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HIGH-RESOLUTION NICHE MODELS VIA A CORRELATIVE APPROACH: COMPARING AND COMBINING CORRELATIVE AND PROCESS-BASED INFORMATION

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RUNNING HEADER: Combining process and correlative models

ABSTRACT

Correlative and process-based approaches to describing the ecological niche in a spatially explicit fashion have often been compared in an adversarial framework. We sought to compare niche models developed via classic (correlative only), niche (process-based information), and hybridized (correlative augmented with process-based derived information) approaches, with the goal of determining if the added effort of process-based model development yielded better model fit. Correlative data layers (i.e., habitat models) included vegetation community types, Euclidean distance statistics, neighborhood analyses, and topographically-derived information. Mechanistic data layers were estimates of thermal suitability derived from field-collected datasets and biophysical calculations, and estimates of prey biomass interpolated from monitoring stations. We applied these models at high resolution (1x1 m pixel size) to habitat occupied by a population of Texas horned lizards (*Phrynosoma cornutum*) located in central Oklahoma. Results suggested that our treatment of process-based information offered dramatically better identification of suitable habitat when compared to correlative information, but that these results were likely due to low variability of niche variable pixel values. Niche layers nearly perfectly predicted lizard locations; the interpretation of these results suggest that lizards occupy habitat based on thermal suitability over the duration of a field season. Given the low variability observed in thermal suitability layers, we question the ecological reality of these predictions. Correlative models may accurately describe the niche at small spatial scales, and may suffice in situations where time and financial resources are limiting constraints on project goals. Process-based

information continues to be an important part of the niche, and may offer additional predictive accuracy via correlative approaches when included in an ecologically meaningful context.

1. INTRODUCTION

The ecological niche was introduced by Hutchinson (1957), and has since served as a conceptual model for the interaction of organisms with each other and their environment. Despite disagreement associated with its description (Whittaker et al., 1973; Hurlbert, 1981; Kearney, 2006; Soberón, 2007; Godsoe, 2010; Angilletta and Sears 2011), the niche concept has been quantified and applied in the form of habitat models that map species' distribution and potential occupancy, with the objective of identifying areas for various conservation goals (Araújo and Guisan, 2006; Guisan and Zimmermann, 2000; Kearney, 2006). Applications include studying relationships between environmental parameters and species richness, examining links between landscape ecology and the persistence of species, predicting potential invasion by non-native species, modeling former or future distributions, and differentiating habitat selection by closely-related species (reviewed in Guisan and Thuiller, 2005; Elith et al., 2006).

A dichotomy between correlative and process-based models (Kearney, 2006; Morin et al., 2007; Morin and Thuiller, 2009; Buckley et al., 2010) is common in the habitat modeling literature, although all distribution models aim to achieve some representation of the niche. Some proponents of process-based models have suggested that an understanding of the underlying mechanism(s) driving species distribution is needed to clearly identify and model axes of the fundamental niche (Kearney and Porter, 2004), whereas others have suggested that focusing solely on the fundamental niche does not provide a complete picture of a species' spatial distribution (Godsoe, 2010) or the underlying biotic interactions that define it. Correlative approaches are not as powerful, explicit, or transferable to novel areas as mechanistic ones (Kearney et al., 2008; Kearney et al., 2009; Bartelt et al., 2010), but for many species they offer a quick, easy, and often robust estimate of occupancy (Tsoar et al., 2007; Barrows et al., 2008; Kharouba et al., 2009; Buckley et al., 2010). Morin and Thuiller (2009) suggested that a more robust estimate of occupancy may be achieved by combining correlative and process-based models, which is the primary aim of this paper.

Collectively, papers referring to "niche" or "habitat" modeling have not shown consistent use of terminology throughout publication history (Hall et al., 1997; Mitchell, 2005; Kearney, 2006). We follow suggestions by Kearney (2006) in describing the various components of space used by animals and how they are modeled. We refer to those variables included in models that lack an explicit mechanism, or for which the basic mechanisms are not reasonably well understood, as "habitat" components. These variables typically form the basis of correlative models (i.e., habitat cover types, soil type, slope and aspect). Variables for which a mechanism is evident are referred to as "niche" components. Given this terminology, the fundamental niche (the portion of habitat in which a population of animals can physiologically survive and reproduce) is best represented by modeling mechanistic approaches (Kearney and Porter, 2004; Kearney et al., 2008). An organism's realized niche, which is contained within the physiological limitations of the fundamental niche, is constrained by refugia from predators and thermal extremes (i.e., cover) and resources over which intraspecific and interspecific competition occur (e.g., food, space).

A potential downfall of any correlative habitat model is the exclusion of operative environmental factors (e.g., thermal environment, Spomer, 1973) from their construction. Organisms are sensitive to their surrounding thermal landscape (Porter and Gates, 1969), and they routinely make decisions that trade-off with other behaviors, such trade-offs resulting from energetic costs and benefits (Huey and Slatkin 1976; Hertz et al., 1993; Angilletta, 2001; Guthery et al., 2005). Including spatially-explicit thermal data, which represent environmental conditions faced by organisms in the decision-making process of habitat selection, should increase the predictive power of model outputs. Another commonly absent factor in habitat modeling is prey availability, which also can determine fine-scale distributions (Soberón, 2007). Some authors attempt to broadly link prey availability to habitat type (Etherington et al., 2009), but such a linkage is less accurate than estimating prey availability as a heterogeneous, spatially explicit phenomenon.

We combined process-based data (spatially-explicit layers of prey availability and thermal suitability) and correlative-based geographic data into models of occupancy, which we refer to as habitat-niche models. We compared these against a typical correlative modeling process that did not include any mechanistically-derived data layers (hereafter habitat-only models), and against a correlative modeling process that included only mechanistically-derived data (hereafter niche-only models). We used the Mahalanobis distance statistic, which has been applied to a variety of conservation questions (Clark et al., 1993; Browning et al., 2005; Watrous et al., 2006; Telesco et al., 2007; Barrows et al., 2008). This technique can provide reliable predictors of occupancy patterns (Johnson and Gillingham, 2005; Hellgren et al., 2007; Tsoar et al., 2007; VanDerWal et al., 2009; Rebelo and Jones, 2010), although they may be outperformed by presence-absence models (Brotons et al., 2004). However, for many cryptic or rare species accurately determining absence points can be difficult (Barrows et al., 2008; Etherington et al., 2009), and so presence-only models offer an alternative.

