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Accounting for geographic variation in species-habitat associations during habitat suitability modeling

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Abstract

Range-wide species conservation efforts are facilitated by spatially explicit estimates of habitat suitability. However, species-environment relationships often vary geographically and models assuming geographically constant relationships may result in misleading inferences. We present the first range-wide habitat suitability model (HSM) for the federally threatened eastern indigo snake (*Drymarchon couperi*) as a case study illustrating an approach to account for known latitudinal variation in habitat associations. Specifically, we modeled habitat suitability using interactive relationships between minimum winter temperature and several a priori environmental covariates and compared our results to those from models assuming geographically constant relationships. We found that multi-scale models including interactive effects with winter temperature outperformed single-scale models and models not including interactive effects with winter temperature. Our top-ranked model had suitable range-wide predictive performance and identified numerous large (i.e., ≥1000 ha) potential habitat patches throughout the indigo snake range. Predictive performance was greatest in southern Georgia and northern Florida likely reflecting more restrictive indigo snake habitat associations in these regions. This study illustrates how modeling interactive effects between temperature and environmental covariates can improve the performance of HSMs across geographically varying environmental gradients.

KEYWORDS
conservation, *Drymarchon couperi*, eastern indigo snake, species distribution model

INTRODUCTION

The importance of landscape-scale conservation to maintain population viability and connectivity has been increasingly recognized (Hoctor et al., 2000; Watson et al., 2014), particularly as anthropogenic landscape changes continue to degrade and fragment suitable habitat (Vitousek et al., 1997). Broad-scale conservation efforts are increasingly reliant on spatially explicit estimates of species occurrence, habitat suitability,

connectivity, and population viability to inform on-the-ground management actions (Cabeza & Moilanen, 2001; Chetkiewicz & Boyce, 2009; Grant & Bradbury, 2019). However, many imperiled species have cryptic behaviors, low densities, or small population sizes making it difficult to collect ecological data necessary for developing and implementing conservation strategies (Maxwell & Jennings, 2005). Opportunistic observations can provide critical information for such species, but careful consideration must be given to various biases or spatial

deficiencies in these data (Bradter et al., 2018; Kramer-Schadt et al., 2013).

Habitat suitability models (HSMs) are regularly used to guide species conservation efforts by providing spatially explicit estimates of habitat suitability (Franklin, 2010; Guisan & Thuiller, 2005). Predicted suitability surfaces from HSMs may be used to quantify the amount of habitat already protected and prioritize land conservation strategies (Crawford et al., 2020; Fajardo et al., 2014; Rodriguez et al., 2007), identify potential mortality hotspots (Zeller, Wattles, et al., 2018), and prioritize future reintroduction efforts (Schadt et al., 2002). As HSMs can be developed using only species occurrence data (e.g., presence-only models) (Elith & Leathwick, 2009; Franklin, 2010), they are regularly used for broad-scale conservation applications. However, several challenges often accompany the use of HSMs, most notably the potential for spatial biases in opportunistically collected occurrence data (Kramer-Schadt et al., 2013; Phillips et al., 2009). For example, opportunistic observations may be more prevalent along roads or near access points (Reddy & Davalos, 2003). Several approaches exist for minimizing the inferential consequences of such sampling biases by reducing the density of presence locations (Kramer-Schadt et al., 2013; Veloz, 2009) or altering the distribution of background or available locations based on realized or inferred distributions of sampling effort to approximate sampling biases (Merow et al., 2013; Phillips et al., 2009; Vollering et al., 2019).

Another challenge in the development of broad-scale HSMs is the presence of geographic variation in species-environment relationships due to regional differences in climate, topography, or vegetation communities (Shirk et al., 2014; Doherty et al., 2016; Wan et al., 2017). Such differences represent an extension of the broader issue of transferability in HSMs, which is a widely recognized problem when predicting to novel spatiotemporal conditions (Guisan & Thuiller, 2005; Yates et al., 2018). Assuming stationarity in species-environment relationships, particularly over regional or continental extents, may result in misleading inferences and reduced model performance (Murphy & Lovett-Doust, 2007). Addressing non-stationarity in species-environment relationships can involve estimating separate HSMs for different eco-regions, study areas, or management units (Crawford et al., 2020; Murphy & Lovett-Doust, 2007) or incorporating interactive effects between environmental covariates and discrete regions (Zanini et al., 2009). However, these approaches either require merging spatial predictions from multiple models or may substantially increase model complexity. If species-environment relationships vary consistently across an environmental gradient ordered along a single geographic axis (e.g., latitude), then such variation may be accounted for using interactive effects between environmental covariates and the geographic axis (Becker et al., 2019). Yet, including spatially varying interactive effects in HSMs may increase the risk of model over-fitting and result in poor predictive performance if results are extrapolated to novel spatiotemporal conditions (Merow et al., 2014; Yates et al., 2018). To date, relatively little attention has been paid to directly modeling geographic variation in species-habitat relationships (Becker et al., 2019; Merow et al., 2014).

In this study, we developed the first range-wide HSM for the U.S. federally threatened eastern indigo snakes (*Drymarchon couperi*; hereafter referred to as DRCO) as a case study of modeling habitat suitability for an imperiled species with limited data availability and known latitudinal variation in habitat associations. DRCO are large (>2.4 m) colubrid snakes native to the southeastern U.S. (Enge et al., 2013; Stevenson et al., 2009) that exhibit marked latitudinal variation in spatial and habitat ecology across their range. During winters in the northern portion of their range (i.e., southern Georgia and northern Florida), DRCO are restricted to patches of xeric soils (i.e., sandhills) containing gopher tortoises (*Gopherus polyphemus*), whose burrows are used as refugia (Bauder et al., 2017; Hyslop et al., 2009; Stevenson et al., 2003). During the summer, DRCO in this region use a diversity of upland and wetland habitats; therefore, they may migrate 5–7 km from overwintering sites (Hyslop et al., 2014). In contrast, DRCO become less dependent on *G. polyphemus* burrows with increasing winter temperatures; therefore, within peninsular Florida region, DRCO may occupy habitats devoid of *G. polyphemus* (Bauder et al., 2016a; USFWS, 2019). Within peninsular Florida, DRCO use a greater diversity of habitats throughout the year and may occur in varying degrees of urban and agricultural development (Bauder et al., 2018; USFWS, 2019).

Therefore, we tested whether modeling environmental covariates interactively with winter temperature would improve the performance of a range-wide HSM for DRCO. Previous research has also shown that DRCO show scale-specific responses to habitat features (Bauder et al., 2018, 2020). Hence, we predicted that multi-scale models with latitudinally varying environmental relationships would outperform single-scale models and models with constant environmental relationships.

METHODS

Study area

We defined the extent of our modeling area to approximate the contemporary distribution of DRCO (Figure 1;

Enge et al., 2013). Additional details are provided in Appendix S1. Natural vegetation communities occupied by DRCO within this area included xeric sandhill and scrub, mesic pine flatwoods, hardwood hammocks, coastal hammocks and dunes, and forested and non-forested wetlands. Anthropogenically altered communities were widespread and included urban and rural developments, agriculture, improved pasture, citrus, and commercial forest stands. Vegetation communities predominately restricted to southern Florida included mangrove swamps, Everglades marshes and stormwater control wetlands, and sugar cane.

Data selection

We compiled observations of DRCO from multiple sources, including previous studies (Enge et al., 2013; Moulis, 1976), museum records, research and monitoring projects, environmental impact assessments, and state and federal agency databases (Appendix S1, Table S1). We examined each observation to determine its veracity, retaining only those that were verified (i.e., with a photo or video at the time of submission) or reported from

reliable sources during 2000–2020 ($n = 3334$). Furthermore, we randomly subsampled observations to maintain a minimum inter-observation distance of 500 m (approximate radius of a DRCO home range in peninsular Florida; Bauder et al., 2018) to reduce the effects of spatial clustering and autocorrelation among observations (Kramer-Schadt et al., 2013; Veloz, 2009). This resulted in a total of 1215 DRCO observations for developing our HSM (Figure 1).

