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Ecological Niche Models for Bat Species of Greatest Conservation Need in Louisiana

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Abstract

Many mammal taxa in Louisiana are experiencing population declines or are at-risk of extinction, including the bat species *Eptesicus fuscus* (Big Brown Bat), *Myotis austroriparius* (Southeastern Myotis), and the threatened *M. septentrionalis* (Northern Long-eared Bat). Understanding species distributions is a critical component of conservation. Occurrence records for these three Chiropteran species from across the United States were used to generate ecological niche models to determine areas of suitable habitat in Louisiana as well as the United States. Suitable habitat for *E. fuscus* was found throughout the United States, and the most suitable habitat in Louisiana was in the northeastern portion of the state. *Myotis austroriparius* had highly suitable habitat throughout Louisiana and the southeastern United States. In Louisiana, *M. septentrionalis* had patchy areas of suitable habitat that included managed and preserved forests throughout the state; this patchiness was expected, as Louisiana is on the edge of the distribution of *M. septentrionalis*, which is found mainly in the northeastern U.S. The Kisatchie National Forest and Tunica Hills Management Area were areas of highly suitable habitat in Louisiana for all three species of bats and should be considered top priority for conservation.

Key words: Chiroptera, ecological niche model, *Eptesicus*, Louisiana, MaxEnt, *Myotis*

Introduction

Wildlife species worldwide face many threats (e.g., climate change, habitat degradation and loss, and other anthropogenic influences; Crooks et al. 2017; Pimm and Raven 2000; Thomas et al. 2004), and bats in particular face additional challenges such as human misperceptions (Kingston 2015; Hoffmaster et al. 2016), windmill mortalities (Johnson et al. 2004), loss of natural and artificial roosts (Voigt et al. 2015), and in North America, white-nose syndrome (Blehert et al. 2009; Frick et al. 2010). Although surrounding states have been affected by white-nose syndrome (WNS), recent bat surveys in Louisiana have found no evidence of WNS or the fungus causing the disease (*Pseudogymnoascus destructans*) based on ultraviolet illumination and genetic analyses of skin swabs (Limon et al. 2019). This suggests that Louisiana could be a vital refuge for bat species severely affected by WNS elsewhere within their distributions (Stevens et al. 2017).

Recent bat surveys in Louisiana indicate that some species are more widely distributed than previously thought. For example, *Eptesicus fuscus* was known from only twelve parishes in Louisiana until a recent survey expanded their distribution to include twelve additional parishes (Lowery 1974; Stevens et al. 2017). The same study (Stevens et al. 2017) detected new parish records (number of new records in parentheses) for *Myotis austroriparius* (16), *M. septentrionalis* (3), *Corynorhinus rafinesquii* (14), *Perimyotis subflavus* (8), and *Lasiurus seminolus* (6). A critical component to any successful conservation plan is survey and assessment of species distributions and abundances; these new records demonstrate that there is still much to learn about bat distributions in Louisiana.

The Louisiana Department of Wildlife and Fisheries recently listed several bat taxa as Species of Greatest Conservation Need (SGCN) in the state (Holcomb et al. 2015). Three of those are *Eptesicus fuscus* (Big Brown Bat), *Myotis austroriparius* (Southeastern Myotis), and the federally threatened *M. septentrionalis* (Northern Long-eared Bat). A crucial step to improve the conservation status of SGCN is habitat conservation (Holcomb et al. 2015), and ecological niche models (ENMs) can be used to predict areas that are highly suitable and, therefore, of high conservation priority (Guisan and Zimmermann 2000; Peterson 2001; Phillips et al. 2006; Elith and Leathwick 2009). Although the use of ENMs to predict bat distributions is increasing, there is still a need for more research in the United States (Razgour et al. 2016).

Our objective was to determine areas of highly suitable habitat for each of these species of bats in Louisiana using ENMs. Moreover, these models could provide valuable information for conservation strategies by revealing areas where these species may exist but have not yet been thoroughly sampled. Because *M. austroriparius* and *M. septentrionalis* are typically found in eastern North America (Jones and Manning 1989; Caceres and Barclay 2000), we predicted similar areas of suitable habitat would occur in northeastern Louisiana, whereas *E. fuscus* was predicted to be found statewide due to it cosmopolitan distribution across the United States (Kurta and Baker 1990).