Here, we developed several models (niche-only, habitat-only and habitat-niche) for the Texas horned lizard (*Phrynosoma cornutum*) in central Oklahoma. This lizard is a cryptically patterned, specialist myrmecophage (Pianka and Parker, 1975) that has suffered localized extirpations across much of its former range (Figure 1), most likely because of a combination of habitat loss and introduced ant fauna (Donaldson et al., 1994; Henke, 2003). Texas horned lizards are ideal candidates for presence-only modeling approaches because of their cryptic nature, which may lead to incorrect assumptions when using techniques that rely on true absences. The dietary specialization (Blackshear and Richerson, 1999) and available physiological data (Prieto and Whitford, 1971) of Texas horned lizards facilitated the inclusion of process-based data in our models. Our goal was to compare predictive performance among each model type (habitat-only, niche-only, and habitat-niche) to determine if predictive accuracy of a fine-scale model was improved by combining mechanistic and correlative datasets, with the expectation that adding process-based data layers to correlative models would increase the accuracy of prediction.

2. METHODS

2.1. Study Area and Field Methods

Texas horned lizards were studied at Tinker Air Force Base (TAFB hereafter), located in Midwest City, Oklahoma (Figure 1), a large (~ 2000 ha), industrial complex on the southeastern edge of the Oklahoma City metropolitan area that serves as a maintenance supply depot for the United States Air Force. Approximately 20% of TAFB is an interconnected network of green space. Within this network, Texas horned lizards occupy approximately 40 ha of mixed-prairie and eastern redcedar (*Juniperus virginiana*) vegetation. We calculated niche models in a 600 x 600 m area within this site (Figure 2).

We used radio-telemetered lizards to obtain location data for niche models. We captured lizards by hand during fortuitous encounter surveys during March–June 2008. We dorsally attached radiotransmitters (model BD-2, 0.95-1.95 g, Holohil Systems Ltd., Ontario, Canada) to individuals using silicone adhesive and small elastic collars placed around individuals' necks (total encumbrance was ≤ 10% of an individual's mass). Lizards were located by homing to their position (R-1000 receiver, Communication Specialists, Orange, CA; Yagi 3-element antennae, Wildlife Materials Inc., Murphysboro, IL) 3-7 times per week. Locations were stored in a GIS database using handheld GPS units (Trimble GeoXT, Terrasync 2.3, Strategic Consulting International, Oklahoma City, OK).

Radiotransmitter packages were designed to reduce individual encumbrance, and were removed if loss of mass caused the transmitter package to exceed 10% of individual mass. Except for mortality and mass-loss events, every attempt was made to continuously track individuals carrying transmitters for continued study. Courtship and mating did not appear to be impacted by transmitter presence (Bogosian et al., 2009). We handled animals as little as possible and minimized disturbance. To this end, lizards tracked to dense vegetation were located to within 1 m of signal position, but were not located visually unless measurements were taken or we needed to confirm a fate if the animal had not moved for several days. For all models, we reduced field-collected data by retaining only telemetered observations to avoid detectability biases toward open areas where lizards were more easily visible and captured (i.e., capture, nesting locations).

2.2. Habitat Variables

We modeled occupancy at a very fine scale (Soberón, 2007; Brambilla et al., 2009) in our study system to lessen the mismatch between the spatial scale of data and that experienced by lizards (Sears et al 2011), attempting to model each ecological component at an appropriate scale (Wiens, 1989). Most habitat models are coarse (> 10 m^2 resolution; Kearney and Porter, 2004; Browning et al., 2005; Barrows et al., 2008), likely due to both the resolution of available datasets and the computing time required for modeling very large areas. We accessed United States Department of Defense GIS datasets that were scaled at ≤ 1 m^2, which allowed us to model the interaction of organisms with habitat and niche layers at a finer scale than previous studies (e.g., Guisan and Thuiller, 2005). All input GIS layers and final models were scaled to 1-m^2 resolution, which were considered appropriate for small, cryptic, ground-dwelling lizards.

Existing GIS datasets, available at TAFB prior to this study, were used in the modeling process. Vegetative communities were mapped on TAFB in 2004 (Dorr et al., 2005; 92% overall accuracy) and over 20 vegetative types were present. We broadly reclassified these communities into 8 main types (Table 1) based on structural type and management regime. This revised vector dataset was converted to a binary raster format for each habitat type, from which Euclidean distance and cell neighborhood statistics were calculated. Euclidean distance layers, indicating the measure of the distance from each target pixel to the nearest pixel of the habitat type in question, were created using the ArcGIS 9.1 (ESRI Inc., Redlands, CA) Spatial Analyst package. Neighborhood statistics were also created using the Spatial Analyst package, and indicated the proportion of pixels containing a habitat type within a circle of a given radius (33 m, based on mean daily movement distances observed).

Additionally, we used existing slope and aspect datasets to produce layers for final models (Table 2). We conducted an initial principal component analysis (PCA) on the correlation matrix of the 17 habitat variables to determine the relative importance of each variable to the overall distribution of Texas horned lizards, with the intention of reducing the dataset for comparison and combination with a limited set of niche variables (see section 2.3). We considered only those components whose overall variance represented a ≥ 30% decrease from the previous eigenvalue (i.e. [previous eigenvalue – current eigenvalue]/current eigenvalue). We retained the 6 GIS layers that had the highest average of absolute value scores for each component that met the eigenvalues criteria in the PCA analysis; these layers were interpreted as having the most impact on final habitat models (Barrows et al., 2008).

2.3. Niche Variables

2.3.1. *Thermal Suitability*.—The dynamics of thermal suitability were modeled using published models of mass-energy balance equations (Porter and Gates, 1969; Porter et al., 2002), with some modifications. We used on-site microclimatic data, available US

Department of Defense GIS datasets, and principles of biophysical ecology (McCullough and Porter, 1971; Gates, 1980; Campbell and Norman, 1998) to develop a model of the relative amount of time habitat was suitable or unsuitable to horned lizard activity via operative temperature (Appendix A). The output layers represent the proportion of those time periods that fall within the preferred temperature range or above the critical thermal maximum (37.0-39.5 °C and 47.9 °C respectively; Prieto and Whitford, 1971) for Texas horned lizards (Table 2).