Environmental data

We considered several environmental covariates that we hypothesized a priori would influence DRCO habitat suitability based on previous research (Table 1). Additional details are provided in Appendix S1. Covariates included land cover classes (undeveloped upland, wetland, urban, and agriculture), soil drainage, topographic position index (TPI; a measure of topographic complexity), canopy and vegetation cover (enhanced vegetation index [EVI]), and fire frequency. As DRCO are positively associated with habitat heterogeneity and edge
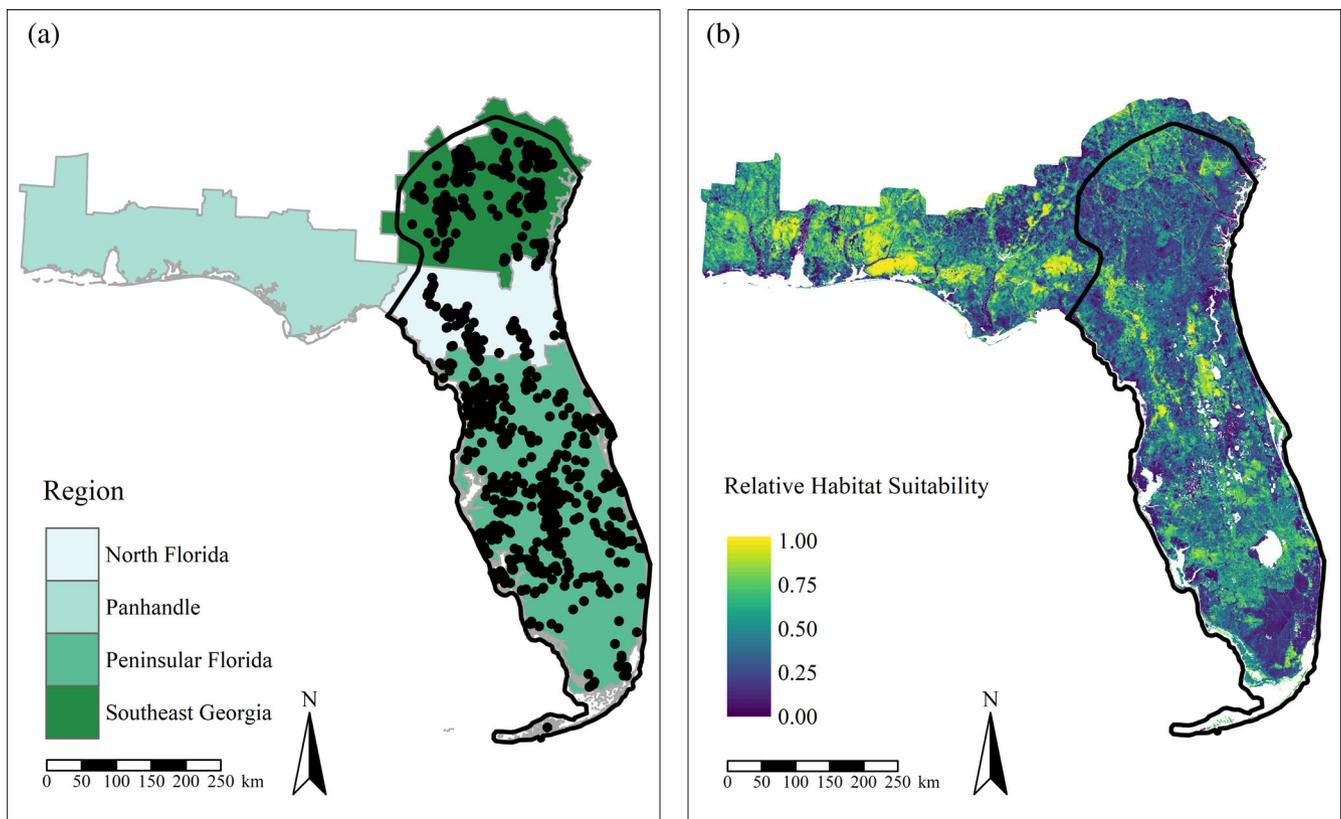
FIGURE 1 Map of habitat modeling study area (a, black outline) based on the contemporary distribution of the eastern indigo snake (*Drymarchon couperi*) and predicted relative habitat suitability (b). Black points represent presence locations from 2000–2020 used to develop the habitat suitability model. We also present the four eastern indigo snake management regions defined by the U.S. Fish and Wildlife Service in the Species Status Assessment (USFWS, 2019)

TABLE 1 Environmental covariates and a priori hypothesized relationships considered for an eastern indigo snake (*Drymarchon couperi*) range-wide habitat suitability model

Covariate	Description	Hypothesized relationship	References
Undeveloped upland	Undeveloped non-wetland land covers (e.g., scrub, sandhill, upland and coastal hammocks, flatwoods, prairie, shrub, commercial forest, unimproved pasture/woodland, rural)	Positive	Bauder et al. (2018), Enge et al. (2013), Hyslop et al. (2014)
Undeveloped upland edge	Undeveloped upland edge pixels	Positive	Bauder et al. (2018, 2020)
Wetland*	Forest and non-forested fresh and saltwater wetlands, canals, and ditches	Positive at intermediate levels (Q), weakest at warmer winter temperatures	Hyslop et al. (2014), USFWS (2019)
Wetland edge	Wetland edge pixels	Positive	Bauder et al. (2018, 2020)
Urban	High, medium, and low density urban, roads, barren, extractive	Negative, weakest at warmer winter temperatures	Bauder et al. (2018) Breininger et al. (2004, 2012)
Agriculture	Citrus, sugarcane, improved pasture, and other commercial agriculture	Negative, weakest at warmer winter temperatures	Bauder et al. (2018)
EVI	Enhanced vegetation index (June–August)	Positive	DRCO are positively associated with vegetated habitats
SD EVI	Standard deviation of EVI	Positive	Bauder et al. (2018, 2020)
Canopy cover*	Percent canopy cover (CC)	Negative and positive at cooler and warmer winter temperatures, respectively. Strongest positive effect at intermediate levels (Q).	Hyslop et al. (2009, 2014)
SD CC	Standard deviation of CC	Positive	DRCO are positively associated with habitat heterogeneity
Deciduous index	Difference between May–July and December–February EVI divided by the maximum EVI (1999–2016, Crawford et al., 2020)	Positive at intermediate levels (Q)	Hyslop et al. (2009, 2014)
Fire frequency*	Proportion of years an area burned during 2001–2016 (MODIS) and the presence of a burn during 2006–2016 (LANDFIRE, Crawford et al., 2020)	Positive, strongest at cooler winter temperatures	Hyslop et al. (2009, 2014)
Soil drainage*	Soil drainage class (well-, moderately-, or poorly drained, Crawford et al., 2020)	Positive, strongest at cooler winter temperatures	Bauder et al. (2017), Hyslop et al. (2009, 2014)
TPI*	Topographic position index using 500 m moving window (Crawford et al., 2020)	Positive at intermediate levels, strongest at cooler winter temperatures	DRCO are strongly associated with upland habitats
SD TPI	Standard deviation of TPI	Positive	DRCO are positively associated with habitat heterogeneity

Notes: Interactive terms between winter temperature and each covariate were considered and interactive effects with undeveloped upland were considered for covariates marked with an asterisk. All covariates were modeled using linear relationships except for those modeled as quadratic effects (Q).

(Bauder et al., 2018, 2020), we also considered upland and wetland edges and the standard deviations of TPI, canopy cover, and EVI within moving windows as measures of habitat heterogeneity. Finally, we used mean minimum winter (December 1–February 27) temperature during 1981–2010 from the Climate

Engine (2019) to model latitudinal variation in DRCO habitat associations. All rasters were resampled to 30-m pixels for analyses. We hypothesized that associations with structurally open upland habitats with well-drained soils and frequent fires would be strongest at cooler temperatures, where DRCO are more closely associated with *G. polyphemus* (Bauder et al., 2017; Hyslop et al., 2009, 2014). We also hypothesized that negative associations with urban, agriculture, and wetland would be weakest at warmer temperatures where DRCO are known to use a greater diversity of habitats (Bauder et al., 2018; USFWS, 2019).