Methods

Distribution records.—Geographic coordinates were recorded from positively identified captures of *E. fuscus*, *M. austroriparius*, and *M. septentrionalis* from fieldwork and previously collected museum specimens. Because these three species occur beyond Louisiana, occurrence records from museum collections also were obtained from the Global Diversity International Facility ("GBIF Occurrence - *Eptesicus fuscus*," 2019.; "GBIF Occurrence - *Myotis austroriparius*," 2019.; "GBIF Occurrence - *Myotis septentrionalis*," 2019) to create distribution models. For each species, all records within the continental United States were concatenated and duplicate coordinates were removed (i.e., if multiple occurrences were from the same location, only one occurrence was retained). To reduce spatial autocorrelation, the spThin package in R (Aiello-Lammens et al. 2015) was used to exclude occurrences that were within 10 km of one another while maintaining the maximum number of occurrences. This distance of 10 km was chosen based on environmental heterogeneity and the balance between reducing spatial autocorrelation and retaining too few occurrences to create strong predictive models.

Environmental layers.—Because bat species in Louisiana primarily are insectivores that roost in trees, several climate and soil data variables were used as environmental layers. Precipitation and temperature directly affect vegetation and forest type, each of which affects the availability of roosts (Sherwin et al. 2013; Vasko et al. 2020) and prey (Vician et al. 2018). Additionally, soil characteristics such as pH, nutrient availability, and drainage influence both forest and insect community composition (Vician et al. 2018; Tyler 2020).

Bioclimatic data were obtained from CliMond (Kriticos et al. 2012), which provides WorldClim (Hijmans et al. 2005) temperature and precipitation variables along with solar radiation and soil moisture data. Soil data (e.g., maximum depth of soil, pH, and carbon content) were obtained from a North American Soil Map (Liu et al. 2013). Resolutions for the environmental layers were set to 10 arcmin, the highest resolution available for solar radiation and soil moisture data. Extents and number of cells were standardized for each species using R packages raster (Hijmans 2019), rgdal (Bivand et al. 2020), and RStoolbox (Leutner et al. 2019) as required by MaxEnt (Phillips et al. 2006).

To reduce multicolinearity of climate and soil data, principle components analyses (PCA) were performed for each species. As background extent can affect response curves (Merow et al. 2013), 250 km buffered domains were determined around all occurrences records for each species. Buffer size was chosen based on dispersal distances and home range sizes. Each layer was then cropped for a given species. A correlation matrix was constructed for the cropped environmental layers using RStoolbox (Leutner et al. 2019) and then principle components (PCs) that captured significant amounts of the variation based on the broken-stick model were determined using the evplot R function (Borcard et al. 2011). In the broken-stick model, observed percentages of variance for individual PCs are compared to those expected by random chance, and components that explain more variance than expected are retained (MacArthur 1957; Frontier 1976; Jackson 1993). Retained PCs for each species were used to build ecological niche models in MaxEnt (Phillips et al. 2006, 2020). Environmental variables contributing the most to each PC were identified by extracting correlations between components and variables. Environmental variables with absolute correlations of 0.2 or greater were identified as those making an important contribution to a given PC. The correlation cutoff, while arbitrary, emphasized at least one positive and one negative environmental correlation on each PC axis.

Ecological niche models.—Ecological niche models were generated in MaxEnt to determine areas of high habitat suitability. Using the R kuenm package (Cobos et al. 2019), large numbers of candidate models were created using combinations of environmental PCs, regularization multipliers (parameters that penalize models with greater number of environmental variables to reduce over-fitting; Merow et al. 2013; Morales et al. 2017) and feature classes (mathematical transformations that allow for modeling complexity among the covariates such as linear or quadratic relationships (Merow et al. 2013; Morales et al. 2017)). From the occurrence records retained, 75% were used for training and 25% were reserved for testing accuracy of ENMs. The number of random background points was determined by domain size of each species: *E. fuscus* (35,378), *M. austroriparius* (13,484), and *M. septentrionalis* (21,301). The default logistic output which can be interpreted as the probability of presence (Merow et al. 2013) was selected.