We tested predicted ground temperatures against actual ground temperatures, which were recorded with Thermochron iButtons (Model DS1921H, Maxim Integrated Products/Dallas Semiconductor, Sunnyvale, CA) painted white and placed in stratified random points (2 points per ha) to estimate the accuracy of the model. We collected 30,560 iButton recordings that fell within the spatial and temporal extents of study area and timeframe. Predicted ground temperature was calculated using Eqn. 2 based on the properties at the iButton site (taken from handheld GPS units) required in the above calculations. We compared operative temperatures calculated from estimated (i.e., calculated using Eqn. 2) and recorded (i.e., recorded via iButton rather than estimated from Eqn. 2) for lizards at each time-step (1 time-step = 10-minute increment). Thermal suitability models were calculated using Python scripts (Appendix B).

2.3.2. *Prey Availability Layer*.—We modeled prey availability by interpolating values from monitoring stations via kriging (Oliver and Webster, 1990; Cressie, 1993). We placed bait stations (*n* = 171) and pitfall traps (*n* = 18) at systematically located stations monthly during May–June 2008 to estimate prey abundance. Bait stations contained a mixture of peanut butter and millet in 20 mL scintillation vials, and pitfall traps (266-mL plastic cups) were roughly 1/3 full of propylene glycol with detergent to reduce surface tension. Bait stations were placed in the field during 0600–1200 hours on rain-free days and were collected 1 hour after placement (Lubertazzi and Tschinkel, 2003). Pitfall traps were placed in the field and collected after 72 hours. Invertebrate samples were stored in 70% ethanol until identification. All ants were identified to genus. Identification was based on Fisher and Cover (2007). To estimate biomass, identified insects were dried for 48 hours at 70°C and weighed (mg) using an analytical balance (accurate to 0.0001 mg).

We calculated averages of Formicidae biomass for each bait station or pitfall trap. These values were used to create semivariograms (Cressie, 1993; Schauber et al., 2009) to estimate the spatial structure of invertebrate biomass via ArcGIS Geostatistical Analyst (Kumar et al., 2007). We compared semivariograms of raw, log- and arcsin-transformed averaged values via relative structural variability (RSV; Isaaks and Srivastava, 1989; Schauber et al., 2009), root-mean square error (RMSE; Kumar et al., 2007), and effective ranges relative to study-area size. The best resulting semivariogram model was used to interpolate biomass values to a continuous surface in the ArcGIS Geostatistical Analyst package.

2.4. Niche Modeling

Texas horned lizards are highly active early in the season following emergence from hibernacula (Apr–Jun) when searching for mates and nest sites, but movement distances decline rapidly following nesting (Henke and Montemayor, 1998; Stark et al., 2005). We modeled occupancy during May and June based on the reproductive behavior seen in the literature and at our site (R. W. Moody, Tinker Air Force Base, unpublished data) using the partitioned Mahalanobis distance statistic (Browning et al., 2005; Rotenberry et al., 2006), which requires presence-only data, to model occupancy. The Mahalanobis distance (D^2) is a measure of occupancy based on p variables measured at n locations:

$$D^2(y) = (y - \mu)' \sum{}^{-1} (y - \mu) \tag{1}$$

where y is the $p \times 1$ vector of measurements taken at any point, and μ is the $p \times 1$ vector of means for each environmental data layer (Clark et al., 1993; Rotenberry et al., 2006). To overcome potentially restrictive model output (Knick and Rotenberry, 1998), we partitioned the statistic via principal component analysis performed on the correlation matrix of environmental data taken at animal locations (Rotenberry et al., 2002; Browning et al., 2005; Rotenberry et al., 2006). Partitioned Mahalanobis models emphasize a minimum set of habitat characteristics (compared to an optimum set of habitat characteristics, which a full-rank Mahalanobis model seeks to achieve; Rotenberry et al., 2006), and are calculated by:

$$D^2(y) = \sum_{j=1}^{p} \frac{d_j^2}{\lambda_j} \tag{2}$$

where λ_j is the eigenvalue associated with principal component j, $d_j = (y - \mu)'\alpha_j$, and α_j are the eigenvectors associated with each environmental data layer. Partitioned D^2 scores follow a χ^2 distribution with n+1-p degrees of freedom (where n = total number of components, p = target component), which allows rescaling of the Mahalanobis distance (which can range from 0 to infinity) for ease of display (Rotenberry et al., 2006).

Niche-only models included two thermally-derived and one prey GIS layer; combination niche-habitat models included three niche layers plus the top six habitat layers; and habitat-only layers included only those top six habitat layers. We randomly selected 90 lizard locations to develop models, and retained the remaining (*n* = 437) locations for internal cross-validation. We followed Rotenberry et al.'s (2006) recommendation of a 1:10 ratio of explanatory variables: locations to avoid model overfitting. This resulted in a dataset of 30 lizard locations for niche models, 90 locations for habitat-niche models, and 60 locations for habitat-only models. .

We generated 1,000 pseudo-absence points randomly across the study area using Hawth's Tools Analysis extension in ArcGIS 9.1 (Beyer, 2004), assuming that random points would occupy different habitats (and thus be rated as lower in occupancy) than locations occupied by Texas horned lizards. For the purposes of statistical tests (see below), we selected enough pseudo-absence points to equal the sample size in each validation dataset. We conducted PCA using the correlation matrix of development dataset locations intersected with pixel values of all model layers to determine the components that were most limiting (and thus most likely to be representative of a realized niche; Rotenberry et al., 2006). Mahalanobis distances were calculated using Python scripts (Appendix C).

2.5. Model Validation

Interpretation of principal components (and selection of a "best" component or series of components) is somewhat arbitrary (Browning et al., 2005; Rotenberry et al., 2006), but some general rules of thumb have been used in the literature. The magnitude of change between eigenvalues has been suggested as an initial step in identifying components that may accurately describe limiting habitat features (Rotenberry et al., 2006), and an arbitrary threshold of the absolute value of factor loadings has been proposed as a method to interpret the importance of each layer to the resulting partition (Rotenberry et al., 2006; Barrows et al., 2008). Once a partition of the full-rank D^2 model has been selected, the partitioned model can be calculated for a landscape or a validation dataset, and various model-validation steps can be taken before a final model is produced.

We followed the approach of Barrows et al. (2008) and Rotenberry et al. (2006) in assessing the various strengths and weaknesses of the partitioning process. First, we inspected the eigenvalues for each model and considered those principal components (candidate components hereafter) whose contribution to overall variance represented a ≥ 30% decrease from the previous eigenvalue (i.e. [previous eigenvalue – current eigenvalue]/current eigenvalue). The factor loadings within these partitions that were considered important were those with an absolute value ≥ 0.35.