Selecting background points

Sampling biases in species observations can result in misleading inferences from HSMs, yet selecting background points to reflect those sampling biases can improve model performance (Vollering et al., 2019). As DRCO are frequently detected along roads or observed as road kill, we used the 2016 TIGER roads layer (U.S. Census Bureau, 2016) to measure the distances from each subsampled DRCO observation to the nearest road (excluding interstates). The proportion of DRCO observations in 0 m and 1–30 m distance bins were higher than those of random background points (0.29 vs. 0.07 and 0.15 vs. 0.10 respectively). Therefore, we selected 500,000 background points (497,649 after excluding points with missing values from one or more covariate raster layers) from across our study area while ensuring equal proportions of DRCO observations and background points in the 0 m and 1–30 m distance bins.

Selecting the characteristic scale

We used a pseudo-optimization approach (McGarigal et al., 2016) to identify the spatial scale with the greatest empirical support (i.e., the characteristic scale; Holland et al., 2004) for each environmental covariate. We considered scales of 250, 500, 1000, 2500, and 5000 m (i.e., radii of circular uniform kernels) to capture the movement potential and home range sizes of DRCO across their range (Bauder et al., 2020; Hyslop et al., 2014). Bauder et al. (2020) reported that circular buffers of 242, 667, and 1610 m radii approximated the 2.5th, 50th, and 97.5th quantiles of DRCO home range sizes in peninsular Florida with smaller home range sizes in more urban landscapes. Hyslop et al. (2014) found that DRCO in southern Georgia would move 5000–7500 m from overwintering sandhills to summer habitats. We also measured each covariate directly from the 30 m covariate rasters. We compared covariates across scales by fitting generalized linear models (GLMs) with binomial error distributions containing each covariate at a single scale. We selected the scale with the lowest AIC as the characteristic scale and identified characteristic scales for models with and without an interactive effect between the covariate and winter temperature. Then, we tested for collinearity between all covariates at their characteristic scales. We excluded the upland edge because of its relatively high collinearity with the upland ($r = 0.71$). Collinearity was low to moderate for all other covariates at their characteristic scales ($|r| \leq 0.68$).

Model fitting

We fit our models using binomial GLM in R (R Core Team, 2019) and weighted our background points so that their summed weights equaled to the summed weights of the presence points (Barbet-Massin et al., 2012). We emphasize that the models' predicted values should not be interpreted as probabilities but as indices of relative habitat suitability. We used a modified backward covariate selection approach to build each model. First, we iteratively dropped higher-order (i.e., interactive or quadratic) terms until no improvement in AIC occurred. We then iteratively dropped main-effects terms that were not present in a retained higher-order term. If a main-effects term was dropped, we iteratively dropped higher-order terms before proceeding to drop additional main-effects terms to retain higher-order terms whose corresponding main-effects were also retained. We ceased dropping terms when no improvement in model AIC occurred.

We fit single-scale models, where each covariate was measured at the same spatial scale, and pseudo-optimized multi-scale models including each covariate at its characteristic scale. We fit each model twice, including or excluding interactive effects of temperature, for a total of 14 models. Given the large home-range sizes of DRCO and their high movement potential, we used the 250-m scale as the smallest scale in our multi-scale models. This effectively treats the home range, rather than points within the home range, as the sampling unit meaning that per-pixel suitability values should be interpreted as the suitability of a home range centered on that pixel. Moreover, DRCO in peninsular Florida showed very low inter-sexual home range overlap (Bauder et al., 2016b), although winter spatial overlap can be high for DRCO in southern Georgia while individuals use xeric sandhills for overwintering (Hyslop et al., 2014). Therefore, we consider our HSMs analogous to first-order habitat selection (Johnson, 1980) describing relative habitat suitability for

at least one DRCO rather than a second- or third-order resource selection function (RSF) describing the relative intensity of home ranges or individual animal locations (Fieberg et al., 2021).

Model validation

We used four cross-validation approaches to evaluate model predictive performance. The first was a random 5-fold cross-validation. As this approach may overestimate predictive performance (Radosavljevic & Anderson, 2014; Roberts et al., 2017), we also conducted two spatially blocked cross-validations. First, we divided our modeling area into five east–west bins to include the majority of the north–south environmental gradient within each bin (Roberts et al., 2017). Second, we divided our modeling area into five north–south bins using 5.0, 7.5, 10.0, and 12.5°C as bin boundaries, which also allowed us to evaluate the extrapolation capability of a model. We evaluated model discriminatory ability using the area-under-the-curve (AUC) of the receiver operating characteristic (ROC) (Fielding & Bell, 1997), despite its limited utility for presence-only models (Hirzel et al., 2006), for comparison with other species distribution models using this metric. We evaluated model calibration with the Continuous

Boyce Index (CBI; Boyce et al., 2002, Hirzel et al., 2006), which quantifies the monotonicity between the ratio of predicted to expected points (P:E) and the midpoints of multiple overlapping suitability bins. Values of the CBI closer to one represent increasingly well-calibrated models, although non-linear relationships indicate reduced resolution (i.e., information content) (Hirzel et al., 2006). We used 10,000 random background points selected uniformly across our study area to calculate CBI and create CBI plots (i.e., plots of P:E against habitat suitability) with the default arguments in the *ecospat.boyce* function from the ECOSPAT package (Broennimann et al., 2021). Finally, we conducted a 3-fold cross-validation across the USFWS (U.S. Fish and Wildlife Service) regions to further compare spatial variation in model performance. We used two regions for model training and calculated AUC and CBI for the third region.

Habitat suitability mapping

We predicted relative habitat suitability across the DRCO historical distribution (Figure 1). We first bounded all covariate values outside our modeling area by the minimum or maximum values present in the model-fitting dataset (contemporary range) to reduce any effects of extrapolation to the historic portion of the indigo snake

TABLE 2 Rankings and predictive performances of eastern indigo snake (*Drymarchon couperi*) range-wide habitat suitability models

| Scale | Temperature interaction | AIC | D^2 | Area under the curve | | | Continuous Boyce index | | | No. temperature interactions |
				R	EW bins	NS bins	R	EW bins	NS bins	
Multi-scale	Yes	1329.2	0.23	0.803	0.787	0.756	1.000	1.000	0.998	4
Multi-scale	No	1342.5	0.21	0.794	0.775	0.769	0.999	0.998	0.990	NA
1000 m	Yes	1351.9	0.21	0.792	0.770	0.691	1.000	0.998	0.953	6
500 m	Yes	1356.7	0.21	0.790	0.774	0.689	0.999	0.999	0.986	8
250 m	Yes	1359.2	0.21	0.793	0.778	0.728	1.000	0.998	0.975	8
2500 m	Yes	1378.2	0.19	0.782	0.755	0.645	0.993	0.991	0.891	7
1000 m	No	1386.9	0.18	0.779	0.760	0.738	0.994	0.997	0.975	NA
5000 m	Yes	1390.2	0.19	0.775	0.745	0.627	0.989	0.997	0.857	7
250 m	No	1393.6	0.19	0.780	0.766	0.758	1.000	1.000	0.990	NA
500 m	No	1394.0	0.18	0.776	0.759	0.747	1.000	0.999	0.990	NA
2500 m	No	1414.8	0.16	0.769	0.749	0.712	0.981	0.985	0.979	NA
5000 m	No	1430.5	0.15	0.757	0.720	0.673	0.991	0.987	0.981	NA
Base	Yes	1441.5	0.18	0.769	0.754	0.693	0.999	0.999	0.998	5
Base	No	1481.2	0.15	0.750	0.733	0.717	0.999	1.000	0.997	NA