All models were evaluated, and the best models were selected based on: (1) statistical significance using partial receiver operating characteristics (ROCs), (2) prediction ability by determining how accurately test data is predicted (omission rates), and (3) model fit and complexity in which overfit models are penalized (AICc), in that order (Cobos et al. 2019). More specifically, statistical significance of partial ROCs was determined by bootstrap resampling half of the data used for testing, and probabilities were calculated by counting proportion of replicates for which AUC is less than or equal to 1.0 (Peterson et al. 2008). Omission rates measured the performance of the model and indicated the proportion of known localities that were not predicted to be highly suitable habitat (Phillips et al. 2006) preferably below 5% (Anderson et al. 2003). Models that met both of the previous standards were then evaluated to determine which had a Δ AICc less than or equal to 2 (Warren and Seifert 2011). This procedure was implemented in the kuenm package (Cobos et al. 2019).

Final models were replicated ten times. The contribution of each PC variable to the final ENM based on permutation importance was determined. Permutation importance was measured by randomly permuting the values of a variable and recalculating the training AUC (Phillips et al. 2006). Larger decreases (normalized to be percentages) in AUCs indicate a greater importance of that variable to the ENM. Final models were used to predict areas of high habitat suitability not only in Louisiana, but throughout the United States.

Results

Distribution records.—After removing duplicates, 1,666 records were retained for *E. fuscus* from the initial dataset of 2,949 individuals, and 1,239 records were kept for training and 427 for testing. For *M. aus-*

troriparius, 144 records were retained after removing duplicates and thinning from the original 277 in the dataset. There were 108 *M. austroriparius* records in the training data set and 36 in the testing data set. For *M. septentrionalis*, our initial records included 265 bats that were thinned to 148 individuals with 108 records for training and 40 records for testing the model.

Environmental layers.—For *E. fuscus*, five principal components (hereafter referred to as PC 1–5) were significant based on the broken-stick model and together captured the majority of variation of climatic and soil variables among sites with presence (73.1%, Table 1). Principle component 1 (30.4%) characterized sites of greater daily temperature fluctuations, high amounts of radiation, and low amounts of soil moisture. For PC2 (18.5%), larger positive values were correlated with less extreme cold temperature anomalies and higher minimum temperatures, whereas negative values reflected more extreme ranges in temperature as well as greater variability in temperature and radiation. Larger values on PC3 (10.2%) were related to environmental characteristics during wetter times of the year such as higher temperature, greater radiation, and more precipitation. Negative values along this axis were correlated with moisture variability and solar radiation during dry periods. Principle component 4 (7.7%) was a soil gradient that ran from silty soils at higher values to sandy soils and soils with higher nutrient-fixing capacities at lower values. Principle component 5 (6.4%) also was a soil gradient with sandy and compacted soils found at higher values and soils with greater organic matter found at lower values.

For *M. austroriparius*, five principle components also were significant, which accounted for 76.8% of the variation among sites of presence regarding environmental variables measured (Table 1). The first PC (33.8%) axis was a gradient where positive values represented sites with large variations in precipitation throughout the year and negative values represented sites with high amounts of soil moisture and precipitation. The second principle component (22.9%) represented variation in temperature and radiation. Specifically, milder cold seasons, less extreme cold temperature anomalies, warmer mean temperatures, and higher amounts of solar radiation characterized sites with more positive values on PC2. Conversely, negative values were correlated with greater temperature and radiation variability as well as more extreme temperature ranges. Principle component 3 (7.7%) was a soil gradient with clay soils, soils with higher nutrient-fixing capacities, and higher organic content at higher positive values and sandy and compacted soils at more negative values. On PC4 (7.0%), more compacted soils, greater solar radiation during the driest portion of the year, and higher soil moisture variability were found at higher values of the axis. Toward more negative values were sites with higher temperature during the wettest season and soils with more organic content. The fifth principle component (5.4%) also was a soil gradient with deeper soils related to more positive values and higher percentage of gravel related to more negative values.