For all candidate components, we calculated Mahalanobis distance scores for pixels associated with cross-validation locations and pseudo-absence locations and tested for a relationship between lizard presence or absence and model prediction using logistic regression, where the dependent variable was the occurrence of a lizard at a point (pseudo-absence points were considered absences) and the predictor variable was the model output (i.e., *p*-value taken from D^2 score) at that point. We used AIC scores to determine top candidate components whose scores were within 2.0 AIC units of the top model, as well as having statistically significant results from the logistic-regression analyses (Barrows et al., 2008). We compared all components satisfying the eigenvalues criteria using lizard and pseudo-absence locations via a receiver-operating-characteristic curve (ROC; Zweig and Campbell, 1993; Fielding and Bell, 1997) to estimate the area under the curve (AUC; Pearce and Ferrier, 2000; Hand and Till, 2001) using SigmaPlot 10.0. Our overall test statistic for comparison between niche-only, habitat-niche, and habitat-only components was the AUC score of the best candidate principal component.

3. RESULTS

3.1. Lizard Capture, Telemetry, and Habitat Variables

We captured 19 lizards during the study period (10 males, 9 females), and obtained 527 locations. PCA of habitat variables suggested that the six most important GIS layers that explained horned lizard locations were mixed bare ground, shrub, unmowed grass, neighborhood unmowed grass, distance to bare ground, and distance to unmowed grass (Table 3).

3.2. Niche Variables

Ground temperature was not well-estimated by the technique used (difference between predicted and field-measured $T(z,t)$ = -1.08 ± 0.02, -36.20 – 10.97 [mean ± SE, range °C]). However, the resulting operative temperature estimates from field-measured versus predicted ground temperatures did not vary widely (difference between T_e from predicted and field-measured $T(z,t)$ = 0.00 ± 0.00, -0.05 – 0.18 [mean ± SE, range °C]). Therefore, we estimated T_e using ground temperatures as calculated in Eqn. 2 (Appendix A).

We collected and identified ca. 48,000 invertebrates during the study period, with ants composing > 96% of the samples and 44% of the biomass. Other sampled orders that composed large proportions of the biomass included the beetles (Coleoptera, 32%)

and isopods (Isopoda, 16%). Ant diversity was represented by 10 genera, although 3 genera (*Crematogaster, Dorymyrmex*, and *Monomorium*) composed roughly 90% of both count and biomass within the Formicidae. Semivariograms (Figure 3), RMSE and RSV values of raw and transformed data suggested that arcsin-transformed values showed the best spatial structure of our dataset. Semivariance appeared to reach the sill at approximately 30 m for all semivariograms, and overall variance was very high for each interpolation approach, suggesting prey distribution was highly patchy. Arcsin-transformed biomass values were interpolated and used as surface rasters for the partitioned Mahalanobis model.

3.3. Niche Modeling and Validation

Initial evaluation of eigenvalue spacing of PCA suggested that between 30-70% of the components of each modeling approach may offer explanatory variables for lizard distribution. Components that explained very little of the overall variance were not tested (i.e., logistic regression, ROC analyses, etc.) further; this pattern was only observed in habitat-niche and habitat-only models.

Results of AIC model selection for top D^2 partitions suggested only one top candidate component for each model type (all $\chi^2 \geq 78.20$, all $p < 0.01$, Table 4). Habitat variables were more important in habitat-niche components than niche variables; niche variables were considered important in only one habitat-niche component based on our criterion. In top candidate habitat-niche and habitat-only components, the same three habitat layers (mixed bare ground, shrub, and unmowed grass) were important variables.

The top candidate habitat-only component emphasized the same binary variables as the top candidate habitat-niche component, effectively reaching the same AUC score

(0.682 ± 0.018; 0.680 ± 0.018 for habitat-niche and habitat-only, respectively, Figure 4). Eigenvectors for the top candidate habitat-niche component (Table 4) did not emphasize either thermal or prey niche layers. Eigenvectors for niche variables in the habitat-niche component were near zero, suggesting that these values did little to increase the D^2 score for pixels, and nearly cancelled each other out directionally. The AUC score for the top candidate niche-only component was higher (0.978 ± 0.007) than either habitat-niche or habitat-only model (Table 4).

4. DISCUSSION

The top candidate niche-only component outperformed habitat-niche and habitat-only components via AUC scores. However, these results may be due to low variance in some of our niche data (see next paragraph). Additionally, the top candidate habitat-niche component did not perform any better than the top candidate habitat-only component. This result suggests that niche variables are better at explaining lizard habitat occupancy than habitat variables, but that this descriptive power is lessened when the two different kinds of information are combined. Similar patterns are revealed when inspecting ΔAIC scores for logistic regression models (Table 4). These results suggested only one candidate component per model type, and AUC scores for components with no support (high ΔAIC values) were larger than those ranked as candidate components. The only exception was in habitat-niche components; component 9 (least support) had the second highest AUC score compared with the candidate component (component 8). We interpret this deviation from the observed pattern to be a result of the GIS layers that had the largest eigenvector for this component (both thermal layers).

Inspection of thermally-derived niche layers revealed very low variability across the study area (Figure 5). The partitioning process of the Mahalanobis distance statistic emphasizes those layers with low variability in the smallest component (Rotenberry et al., 2006), and it is likely that the high AUC score seen in the niche-only component is a result of two of three variables (both thermally-derived layers) used showing little range and variation across the study area. Our ROC curves (from which AUC scores are calculated) were based on pseudo-absence and lizard locations. Random spatial distribution of pseudo-absence locations increased the proportion that occurred within forested habitat (which lizards never used), which would have different thermal properties than the rest of the study area. Pseudo-absence locations in pixels of forested habitat offered model predictions of better performance (i.e., forested habitat had less time within preferred temperature ranges than non-forested habitat), but the overall homogeneity of D^2 results in our candidate niche-only model offered little variation for ROC analyses to discriminate between suitable and unsuitable sites. The range of values that our niche-only model presented was very low (0.89 – 1.00), leading us to question the utility of such results in the context of species distribution modeling. These factors, when combined with the correlative approach taken by the Mahalanobis distance statistic, gives the impression that thermally-derived layers (which heavily weighted final D^2 scores in our results) can nearly perfectly predict lizard locations. We question the ecological validity of these results in light of the near-homogeneity of the niche model output (Figure 5 – note the different scales per panels).