Notes: The scales in this table represent the scale at which all covariates in the model were measured except the multi-scale models in which scale was pseudo-optimized for each covariate. Temperature interaction refers to whether or not an interactive effect of temperature was allowed with each covariate. D^2 is proportion of deviance explained. Models were cross-validated using either random 5-fold cross-validation (R) or 5-fold cross-validation with geographic bins. North–south (NS) bins reflected a north–south temperature gradient and East–west (EW) bins reflected an east–west gradient with each bin spanning approximately the entire latitudinal extent of the indigo snake distribution.
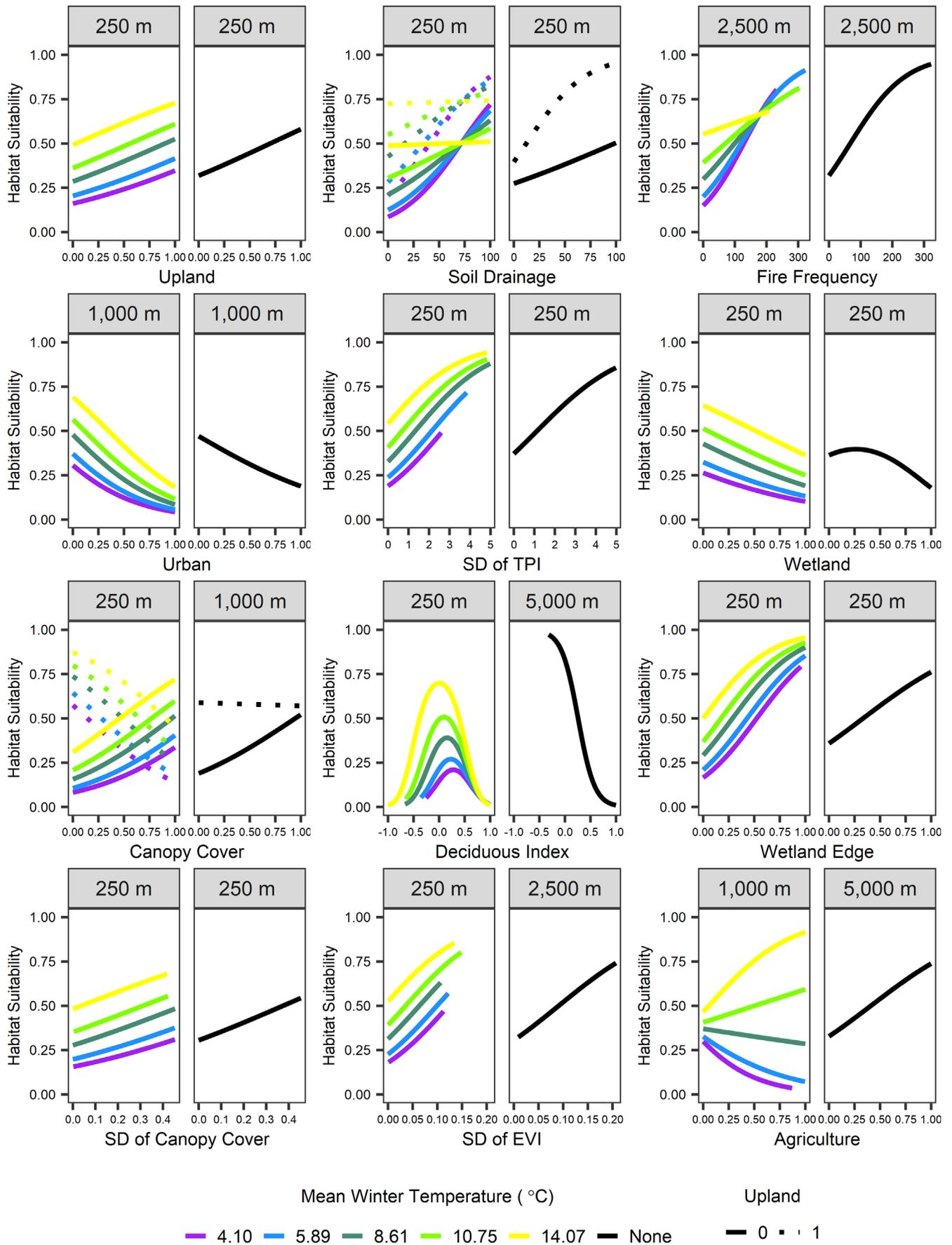
FIGURE 2 Legend on next page.

TABLE 3 Regional predictive performance of eastern indigo snake (*Drymarchon couperi*) habitat suitability models through regional cross-validation

	Multi-scale with temperature interactions		Multi-scale with no temperature interactions	
	AUC	CBI	AUC	CBI
USFWS region				
Georgia	0.828	0.995	0.783	0.990
North Florida	0.812	0.964	0.820	0.836
Peninsular Florida	0.755	0.862	0.692	0.820
Temperature bin				
2.86–5.0°C	0.830	0.998	0.777	0.987
5.0–7.5°C	0.794	0.972	0.791	0.888
7.5–10.0°C	0.784	0.971	0.813	0.987
10.0–12.5°C	0.740	0.991	0.765	0.995
12.5–17.7°C	0.779	0.939	0.784	0.903
East–west bin				
1	0.814	0.991	0.806	0.968
2	0.856	0.986	0.825	0.988
3	0.813	0.994	0.797	0.982
4	0.729	0.995	0.742	0.993
5	0.755	0.988	0.730	0.836

Notes: Results are presented from the two pseudo-optimized multi-scale models with and without interactive effects of temperature. All statistics were calculated using the specified region as testing data and data from all other regions as training data. USFWS Regions are as defined in the Species Status Assessment (USFWS, 2019) and east–west bin numbers go from east to west.

Abbreviations: AUC, area under the curve; CBI, continuous Boyce Index.

range. We also created a categorical habitat suitability map representing unsuitable, low, medium, and high suitability to provide an alternative representation of habitat suitability in the presence of non-linear CBI plots as described above in Model validation. We use the word "unsuitable" in a relative sense and do not mean to imply that DRCO are absent in areas denoted as unsuitable. We defined the threshold between unsuitable and low to include 95% of our DRCO observations (i.e., 95% sensitivity). The threshold between low and medium was the suitability value at which the predicted:observed ratio in the CBI plot was one (Hirzel et al., 2006). The threshold between medium and high approximated an inflection

point within the CBI plot (Hirzel et al., 2006). We determined these thresholds using our three cross-validation approaches and selected the median value across approaches as the final threshold value. We delineated all contiguous patches that were low, medium, or high, medium or high, or only high suitability that were ≥ 250, 1000, or 5000 ha to account for varying estimates of the minimum area needed for viable DRCO populations (1000 ha, Moler, 1992; >8000 ha, Bauder, 2019). To account for potential barrier effects of roads (Bauder et al., 2018; Breininger et al., 2004, 2012), we split patches that were bisected by interstates. Finally, we calculated the total patch area across size and suitability classes for each USFWS region and the proportion of habitat patch area for each size that overlapped conservation land using the U.S. Geological Survey Protected Areas Database (U.S. Geological Survey, 2020).

RESULTS

To build our HSM, we used 438, 99, and 678 DRCO observations from southeast Georgia, north Florida, and peninsular Florida, respectively. The characteristic scale of 11 of our 14 covariates was 250 m when an interactive effect of temperature was included (Appendix S1, Table S2). Three covariates (agriculture, fire frequency, and urban) had characteristic scales ≥1000 m. Seven of these 14 covariates had characteristic scales ≥1000 m when excluding the interactive effect of temperature.

The multi-scale model with pseudo-optimized scales and interactive effects of temperature was the top-ranked model followed by the multi-scale model without temperature effects (Table 2). Single-scale models including temperature interactions always outperformed their corresponding models without temperature interactions (Table 2). Suitability was positively associated with upland, SD of TPI, wetland edge, and SD of EVI. It was negatively associated with urban and wetland regardless of the temperature (Figure 2). The interactive effect with temperature was retained in the multi-scale model for four covariates (soil drainage, fire frequency, deciduous index, and agriculture; Appendix S1, Table S3). Five to eight temperature interactive effects were retained in the single-scale models (Table 2). The association between soil drainage and fire frequency was strongly positive at cooler winter temperatures and virtually absent in southern Florida. In contrast, agriculture had a strong positive effect in southern Florida.