Six principle components characterized environmental conditions within the distribution of *M. septentrionalis* and comprised 81.7% of this variation (Table 1). The first principle component (31.7%) consisted of a gradient from high amounts of soil moisture and precipitation to high amounts of solar radiation and greater precipitation variability. Positive values on PC2 (25.3%) were related to sites with higher mean temperatures in winter, overall warmer temperatures, and milder cold temperature anomalies. Negative values on this axis were related to sites with larger ranges of extreme temperature conditions and more variability in temperature and radiation throughout the year. Principle component 3 (8.0%) was a soil gradient with sites containing higher amounts of silt and organic matter at higher positive values and sites with higher amounts of compacted and sandy soils at more negative values. The fourth PC (6.7%) was another soil gradient with positive values representing sites with soils having higher organic content and higher nutrient-fixing capacity. Principle component 5 (5.2%) was yet another soil gradient with soils containing high amounts of clay and higher nutrient-fixing capacity found at higher positive values and more gravely soils at more negative values. The last PC (4.7%) included in analyses was a mixture of climate and soil variables with deeper soils and higher amounts of temperature and radiation during the wettest quarter found at higher positive values and more gravely soils at more negative values.

Ecological niche models.—For *E. fuscus*, there was only one candidate model that was statistically significant and had an omission rate below 5% and a

Table 1. Contributions of environmental variables to principle components used to construct ecological niche models for *Eptesicus fuscus*, *Myotis austroriparius*, and *M. septentrionalis*. Strongest correlations are in bold. T = temperature; Q = quarter; MI = moisture index; Rad = radiation; Ann = annual; Wk = week; Rg = range; Top = topsoil; Sub = subsoil.