The scale at which we applied niche factors may have influenced our results. Thermal data were estimated over the course of the mating and nesting season and were expressed on the landscape as a proportion of the amount of time pixel temperatures fell within a preferred range or above a critical maxima. Our approach sought to summarize the fluctuation of short-term patterns and express them in a convenient format that allowed for inclusion in correlative niche models, but our results suggest that this approach did not produce ecologically meaningful output. Our thermal layers showed little overall range (n = 90, 0.00 – 0.02, 0.00 – 0.08 for a_ctmax, w_tpref, respectively) or variation at lizard locations (mean ± SE: 0.01 ± 0.00, 0.06 ± 0.00 for a_ctmax and w_tpref, respectively).

Lizards are likely responding to operative temperature at a finer temporal scale (i.e., from minutes to hourly response timeframes) than is represented in our dataset (i.e., where the spatial representation of landscape thermal suitability is for a 2 month period; see Sears et al. 2011). Lizards actively thermoregulate throughout a daily cycle, and follow patterns that allow them to efficiently interact with their habitat for energetic requirements (Heath, 1962; Heath, 1965). These behaviors may occur at a shorter temporal scale than can be modeled effectively over long durations, and thermal suitability may not be easily represented in correlative procedures. Additionally, the spatial scale at which thermal mechanisms seem to constrain distributions is likely larger than the scope of our study (Kearney et al., 2008; Kearney et al., 2009). The importance of thermal and nutritional constraints on mate-seeking and nesting strategies should not be downplayed, however; rather, at a local spatial scale, our data suggest that these factors may not be easily expressed in a correlative modeling approach or combined with temporally coarser habitat GIS layers.

The consistency of habitat-only eigenvectors that influenced final D^2 scores and the relatively low AUC scores (Table 4) suggests that habitat variables explain lizard site occupancy only marginally, and may not be optimal descriptors of the niche (Figure 5). Our AUC scores (~0.7) for habitat-niche and habitat-only models were not as high as other scores seen in the literature (i.e., Barrows et al., 2008; Hu and Jiang, 2010), suggesting that our approach did not capture the essential components of the niche required to accurately predict site occupancy by horned lizards. This result was unexpected, as prey items and habitat features have been shown to be important factors in horned lizard behavior (Pianka and Parker, 1975) and habitat use (Whiting et al., 1993). Nevertheless, the habitat variables in the best-performing habitat and habitat-niche models were bare ground/mixed vegetation, shrub, and unmowed grass, which were consistent with preferences of Texas horned lizards for a mosaic of bare ground, herbaceous vegetation, and woody cover (Whiting et al., 1993, Burrow et al., 2001).

The lack of importance of prey distribution is not consistent with the expectation that it would influence fine-scale distribution (Soberón, 2007). Dietary specialization of Texas horned lizards on ants (Pianka and Parker, 1975; Whitford and Bryant, 1979) led to our prediction that prey distribution across a landscape would be a leading factor in the distribution of the Texas horned lizard. However, none of the best-performing components in the present study had high factor loadings for the prey layer. High variance seen in semivariograms suggests that interpolation results may not accurately represent prey availability for lizards on our study site. The estimation of ant biomass via interpolation is novel to our knowledge, and it may not be appropriate for a mobile rather than a sessile prey item (i.e., Lovvorn et al., 2009).

A niche dataset missing from our models is predator distribution (Kliskey and Byrom, 2004; Schauber et al., 2009). Texas horned lizards have a variety of antipredator behavioral strategies (Pianka and Parker, 1975; Sherbrooke, 2008), and are not a main prey item for any predator, although they are taken occasionally by a wide range of taxa (Sherbrooke, 1990; Sherbrooke, 1991; Sherbrooke, 2008). We could not represent predation risk in a spatially-explicit fashion for this model because of the diversity of predators and a logistical inability to map their distribution at a seasonal scale. However, future habitat-niche models could develop such a distribution through spatially-explicit measurement of predation rates on simulated prey (Connors et al., 2005; Shepard, 2007) or predator activity level (Schauber et al., 2009).

Our results offer some suggestions for future attempts of combining niche and habitat variables into single-output models. Future applications should focus on a more meaningful metric of interaction with thermal landscapes. For example, Kearney and Porter (2004) expressed thermal GIS layers as the minimum number of degree-days required by a clutch of *Heteronotia binoei* eggs to hatch, and Lovvorn et al. (2009) expressed viable habitat as pixels where energy intake was greater than energy cost. Angilletta et al. (2009) compared predicted and measured temperatures at nest sites via a spatially-explicit model of soil temperatures. Application of prey and predator spatial distribution is not as easily achieved, but future research may benefit from comparing suitability models for those taxa as input features for a study species' own ecological niche model.

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FIGURE HEADERS

Figure 1. (A) Location of Tinker Air Force base within Texas horned lizard historic range (adapted from Sherbrooke 2003) and (B) aerial photo of Tinker Air Force Base.