FIGURE 2 Predicted relationships between eastern indigo snake (*Drymarchon couperi*) relative habitat suitability and landscape covariates at their characteristic scales with and without an interactive effect of temperature. Predictions were made using the final multi-scale pseudo-optimized model holding all other covariates constant at their mean values. Temperature values represent the midpoint temperatures within the five temperature bins used in the cross-validation analysis
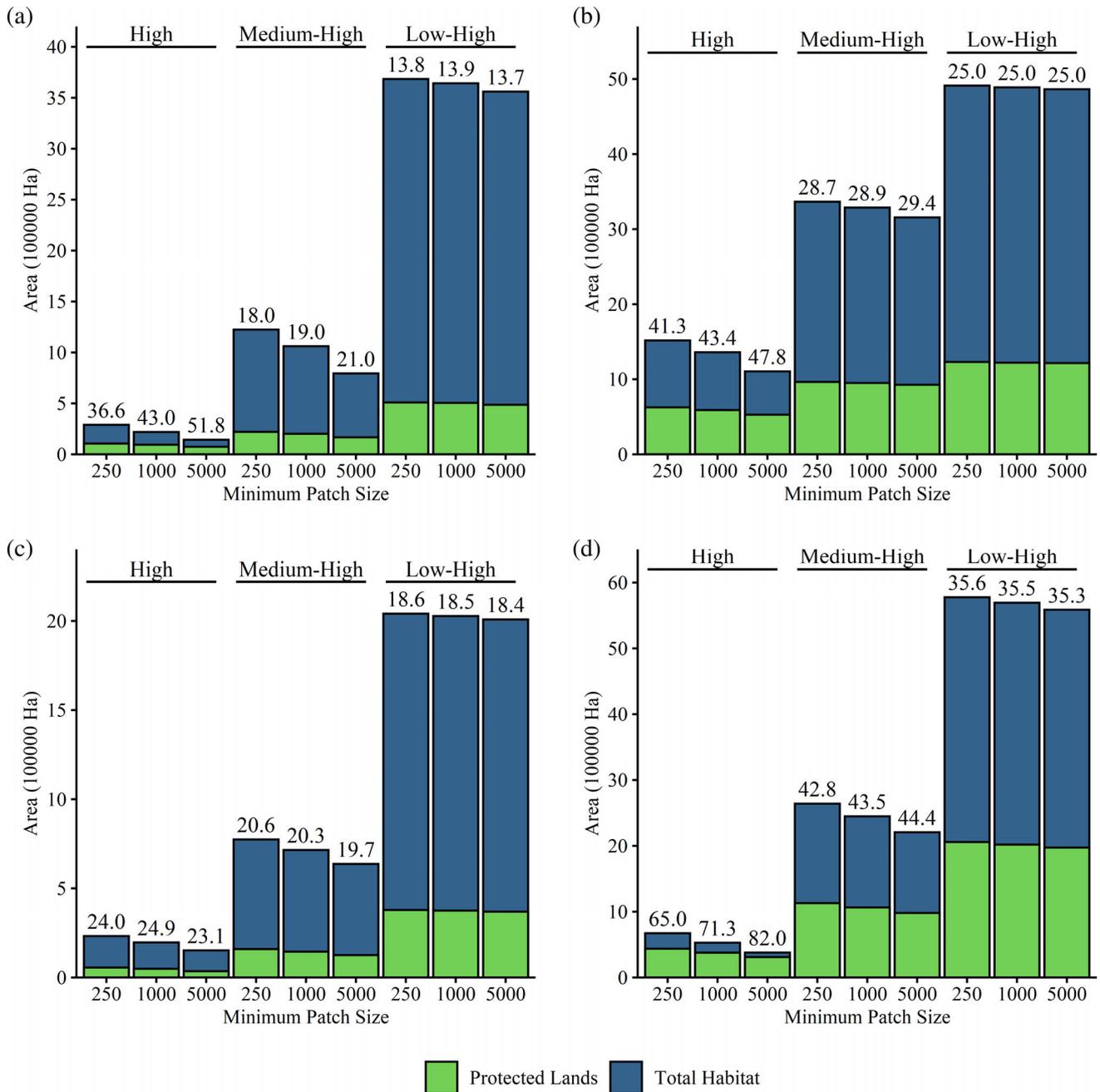
FIGURE 3 The amount and percent (shown above bars) of potentially suitable eastern indigo snake (*Drymarchon couperi*) habitat patches protected in the four U.S. Fish and Wildlife Service Conservation Regions (a: Georgia, b: Panhandle, c: north Florida, d: peninsular Florida; USFWS, 2019). Habitat patches were defined using three minimum patch size thresholds (250, 1000, and 5000 ha) and three minimum suitability thresholds (low, medium, and high suitability)

Moreover, the quadratic effect of the deciduous index was also strongest in that region (Figure 2). Habitat suitability in areas with large amounts of upland land cover was highest when canopy cover was low, whereas suitability was highest when canopy cover was high in areas with no upland land cover (Figure 2).

The multi-scale model generally had the highest predictive performance across cross-validation approaches (Table 2). Predictive performance was highest using random 5-fold cross-validation and lowest when cross-validating by north–south bins (Table 3). Model predictions were generally the best in southern Georgia and poorest in southern peninsular Florida. Performance was as good or better using the pseudo-optimized model with temperature interactions compared to the pseudo-optimized model without temperature interactions (Table 3).

We used thresholds of 0.21, 0.47, and 0.71 to define our suitability categories (Appendix S1, Figure S1). Highly suitable habitats were mostly concentrated along riverine sand ridges in southern Georgia and central peninsular Florida, while suitability was lowest in large urbanized and wetland areas (e.g., Okefenokee Swamp, Everglades; Figure 1). The Florida Panhandle contained a much higher percentage of potentially suitable habitat than other regions (Appendix S1, Table S4). The percentage of protected potential habitat patches was relatively insensitive to patch size but decreased markedly as lower suitability classes were considered (Figure 3).

DISCUSSION

Our study showed that considering interactive relationships between a priori selected environmental covariates and temperature in a HSM can successfully capture geographic variation in species-habitat associations. Both multi- and single-scale HSMs allowing interactive effects of winter temperature with environmental covariates had greater empirical support and predictive performance than models without these interactive effects. While previous research across taxa has illustrated the superior predictive performance of multi-scale HSMs (Macdonald et al., 2019; Mateo-Sanchez et al., 2016; Wan et al., 2018), we found that even single-scale models with interactive temperature effects always outperformed their corresponding model without interactive temperature effects. This suggests that considering both multi-scale and geographical variation in species-habitat associations is important for improving the performance of HSMs. The strong performance of our multi-scale model with interactive temperature effects when cross-validating across north–south bins across the temperature gradient suggests that this model was not overfitted. Therefore, it was less susceptible to poor out-of-sample predictive performance. Furthermore, latitudinal variations in predicted covariate relationships were consistent with our a priori hypotheses. For example, covariates indicative of potential *G. polyphemus* habitat, specifically soil drainage and fire frequency, showed their strongest relationships at cooler temperatures, reflecting the dependence of DRCO on *G. polyphemus* burrows in these regions (Bauder et al., 2017; Hyslop et al., 2009, 2014; Stevenson et al., 2003). Additionally, DRCO were negatively associated with agriculture in southern Georgia and northern Florida but positively associated with agriculture in southern Florida, consistent with DRCO habitat use of canal banks, and abandoned citrus groves in this region (USFWS, 2019). We suggest that modeling geographic variation in species-habitat relationships using interactive effects with factors varying across a study gradient

(e.g., temperature) offers a useful approach for modeling habitat suitability across diverse environments within a single model.