Environmental variable	*E. fuscus*					*M. austroriparius*					*M. septentrionalis*					
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC6
Ann mean T	0.12	**0.25**	0.11	0.08	0.01	0.01	**0.27**	0.10	0.02	0.04	0.01	**0.26**	0.06	0.02	0.00	0.08
Mean diurnal T rg	0.20	−0.04	−0.02	−0.02	0.02	0.18	0.02	−0.11	0.05	−0.04	−0.19	0.10	−0.09	0.03	−0.04	−0.08
Isothermality	0.18	0.17	−0.10	−0.07	−0.02	0.08	**0.23**	−0.09	−0.06	−0.12	−0.06	**0.23**	−0.10	0.07	−0.05	−0.09
T seasonality	−0.12	**−0.24**	0.14	0.03	0.01	0.01	**−0.27**	0.02	0.08	0.12	−0.04	**−0.25**	0.06	−0.05	0.04	0.10
Max T - warm wk	0.17	0.14	0.15	0.14	0.01	0.10	0.19	0.12	0.13	0.17	−0.08	**0.22**	0.10	−0.01	0.01	0.14
Min T - cold wk	0.12	**0.27**	−0.02	0.06	−0.01	−0.03	**0.27**	0.06	−0.02	−0.02	0.04	**0.26**	0.03	0.02	−0.02	0.02
T ann rg	−0.04	**−0.27**	0.13	0.02	0.02	0.10	**−0.23**	−0.01	0.09	0.11	−0.11	**−0.22**	0.03	−0.03	0.04	0.07
Mean T - wet Q	0.05	0.09	**0.36**	0.01	0.00	0.11	0.05	0.02	**−0.26**	0.15	−0.08	0.08	0.13	0.08	−0.10	0.31
Mean T - dry Q	0.12	**0.22**	−0.17	0.05	0.01	−0.07	**0.24**	0.06	0.16	−0.05	0.07	**0.25**	−0.02	0.02	0.06	−0.07
Mean T - warm Q	0.11	0.20	**0.20**	0.13	0.02	0.03	**0.22**	0.15	0.09	0.15	−0.01	**0.24**	0.12	−0.00	0.02	0.16
Mean T - cold Q	0.14	**0.26**	0.02	0.05	0.00	0.00	**0.28**	0.05	−0.01	−0.01	0.02	**0.27**	0.02	0.03	−0.01	0.02
Ann precip	−0.19	0.19	−0.03	0.06	−0.00	**−0.23**	0.05	0.04	0.07	0.03	**0.23**	0.08	0.04	−0.04	0.03	0.03
Precip - wet wk	−0.13	**0.20**	−0.04	−0.02	−0.09	−0.19	0.10	0.05	0.01	0.12	0.19	0.10	0.08	0.00	0.02	0.14
Precip - dry wk	−0.18	0.15	0.02	0.09	0.10	**−0.22**	0.05	0.01	0.09	−0.07	**0.22**	0.08	−0.03	−0.04	0.04	−0.09
Precip seasonality	0.15	−0.01	0.03	−0.13	−0.15	**0.21**	0.01	−0.02	−0.10	0.05	**−0.21**	−0.03	0.03	0.07	−0.04	0.11
Precip - wettest Q	−0.15	0.19	−0.05	−0.01	−0.09	**−0.21**	0.07	0.04	−0.00	0.12	**0.21**	0.08	0.08	−0.01	0.02	0.14
Precip - driest Q	−0.18	0.16	0.01	0.09	0.09	**−0.22**	0.06	0.02	0.09	−0.05	**0.22**	0.09	−0.02	−0.04	0.03	−0.07
Precip - warm Q	−0.16	0.14	**0.22**	−0.02	0.01	−0.20	0.04	0.00	−0.14	0.14	**0.21**	0.03	0.08	0.02	−0.04	0.20
Precip - cold Q	−0.13	0.18	**−0.21**	0.04	−0.01	**−0.21**	0.09	0.02	0.12	−0.04	**0.21**	0.11	−0.03	−0.03	0.05	−0.07
Ann mean rad	0.20	0.16	0.06	0.01	0.02	0.14	**0.20**	0.06	0.08	0.07	−0.09	**0.24**	−0.02	0.07	0.05	−0.01
High weekly rad	0.20	−0.04	−0.13	0.03	−0.03	0.17	0.00	0.07	0.15	0.17	**−0.20**	0.09	0.01	0.04	0.10	0.00
Low weekly rad	0.16	**0.21**	0.13	−0.02	0.03	0.10	**0.25**	0.04	0.01	0.00	−0.05	**0.26**	−0.02	0.08	0.02	−0.01
Rad seasonality	−0.11	**−0.23**	−0.17	−0.00	−0.04	−0.04	**−0.27**	−0.02	0.03	0.05	0.00	**−0.26**	0.02	−0.05	0.02	0.01
Rad - wet Q	0.04	−0.04	**0.37**	0.03	0.01	0.13	−0.12	−0.01	−0.17	0.17	−0.15	−0.01	0.13	0.00	−0.11	0.22

Table 1. (cont.)