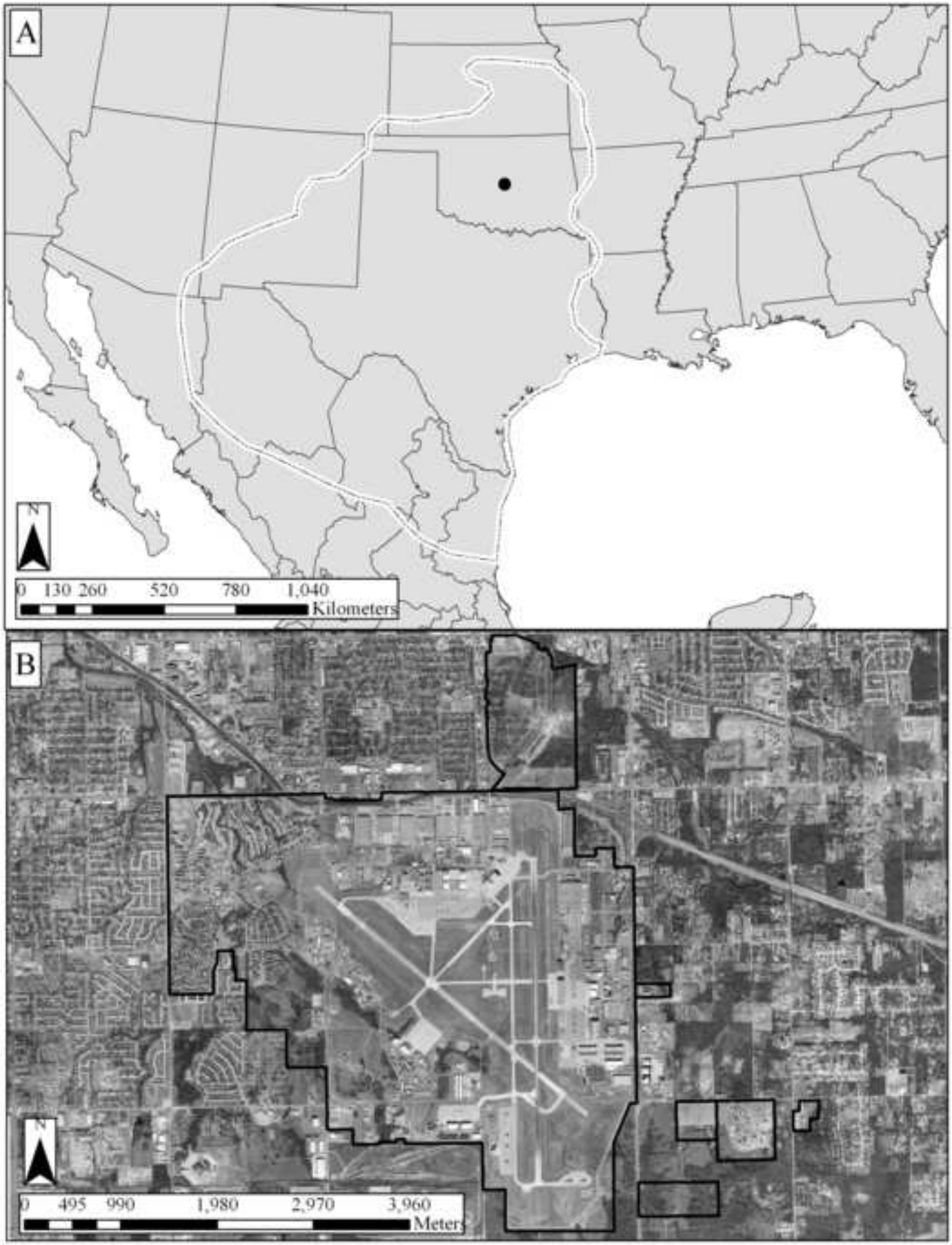
Figure 2. Study area located within Tinker Air Force Base, Midwest City, Oklahoma.

Figure 3. Semivariograms of raw and transformed (ln – natural log, arcsin – arcsine) Formicidae biomass datasets used to create surface maps of prey availability for Texas horned lizards on Tinker Air Force Base during May-June 2008.

Figure 4. Receiver operator characteristic (ROC) plots and area under the curve (AUC) scores for top candidate (A) niche-only, (B) habitat-niche, and (C) habitat-only models calculated for Texas horned lizards on Tinker Air Force Base during 2008. Random classifier curves included.

Figure 5. Index of suitability of study area (Tinker Air Force Base, Oklahoma City Metropolitan area) based on probability values taken from Mahalanobis distance statistic scores for niche-only (A), habitat-niche (B), and habitat-only (C) components via partitioned Mahalanobis distance statistic for Texas horned lizards on Tinker Air Force Base during 2008. Note the different scales per panel.

Figure1


A
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Kilometers
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Meters

Figure2

Figure3

Click here to download high resolution image

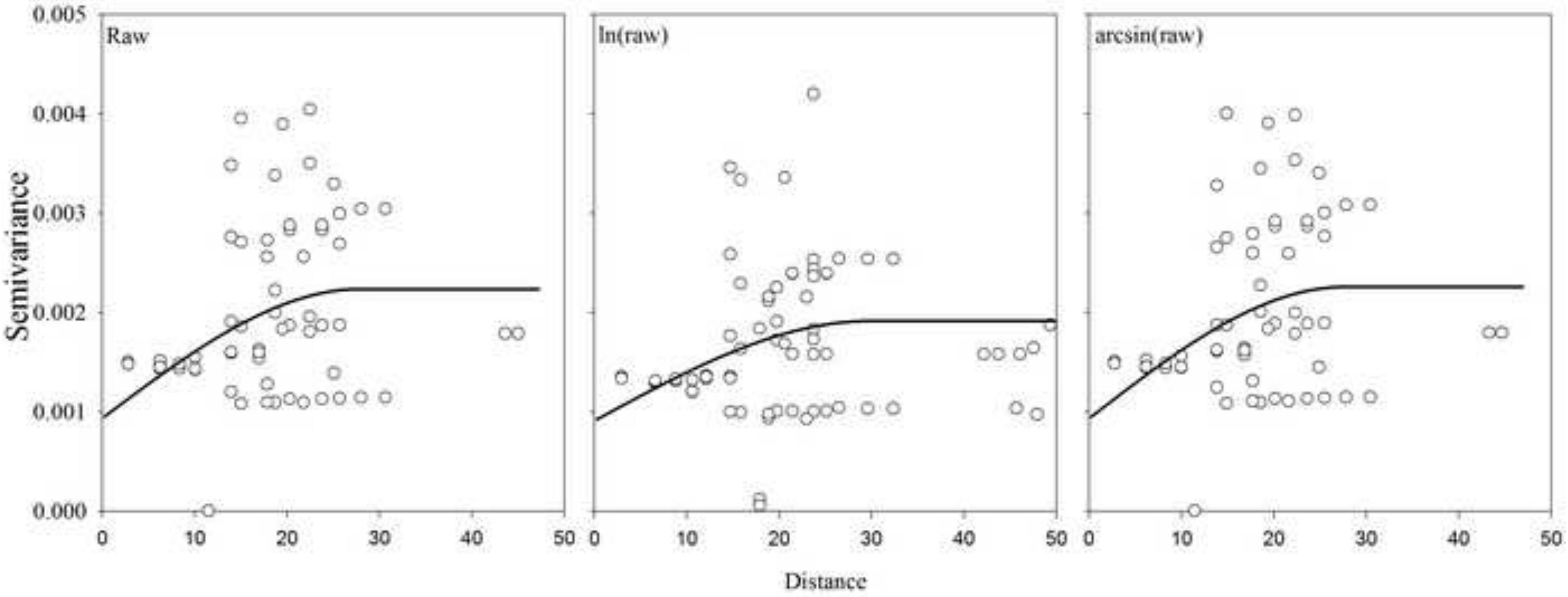
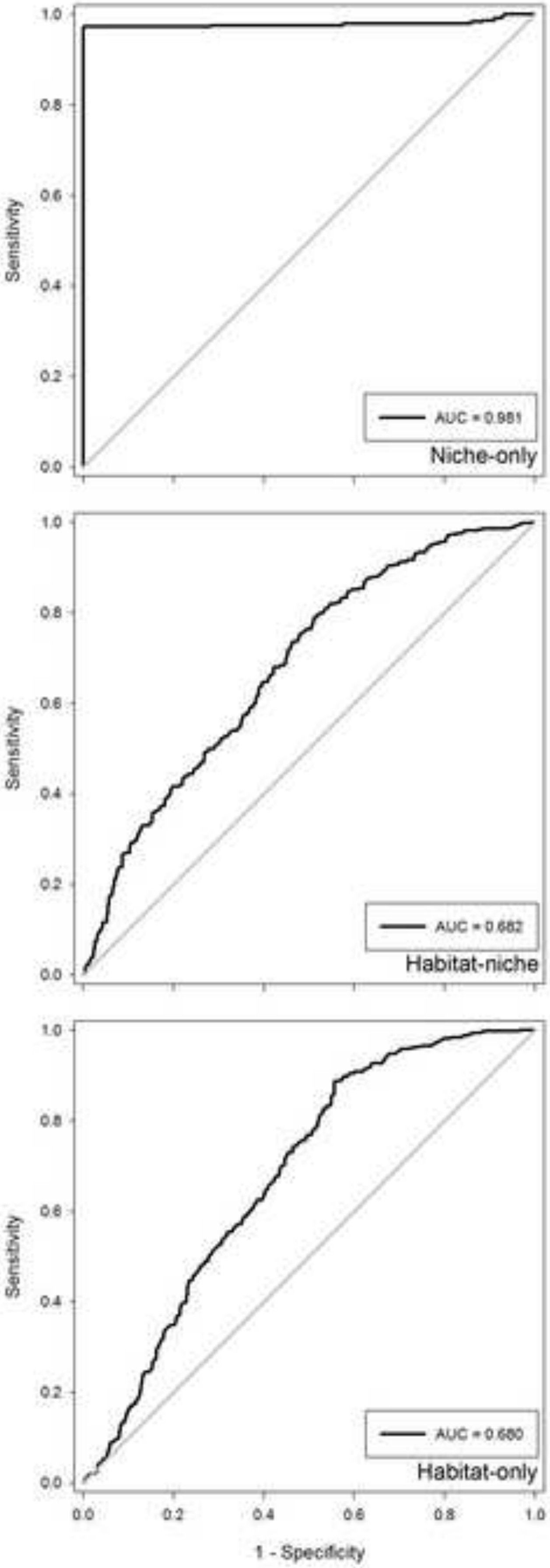