Several covariates showed consistent relationships with suitability independent of temperature. In particular, upland and urban showed strong positive and negative effects, respectively, on DRCO habitat suitability. However, the consistently negative association with wetland independent of temperature was surprising given observations of DRCO use of wetlands (Hyslop et al., 2014). One possible explanation is that many of our Georgia observations came from winter DRCO monitoring projects when DRCO are most closely associated with xeric sandhills and relatively easy to detect (Bauder et al., 2017; Stevenson et al., 2003). As a result, our model may be biased towards winter DRCO habitats in southern Georgia and northern Florida in comparison to habitats in peninsular Florida. Sampling effort across sandhills in southern Georgia was highly variable, both temporally and spatially, during the years in which our data were collected, limiting our ability to account for spatial variation in sampling effort. Nevertheless, habitat suitability was positively associated with wetland edge, consistent with prior research indicating that DRCO may predominantly select mosaics of upland and wetland habitats (Bauder et al., 2018, 2020). Therefore, we encourage caution when inferring summer habitat suitability from our model in the northern part of the DRCO range as well as additional research to better understand the relative importance of wetland area versus configuration for DRCO. More broadly, the potential regional biases in sampling efforts illustrate the challenges of using opportunistic data when modeling species-habitat associations in the presence of spatial variation in sampling bias.

Model predictive performance varied geographically, being strongest in southern Georgia and weakest in central and southern peninsular Florida. We suggest that this pattern largely reflects latitudinal variation in DRCO habitat associations, specifically the more stringent habitat associations of DRCO in southern Georgia and northern Florida with regards to *G. polyphemus* burrows. The specific habitat requirements of *G. polyphemus* in these regions (i.e., well-drained soils, open canopy, sufficient ground cover forage) (Auffenberg & Franz, 1982; Mushinsky et al., 2006) likely increased model discriminatory ability with regards to suitable DRCO habitat. In contrast, DRCO in peninsular Florida, particularly the southern third, use a greater diversity of habitat types including unimproved cattle pasture, mangroves, canal banks, and urban edges (Bauder et al., 2018; USFWS, 2019). This trend towards increasing habitat generalization with decreasing winter temperature likely made it difficult for our model to discriminate between potentially suitable and unsuitable DRCO habitats. Similarly, Mateo-Sanchez et al. (2016) found that HSMs for

the brown bear (*Ursus arctos*) performed poorly during seasons when bears used a greater diversity of environmental conditions. While such plasticity in DRCO habitat requirements is likely an asset for their persistence within peninsular Florida, it also increases the challenges of modeling habitat suitability in this region, which may have important implications for regulatory and permitting efforts. Therefore, we encourage additional monitoring of DRCO in peninsular Florida, particularly in anthropogenically dominated landscapes, to better understand DRCO occurrence and habitat associations in this region.

We acknowledge additional limitations when drawing inferences from our results. First, our data were mainly opportunistic and may reflect biases associated with accessibility. Increasing the number of background points in close proximity to roads to match the frequency that indigo snakes were observed near roads likely mitigated this bias by capturing any differences among covariates that occurred near roads when compared to areas farther away from roads. Second, our data were relatively sparse within southern Florida compared to southern Georgia. Given our model's poorer predictive performance and greater DRCO habitat use-plasticity in this region, we encourage caution when applying our model to this region. Third, our HSM did not incorporate the effects of population isolation, recolonization, or localized extinction. These demographic processes may result in mismatches between a species' present occurrence and habitat conditions (Waldron et al., 2008; Welch et al., 2007). Finally, given the challenges of detecting DRCO, particularly in peninsular Florida (Bauder et al., 2017; Bauder & Barnhart, 2014), we recommend not using our HSM to infer the presence or absence of DRCO at any specific site but rather as a potential tool to prioritize sites for more intensive inventory and monitoring efforts.

Our results provide the first empirical range-wide HSM for DRCO, which can assist and guide future conservation efforts by prioritizing future land protection efforts, identifying potential linkages among existing protected lands, and helping identify sites for ongoing reintroduction efforts (USFWS, 2019). Our results and previous research emphasize the importance of large tracts of heterogeneous upland habitats for DRCO. While our results suggest that potentially suitable DRCO habitat is regionally widespread, we encourage further research in four specific topics. First, we encourage additional field-based surveys to verify the presence of DRCO within potentially suitable patches. Second, our results can be used to identify gaps in the existing network of conservation lands. Third, we recognize that our thresholds for defining suitability classes may not be ideal for all conservation applications and encourage managers to consider how different threshold values may affect their management objectives. In particular, the threshold between

unsuitable and low suitability may need to be lower in situations where a more liberal definition of potentially suitable habitat is warranted. Finally, we encourage additional efforts to empirically delineate and quantify potential DRCO population units using our estimates of habitat suitability in conjunction with population viability modeling.

CONCLUSIONS

Broad-scale estimates of habitat suitability that account for geographic variation in species ecology are essential for successful implementation of regional conservation programs. Our work demonstrated how a continuous environmental predictor, specifically winter temperature, can be used to model geographic variation in habitat associations across a species' range, resulting in more accurate model predictions. We suspect that this methodology is broadly applicable to other taxa exhibiting spatial variation in habitat associations along relatively simple geographic gradients. We encourage future research to evaluate this hypothesis, particularly in study systems with spatially complex geographical variations in habitat associations. As interactive effects may reduce model transferability to novel environments, we encourage practitioners of our approach to use rigorous spatially explicit cross-validation to validate model predictions. Finally, the opportunistically collected data used in this project not only highlight the utility of these datasets, but also that sampling biases and inconsistences across large areas are often present. These biases should be addressed during the modeling process, and the consequences of spatial sampling biases on interpreting model predictions should be acknowledged.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Eastern indigo snake point locations were not made available because of collecting concerns but are available from the U.S. Fish and Wildlife Service by contacting the Georgia Ecological Services Field Office. All other data sets for this research are archived on Figshare: https://doi.org/10.6084/m9.figshare.c.5461809.

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REFERENCES

Auffenberg, Walter, and Richard Franz. 1982. "The Status and Distribution of the Gopher Tortoise (*Gopherus polyphemus*)." In *North American Tortoises: Conservation and Ecology*, edited by R. Bruce Bury, 95–126. Washington, DC: U.S. Fish and Wildlife Service.

Barbet-Massin, Morgane, Frédéric Jiguet, Cécile Hélène Albert, and Wilfried Thuiller. 2012. "Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?" *Methods in Ecology and Evolution* 3: 327–38.

Bauder, Javan M. 2019. "Population Viability and Connectivity of the Federally Threatened Eastern Indigo Snake in Central Peninsular Florida." Dissertation (PhD), University of Massachusetts Amherst, Massachusetts.

Bauder, Javan M., and Patrick Barnhart. 2014. "Factors Affecting the Accuracy and Precision of Triangulated Radio Telemetry Locations of Eastern Indigo Snakes (*Drymarchon couperi*)." *Herpetological Review* 45: 590–7.

Bauder, Javan M., David R. Breininger, M. Rebecca Bolt, Michael L. Legare, Christopher L. Jenkins, Betsie B. Rothermel, and Kevin McGarigal. 2016a. "Seasonal Variation in Eastern Indigo Snake (*Drymarchon couperi*) Movement Patterns and Space Use in Peninsular Florida at Multiple Temporal Scales." *Herpetologica* 72: 214–26.

Bauder, Javan M., David R. Breininger, M. Rebecca Bolt, Michael L. Legare, Christopher L. Jenkins, Betsie B. Rothermel, and Kevin McGarigal. 2016b. "The Influence of Sex and Season on Conspecific Spatial Overlap in a Large, Actively-Foraging Colubrid Snake". *PloS One* 11: e0160033.

Bauder, Javan M., Dirk J. Stevenson, Christopher S. Sutherland, and Christopher L. Jenkins. 2017. "Occupancy of Potential Overwintering Habitat on Protected Lands by Two Imperiled Snake Species in the Coastal Plain of the Southeastern United States." *Journal of Herpetology* 51: 73–88.