Environmental variable	*E. fuscus*					*M. austroriparius*					*M. septentrionalis*					
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC6
Rad - dry Q	0.12	0.13	**−0.25**	−0.05	−0.00	−0.03	**0.20**	0.07	**0.22**	−0.08	0.05	0.18	−0.10	0.06	0.15	−0.18
Rad - warm Q	0.20	−0.04	−0.09	0.08	−0.02	0.18	−0.00	0.10	0.17	0.15	−0.20	0.10	0.04	0.01	0.11	0.02
Rad - cold Q	0.15	**0.21**	0.15	−0.04	0.03	0.10	**0.25**	0.04	−0.01	−0.01	−0.04	**0.25**	−0.03	0.09	0.03	−0.02
Ann mean MI	−0.23	0.10	−0.03	0.02	0.02	**−0.23**	−0.02	0.03	0.02	0.01	**0.24**	−0.03	0.02	−0.03	0.03	0.00
High weekly MI	−0.20	0.14	−0.13	−0.00	−0.03	**−0.23**	0.00	0.03	0.06	0.02	**0.24**	−0.00	0.02	−0.05	0.04	−0.01
Low weekly MI	−0.23	0.04	0.12	0.01	0.06	**−0.22**	−0.05	0.00	−0.08	−0.00	**0.22**	−0.08	0.03	−0.01	−0.01	0.06
MI seasonality	0.13	0.09	**−0.28**	−0.06	−0.09	0.03	0.11	0.03	**0.21**	−0.10	−0.04	0.15	−0.05	−0.04	0.09	−0.18
Mean MI - wet Q	−0.21	0.13	−0.13	0.00	−0.02	**−0.23**	0.00	0.03	0.06	0.00	**0.24**	−0.00	0.01	−0.04	0.04	−0.02
Mean MI - dry Q	−0.23	0.05	0.11	0.01	0.06	**−0.22**	−0.04	0.01	−0.08	0.02	**0.23**	−0.07	0.02	−0.01	−0.01	0.06
Mean MI - warm Q	−0.21	0.09	0.15	−0.06	0.03	**−0.21**	0.01	−0.02	−0.16	0.06	**0.22**	−0.06	0.02	0.03	−0.02	0.10
Mean MI - cold Q	−0.20	0.11	−0.16	0.04	0.02	**−0.23**	−0.01	0.03	0.09	−0.02	**0.24**	0.01	0.00	−0.05	0.04	−0.04
Dominant Soil %	−0.06	−0.02	0.07	−0.04	0.06	0.01	−0.05	−0.04	−0.04	−0.08	0.02	−0.04	−0.06	−0.01	0.14	0.06
Max soil depth	−0.05	0.07	0.10	0.17	0.02	−0.07	0.03	0.02	0.07	**0.40**	0.03	0.10	0.09	−0.01	−0.06	0.32
Sub cation	0.04	0.01	0.08	**−0.29**	−0.15	0.10	−0.02	**0.27**	−0.07	−0.07	−0.03	−0.08	0.08	**0.21**	0.42	−0.09
Sub clay fraction	0.00	0.02	0.06	**0.26**	−0.17	−0.03	−0.05	**0.27**	0.17	−0.01	−0.02	0.09	**0.25**	−0.13	0.19	−0.06
Sub gravel content	0.01	−0.03	**−0.23**	0.01	0.10	−0.01	−0.03	−0.11	−0.03	**−0.45**	0.02	−0.00	−0.13	−0.07	−0.27	−0.38
Sub organic carbon	−0.04	0.01	0.03	−0.14	**−0.33**	−0.03	0.03	**0.26**	**−0.31**	0.03	0.02	−0.03	**0.22**	**0.39**	−0.14	−0.11
Sub pH	0.09	−0.13	0.00	**0.24**	0.10	0.15	−0.05	−0.00	0.13	0.09	−0.17	−0.00	0.00	−0.20	0.05	0.04
Sub bulk density	−0.03	−0.07	−0.03	**0.22**	**0.30**	−0.03	−0.04	**−0.21**	**0.27**	0.12	0.01	0.02	**−0.24**	**−0.31**	0.17	0.13
Sub sand fraction	−0.02	−0.02	−0.01	**−0.21**	**0.38**	0.01	0.12	**−0.36**	−0.16	0.09	0.03	−0.06	**−0.39**	0.18	−0.06	0.16
Sub silt fraction	−0.02	−0.06	−0.01	**0.35**	−0.19	−0.01	−0.16	0.19	**0.20**	−0.01	−0.03	0.01	**0.30**	**−0.30**	−0.05	−0.12
Top cation	0.01	−0.00	0.09	**−0.34**	−0.13	0.11	0.00	**0.28**	−0.11	−0.13	0.00	−0.10	0.03	**0.23**	0.42	−0.09
Top clay fraction	0.03	−0.00	0.11	**−0.20**	−0.08	0.08	0.00	**0.24**	0.06	**−0.25**	−0.01	−0.06	0.03	0.05	0.49	−0.13
Top gravel content	0.04	0.00	−0.20	−0.06	0.08	0.01	0.00	−0.09	−0.03	**−0.47**	0.02	0.02	−0.14	−0.05	−0.25	−0.39
Top organic carbon	−0.05	0.02	0.03	−0.16	**−0.34**	−0.03	0.02	**0.26**	**−0.32**	0.03	0.03	−0.04	**0.22**	**0.40**	−0.13	−0.10
Top pH	0.18	−0.11	−0.00	0.15	0.06	0.20	−0.01	0.01	0.10	−0.01	−0.19	0.03	−0.01	−0.18	0.06	0.01

Table 1. (cont.)