Figure4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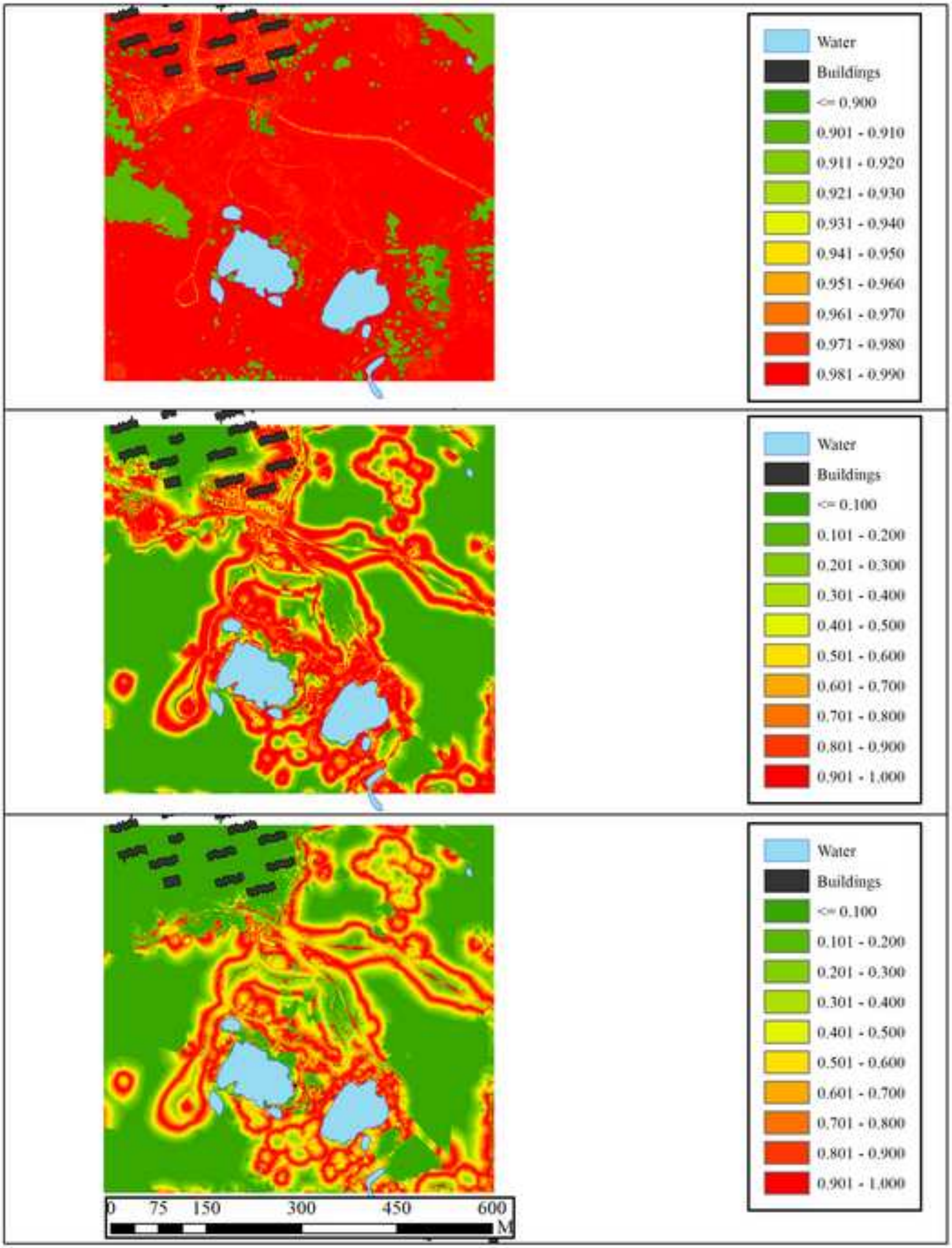
0.0
0.2
0.4
0.6
0.8
1.0
AUC = 0.981
Niche-only
AUC = 0.682
Habitat-niche
AUC = 0.680
Habitat-only
1 - Specificity

Figure5


Water
Buildings
<= 0.900
0.901 - 0.910
0.911 - 0.920
0.921 - 0.930
0.931 - 0.940
0.941 - 0.950
0.951 - 0.960
0.961 - 0.970
0.971 - 0.980
0.981 - 0.990
Water
Buildings
<= 0.100
0.101 - 0.200
0.201 - 0.300
0.301 - 0.400
0.401 - 0.500
0.501 - 0.600
0.601 - 0.700
0.701 - 0.800
0.801 - 0.900
0.901 - 1.000
Water
Buildings
<= 0.100
0.101 - 0.200
0.201 - 0.300
0.301 - 0.400
0.401 - 0.500
0.501 - 0.600
0.601 - 0.700
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Tables

Table 1. Reclassified vegetative communities on Tinker Air Force Base, central Oklahoma, during May-June 2008.

