPENDIX

Appendix. Environmental covariates included in the study for Mexican spotted owl nesting and roosting habitat suitability modeling, with the class of each covariate and the source of data.

Number	Covariate	Description	Class	Source
1	Cumulative Degree-Days*	Cumulative temperature (Celsius)	Climatic	NPN
2	Monsoon Season Precipitation	Average precipitation from June to September (mm)	Climatic	PRISM
3	Edge Density	Ratio of sum of edge lengths to minimum total length of edge of a constant reference area	Composition	LANDFIRE
4	Proximity	Spatial context of a habitat	Composition	LANDFIRE

Number	Covariate	Description	Class	Source
		patch in relation to its neighbors		
5	Canopy	Percent canopy cover	Composition	LANDFIRE
6	Mixed Ponderosa Pine	Proportion of mixed ponderosa pines	Composition	LANDFIRE
7	Slope Position Index	Steepness at each cell of a raster surface	Topographic	LANDFIRE
8	Insolation	Amount of solar radiation reaching a given area (Wh/m^2)	Topographic	LANDFIRE
9	Roughness	Degree of irregularity of the surface	Topographic	LANDFIRE
10	Slope	Slope (degrees)	Topographic	LANDFIRE
11	TPI (Topographic	A measure of the relative	Topographic	LANDFIRE

Number	Covariate	Description	Class	Source
	position index)	elevation of a point on a topographic surface compared to its surrounding area.		
12	TRI (Topographic roughness index)	A measure of the complexity of a topographic surface, such as a landscape	Topographic	LANDFIRE
13	Curvature	A measurement for understanding to what extent the landscape is curved	Topographic	LANDFIRE

*We divided values of the accumulated degree days by 1.8 to convert it from fahrenheit to celsius.