Bauder, Javan M., David R. Breininger, M. Rebecca Bolt, Michael L. Legare, Christopher L. Jenkins, Betsie B. Rothermel, and Kevin McGarigal. 2018. "Multi-Level, Multi-Scale Habitat Selection by a Wide-Ranging Ranging Federally Threatened Snake." *Landscape Ecology* 33: 743–63.

Bauder, Javan M., David R. Breininger, M. Rebecca Bolt, Michael L. Legare, Christopher L. Jenkins, Betsie B. Rothermel, and Kevin McGarigal. 2020. "Movement Barriers, Habitat Heterogeneity or Both? Testing Hypothesized Effects of Landscape

Features on Home Range Sizes in Eastern Indigo Snakes." *Journal of Zoology* 311: 204–16.

Becker, Elizabeth A., Karin A. Forney, Jessica V. Redfern, Jay Barlow, Michael G. Jacox, Jason J. Roberts, and Daniel M. Palacios. 2019. "Predicting Cetacean Abundance and Distribution in a Changing Climate." *Diversity and Distributions* 25: 626–43.

Boyce, Mark S., Pierre R. Vernier, Scott E. Nielsen, and Fiona K.A. Schmiegelow. 2002. "Evaluating Resource Selection Functions." *Ecological Modelling* 157: 281–300.

Bradter, Ute, Louise Mair, Mari Jonsson, Jonas Knape, Alexander Singer, and Tord Snall. 2018. "Can Opportunistically Collected Citizen Science Data Fill a Data Gap for Habitat Suitability Models of Less Common Species?" *Methods in Ecology and Evolution* 9: 1667–78.

Breininger, David R., Michael L. Legare, and Rebecca B. Bolt. 2004. "Eastern Indigo Snakes (*Drymarchon Couperi*) in Florida: Influence of Edge on Species Viability." In *Species Conservation and Management: Case Studies*, edited by H. Resit Akcakaya, Mark Burgman, Oskar Kindvall, Chris Wood, Per Sjögren-Gulve, Jeff Hatfield, and Michael McCarthy, 299–311. New York: Oxford University Press.

Breininger, David R., Marc J. Mazerolle, M. Rebecca Bolt, Michael L. Legare, John H. Drese, and James E. Hines. 2012. "Habitat Fragmentation Effects on Annual Survival of the Federally Protected Eastern Indigo Snake." *Animal Conservation* 15: 361–8.

Broennimann, Olivier, Valeria Di Cola, and Antoine Guisan. 2021. ecospat: Spatial Ecology Miscellaneous Methods. R package version 3.2. https://CRAN.R-project.org/package=ecospat (accessed April 15, 2020).

Cabeza, Mar, and Atte Moilanen. 2001. "Design of Reserve Networks and the Persistence of Biodiversity." *Trends in Ecology & Evolution* 16: 242–8.

Chetkiewicz, Cheryl-Lesley B., and Mark S. Boyce. 2009. "Use of Resource Selection Functions to Identify Conservation Corridors." *Journal of Applied Ecology* 46: 1036–47.

Climate Engine. 2019. "Climate Engine." http://climateengine.org (accessed April 15, 2020).

Crawford, Brian A., John C. Maerz, and Clinton T. Moore. 2020. "Expert-Informed Habitat Suitability Analysis for at-Risk Species Assessment and Conservation Planning." *Journal of Fish and Wildlife Management* 11: 130–50.

Doherty, Kevin E., Jeffrey S. Evans, Peter S. Coates, Lara M. Juliusson, and Bradley C. Fedy. 2016. "Importance of Regional Variation in Conservation Planning: A Rangewide Example of the Greater Sage-Grouse." *Ecosphere* 7: e01462.

Elith, Jane, and John R. Leathwick. 2009. "Species Distribution Models: Ecological Explanation and Prediction across Space and Time." *Annual Review of Ecology, Evolution, and Systematics* 40: 677–97.

Enge, Kevin M., Dirk J. Stevenson, Matthew J. Elliot, and Javan M. Bauder. 2013. "The Historical and Current Distribution of the Eastern Indigo Snake (*Drymarchon couperi*)." *Herpetological Conservation and Biology* 8: 288–307.

Fajardo, Javier, Janeth Lessmann, Elisa Bonaccorso, Christian Devenish, and Jesus Munoz. 2014. "Combined Use of Systematic Conservation Planning, Species Distribution Modelling, and Connectivity Analysis Reveals Severe Conservation Gaps in a Megadiverse Country (Peru)." *PLoS One* 9: e114367.

Fieberg, John, Johannes Signer, Brian Smith, and Tal Avgar. 2021. "A 'How To' Guide for Interpreting Parameters in Habitat-Selection Analyses." *Journal of Animal Ecology* 00: 1–17.

Fielding, Alan H., and John F. Bell. 1997. "A Review of Methods for the Assessment of Prediction Errors in Conservation Presence/Absence Models." *Environmental Conservation* 24: 38–49.

Franklin, Janet. 2010. *Mapping Species Distributions: Spatial Inference and Prediction*. New York: Cambridge University Press.

Grant, Tyler J., and Stevan P. Bradbury. 2019. "The Role of Modeling in Monarch Butterfly Research and Conservation." *Frontiers in Ecology and Evolution* 7: 197.

Guisan, Antoine, and Wilfried Thuiller. 2005. "Predicting Species Distribution: Offering More than Simple Habitat Models." *Ecology Letters* 8: 993–1009.

Hirzel, Alexandre H., Gwenaelle Le Lay, Veronique Helfer, Christophe Randin, and Antoine Guisan. 2006. "Evaluating the Ability of Habitat Suitability Models to Predict Species Presences." *Ecological Modelling* 199: 142–52.

Hoctor, Thomas S., Margaret H. Carr, and Paul D. Zwick. 2000. "Identifying a Linked Reserve System Using a Regional Landscape Approach: The Florida Ecological Network." *Conservation Biology* 14: 984–1000.

Holland, Jeffrey D., Daniel D. Bert, and Lenore Fahrig. 2004. "Determining the Spatial Scale of a Species' Response to Habitat." *Bioscience* 54: 227–33.

Hyslop, Natalie L., Robert J. Cooper, and J. Michael Meyers. 2009. "Seasonal Shifts in Shelter and Microhabitat Use of *Drymarchon Couperi* (Eastern Indigo Snake) in Georgia." *Copeia* 2009: 458–64.

Hyslop, Natalie L., J. Michael Meyers, Robert J. Cooper, and Dirk J. Stevenson. 2014. "Effects of Body Size and Sex of *Drymarchon couperi* (Eastern Indigo Snake) on Habitat Use, Movements, and Home Range Size in Georgia." *Journal of Wildlife Management* 78: 101–11.

Johnson, Douglas H. 1980. "The Comparison of Usage and Availability Measurements for Evaluating Resource Preference." *Ecology* 61: 65–71.

Kramer-Schadt, Stephanie, Jürgen Niedballa, John D. Pilgrim, Boris Schröder, Jana Lindenborn, Vanessa Reinfelder, Milena Stillfried, et al. 2013. "The Importance of Correcting for Sampling Bias in MaxEnt Species Distribution Models." *Diversity and Distributions* 19: 1366–79.

Macdonald, David W., Helen M. Bothwell, Żaneta Kaszta, Eric Ash, Gilmoore Bolongon, Dawn Burnham, Özgün Emre Can, et al. 2019. "Multi-Scale Habitat Modelling Identifies Spatial Conservation Priorities for Mainland Clouded Leopards (*Neofelis nebulosa*)." *Diversity and Distributions* 25: 1639–54.

Mateo-Sanchez, María C., Aitor Gastón, Carlos Ciudad, Juan I. García-Viñas, Jorge Cuevas, César López-Leiva, Alfredo Fernández-Landa, et al. 2016. "Seasonal and Temporal Changes in Species Use of the Landscape: How Do they Impact the Inferences from Multi-Scale Habitat Modeling?" *Landscape Ecology* 31: 1261–76.