Habitat type	Description
Bare ground	Ground without vegetation (includes paved surfaces)
Bare ground/mixed vegetation	Ground with sparse vegetation
Forest	Forested areas
Herbaceous vegetation	Vegetated areas without grass or woody plants
Improved grass	Non-native grasses that are mowed routinely
Semi-improved grass	Non-native and native grasses that are mowed periodically
Shrubs and redcedar	Deciduous and coniferous shrubs
Unimproved grass	Native grasses that are not mowed

Table 2. GIS data layers used to develop partitioned Mahalanobis D^2 models for Texas horned lizards during May-June 2008 on Tinker Air Force Base, central Oklahoma.

GIS layer	Layer type	Explanation
asin_form	Niche	Arcsin-transformed value for interpolated prey biomass of target pixel
bin_bg	Habitat	Binary code for bare ground (present or not) at target pixel
bin_ig	Habitat	Binary code for improved grass (present or not) at target pixel
bin_mx	Habitat	Binary code for bare ground/mixed vegetation (present or not) at target pixel
bin_sh	Habitat	Binary code for shrubs (present or not) at target pixel
bin_ug	Habitat	Binary code for unimproved grass (present or not) at target pixel
blk_bg	Habitat	Proportion of pixels in a circular neighborhood around target pixel that are bare ground
blk_ig	Habitat	Proportion of pixels in a circular neighborhood around target pixel that are improved grass
blk_mx	Habitat	Proportion of pixels in a circular neighborhood around target pixel that are bare ground/mixed vegetation
blk_sh	Habitat	Proportion of pixels in a circular neighborhood around target pixel that are shrubs
blk_ug	Habitat	Proportion of pixels in a circular neighborhood around target pixel that are unimproved grass

dst_bg	Habitat	Distance from target cell to nearest pixel of bare ground
dst_ig	Habitat	Distance from target cell to nearest pixel of improved grass
dst_mx	Habitat	Distance from target cell to nearest pixel of bare ground/mixed vegetation
dst_sh	Habitat	Distance from target cell to nearest pixel of shrub
dst_ug	Habitat	Distance from target cell to nearest pixel of unimproved grass
slope	Habitat	Slope of target pixel
sin_asp	Habitat	Sin-transformed value for aspect of target pixel
a_ctmax	Niche	Proportion of time per target pixel that was above critical thermal maximum for Texas horned lizards
w_tpref	Niche	Proportion of time per target pixel that was within preferred temperature range of Texas horned lizards

Table 3. Eigenvectors for habitat GIS layers that consistently dominated factor loadings in those components that satisfied: ([previous eigenvalue – current eigenvalue]/current eigenvalues) ≥ 30%, taken from Texas horned lizard in Oklahoma during May-June 2008. Average = average of absolute values of eigenvectors.

Layer	3	7	12	16	17	Average
binsh	-0.428	0.527	-0.325	0.023	-0.332	0.327
binmx	-0.100	-0.233	0.289	-0.040	-0.621	0.257
dstbg	-0.281	0.123	0.273	0.524	-0.002	0.240
binug	0.184	-0.300	-0.114	0.027	-0.573	0.240
blkug	0.183	0.168	0.398	-0.436	0.005	0.238
dstug	-0.226	0.083	-0.003	-0.667	0.018	0.199
binig	0.209	0.199	-0.193	-0.091	-0.292	0.197
dstsh	0.195	0.492	0.096	0.134	-0.010	0.186
binbg	0.116	0.220	0.201	0.069	-0.289	0.179
blksh	-0.303	0.075	0.429	0.007	0.025	0.168
blkmx	0.405	0.301	0.093	0.023	-0.016	0.168

blkig	0.197	-0.015	0.308	0.164	0.016	0.140
slope_w	-0.350	-0.060	0.218	-0.003	-0.020	0.130
dstig	-0.249	-0.028	-0.271	0.036	0.000	0.117
blkbg	0.170	-0.005	-0.258	0.135	0.001	0.114
dstmx	-0.072	0.200	0.039	-0.093	-0.064	0.093
sin_asp	-0.036	-0.238	0.032	-0.016	0.008	0.066

Table 4. Candidate model logistic regression scores, *p*-values, Akaike's Information Criterion (AIC) scores, area under the receiver operator characteristic curve (AUC) scores, and important eigenvectors (see Table 2) calculated for Texas horned lizards on Tinker Air Force Base, central Oklahoma, during May-June 2008.

Model Type	Partition	χ^2	p	AIC	Δ AIC	AUC (SE)	Important eigenvectors		
Niche-only	3	1097.38	< 0.01	118.24	0.00	0.978 (0.006)	a_ctmax	w_tpref	
	2	< 0.01	1.00	1213.60	1095.36	0.631 (0.019)	asin_form		
Habitat-niche	8	78.20	< 0.01	1137.40	0.00	0.682 (0.018)	bin_mx	bin_sh	bin_ug
	4	4.20	0.04	1211.40	74.00	0.423 (0.019)	dst_sh	dst_ug	
	3	0.20	0.65	1215.40	78.00	0.406 (0.019)	bin_sh	dst_sh	
	5	0.10	0.75	1215.50	78.10	0.525 (0.020)	bin_sh	dst_bg	dst_ug
	9	< 0.01	1.00	1215.60	78.20	0.642 (0.019)	a_ctmax	w_tpref	
Habitat-only	6	80.70	< 0.01	1134.90	0.00	0.680 (0.018)	bin_mx	bin_sh	bin_ug
	2	2.90	0.09	1212.70	77.80	0.404 (0.019)	bin_mx	bin_sh	dst_sh
	3	1.60	0.21	1214.00	79.10	0.465 (0.019)	bin_sh	dst_bg	