Maxwell, David, and Simon Jennings. 2005. "Power of Monitoring Programmes to Detect Decline and Recovery of Rare and Vulnerable Fish." *Journal of Applied Ecology* 42: 25–37.

McGarigal, Kevin, Ho Yi Wan, Kathy A. Zeller, Brad C. Timm, and Samuel A. Cushman. 2016. "Multi-Scale Habitat Selection Modeling: A Review and Outlook." *Landscape Ecology* 31: 1161–75.

Merow, Cory, Matthew J. Smith, and John A. Silander, Jr. 2013. "A Practical Guide to MaxEnt for Modeling Species' Distributions: What it Does, and Why Inputs and Settings Matter." *Ecography* 36: 1058–69.

Merow, Cory, Mathew J. Smith, Thomas C. Edwards, Jr., Antoine Guisan, Sean M. McMahon, Signe Normand, Wilfried Thuiller, Rafael O. Wüest, Niklaus E. Zimmermann, and Jane Elith. 2014. "What Do We Gain from Simplicity Versus Complexity in Species Distribution Models?" *Ecography* 37: 1267–81.

Moler, Paul E. 1992. "Eastern Indigo Snake." In *Rare and Endangered Biota of Florida, Volume III, Amphibians and Reptiles*, edited by Paul E. Moler, 181–6. Gainesville, FL: University Press of Florida.

Moulis, Robert. 1976. "Autecology of the Eastern Indigo Snake, *Drymarchon corais couperi*." *Bulletin of the New York Herpetological Society* 12: 14–23.

Murphy, Helen T., and Jon Lovett-Doust. 2007. "Accounting for Regional Niche Variation in Habitat Suitability Models." *Oikos* 116: 99–110.

Mushinsky, Henry R., Earl D. McCoy, Joan E. Berish, Ray E. Ashton, Jr., and Dawn S. Wilson. 2006. "*Gopherus polyphemus* - Gopher Tortoise." In *Biology and Conservation of Florida Turtles. Chelonian Research Monographs No. 3*, edited by Peter A. Meylan, 350–75. Lunenburg, MA: The Chelonian Research Foundation.

Phillips, Steven J., Miroslav Dudik, Jane Elith, Catherine H. Graham, Anthony Lehmann, John Leathwick, and Simon Ferrier. 2009. "Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data." *Ecological Applications* 19: 181–97.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. http://www.R-project.org/ (accessed June 10, 2021).

Radosavljevic, Aleksandar, and Robert P. Anderson. 2014. "Making Better MAXENT Models of Species Distributions: Complexity, Overfitting and Evaluation." *Journal of Biogeography* 41: 629–43.

Reddy, Sushma, and Liliana M. Davalos. 2003. "Geographical Sampling Bias and its Implications for Conservation Priorities in Africa." *Journal of Biogeography* 30: 1719–27.

Roberts, David R., Volker Bahn, Simone Ciuti, Mark S. Boyce, Jane Elith, Gurutzeta Guillera-Arroita, Severin Hauenstein, et al. 2017. "Cross-Validation Strategies for Data with Temporal, Spatial, Hierarchical, or Phylogenetic Structure." *Ecography* 40: 913–29.

Rodriguez, Jon Paul, Lluis Brotons, Javier Bustamante, and Javier Seoane. 2007. "The Application of Predictive Modelling of Species Distribution to Biodiversity Conservation." *Diversity and Distributions* 13: 243–51.

Schadt, Stephanie, Eloy Revilla, Thorsten Wiegand, Felix Knauer, Petra Kaczensky, Urs Breitenmoser, Ludek Bufka, et al. 2002. "Assessing the Suitability of Central European Landscapes for the Reintroduction of Eurasian Lynx." *Journal of Applied Ecology* 39: 189–203.

Shirk, Andrew J., Martin G. Raphael, and Samuel A. Cushman. 2014. "Spatiotemporal Variation in Resource Selection: Insights from the American Marten (*Martes americana*)." *Ecological Applications* 24: 1434–44.

Stevenson, Dirk J., Karen J. Dyer, and Beth A. Willis-Stevenson. 2003. "Survey and Monitoring of the Eastern Indigo Snake in Georgia." *Southeastern Naturalist* 2: 393–408.

Stevenson, Dirk J., Kevin M. Enge, Lawrence D. Carlile, Karen. J. Dyer, Terry M. Norton, Natalie L. Hyslop, and Richard A. Kilte. 2009. "An Eastern Indigo Snake (*Drymarchon couperi*) Mark-Recapture Study in Southeastern Georgia." *Herpetological Conservation and Biology* 4: 30–42.

U. S. Census Bureau. 2016. "2016 TIGER/Line shapefiles technical documentation." https://www2.census.gov/geo/pdfs/maps-data/data/tiger/tgrshp2016/TGRSHP2016_TechDoc.pdf (accessed April 15, 2020).

U. S. Fish and Wildlife Service. 2019. "Species Status Assessment Report for the Eastern Indigo Snake (*Drymarchon couperi*)." Version 1.1, Atlanta, GA.

U.S. Geological Survey. 2020. "Protected Areas Database of the United States." https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/pad-us-data-overview?qt-science_center_objects=4#qt-science_center_objects (accessed June 15, 2020).

Veloz, Samuel D. 2009. "Spatially Autocorrelated Sampling Falsely Inflates Measures of Accuracy for Presence-Only Niche Models." *Journal of Biogeography* 36: 2290–9.

Vitousek, Peter M., Harold A. Mooney, Jane Lubchenco, and Jerry M. Melillo. 1997. "Human Domination of Earth's Ecosystems." *Science* 277: 494–9.

Vollering, Julien, Rune Halvorsen, Inger Auestad, and Knut Rydgren. 2019. "Bunching up the Background Betters Bias in Species Distribution Models." *Ecography* 42: 1717–27.

Waldron, Jayme L., Shane M. Welch, and Stephen H. Bennett. 2008. "Vegetation Structure and the Habitat Specificity of a Declining North American Reptile: A Remnant of Former Landscapes." *Biological Conservation* 141: 2477–82.

Wan, Ho Yi, Kevin McGarigal, Joseph L. Ganey, Valentin Lauret, Brad C. Timm, and Samuel A. Cushman. 2017. "Meta-Replication Reveals Nonstationarity in Multi-Scale Habitat Selection of Mexican Spotted Owl." *Condor* 119: 641–58.

Wan, Ho Yi, Samuel A. Cushman, and Joseph L. Ganey. 2018. "Habitat Fragmentation Reduces Genetic Diversity and Connectivity of the Mexican Spotted Owl: A Simulation Study Using Empirical Resistance Models." *Genes* 9: 403.

Watson, James E.M., Nigel Dudley, Daniel B. Segan, and Marc Hockings. 2014. "The Performance and Potential of Protected Areas." *Nature* 515: 67–73.

Welch, Shane M., Arnie G. Eversole, and Jeanne Riley. 2007. "Using the Spatial Information Implicit in the Habitat Specificity of the Burrowing Crayfish Distocambarus Crockeri to Identify a Lost Landscape Component." *Ecography* 30: 349–58.

Yates, Katherine L., Phil J. Bouchet, M. Julian Caley, Kerrie Mengersen, Christophe F. Randin, Stephen Parnell, Alan H. Fielding, et al. 2018. "Outstanding Challenges in the Transferability of Ecological Models." *Trends in Ecology & Evolution* 33: 790–802.

Zanini, Flavio, Jerome Pellet, and Benedikt R. Schmidt. 2009. "The Transferability of Distribution Models across Regions: An Amphibian Case Study." *Diversity and Distributions* 15: 469–80.

Zeller, Katherine A., David W. Wattles, and Stephen DeStefano. 2018. "Incorporating Road Crossing Data into Vehicle Collision Risk Models for Moose (*Alces americanus*) in Massachusetts, USA." *Environmental Management* 62: 518–28.

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