Environmental variable	*E. fuscus*					*M. austroriparius*					*M. septentrionalis*					
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC6
Top bulk density	0.09	0.02	0.02	0.07	**0.34**	0.04	0.05	**−0.29**	**0.30**	−0.03	−0.02	0.08	**−0.28**	**−0.28**	0.15	0.10
Top sand fraction	0.01	0.04	0.01	**−0.29**	**0.38**	0.01	0.16	**−0.34**	−0.12	0.07	0.04	−0.01	**−0.41**	0.17	−0.02	0.18
Top silt fraction	−0.02	−0.06	−0.02	**0.33**	**−0.22**	−0.01	−0.18	0.20	0.19	−0.05	−0.02	−0.00	**0.31**	**−0.33**	−0.04	−0.13

delta AICc < 2 (Table 2). The final ENM had a partial AUC of 0.731, which is considered acceptable (Hosmer and Lemeshow 2000). The principle component with the highest permutation importance was PC2 at 45.2% (Table 3). Principle component 3 had the second highest permutation importance (27.6%) followed by PC1 (15.3%), PC4 (11.1%), and PC5 (0.8%). For *E. fuscus*, the most important gradient (PC2) is related to magnitude and variability of temperature and radiation, with highest probability of occurrence in areas with high magnitude and low variability. The final ENM predicted highly suitable habitat throughout most of the southwestern, central, and northeastern United States (Fig 1A) including the northeastern portion of Louisiana (Fig 1B).

There were two models that were statistically significant and had delta AICc < 2 for *M. austroriparius*, but none had omission rates < 5% (Table 2). Of those two models, the final model had the lowest omission rate at 5.7%. This ENM had a partial AUC of 0.887 and the component with the highest permutation importance was PC1 at 51.8% (Table 3). Principle component 2 (26.8%) had the second highest permutation importance. These were followed by PC4 (13.9%), PC5 (5.9%), and PC3 (1.5%). The most important environmental gradient for *M. austroriparius* was PC1, which was related to magnitude and variability of precipitation and soil moisture with the highest probabilities of occurrence in areas with lower precipitation and soil moisture and higher amounts of precipitation variability. The final ENM for *M. austroriparius* predicted areas of high-suitability habitat in the southeastern portion of the United States (Fig. 2A) and throughout most of Louisiana (Fig. 2B).

For *M. septentrionalis*, two candidate models were statistically significant with omission rates < 5% and delta AICc < 2 (Table 2). Of those models, the model with the lowest delta AICc was selected as the final model. The final model had a partial AUC of 0.836 and PC2 had the highest permutation importance of 41.5% (Table 3). PC1 (24.9%) had the next highest permutation importance followed by PC5 (14.8%), PC3 (7.4%), PC6 (6.6%), and PC4 (4.8%). The most important gradient (PC2) is related to magnitude and variability of temperature and radiation with highest probability of occurrence in areas with high magnitude and low variability. The final ENM predicted areas of

Table 2. MaxEnt model results for *Eptesicus fuscus*, *Myotis austroriparius*, and *M. septentrionalis*.

Species	Model	Partial ROC	Omission Rate	Delta AICc	AUC
E. fuscus	M_3_F_qpt	< 0.001	0.049	0.000	0.731
M. austroriparius	M_4_F_h	< 0.001	0.057	0.000	0.887
M. septentrionalis	M_5_F_lph	< 0.001	0.050	0.000	0.836

Table 3. Permutation importance for principle components (PC) for *Eptesicus fuscus*, *Myotis austroriparius*, and *M. septentrionalis*.

Species	PC1	PC2	PC3	PC4	PC5	PC6
E. fuscus	15.3	45.2	27.6	11.1	0.8	NA
M. austroriparius	51.8	26.8	1.5	13.9	5.9	NA
M. septentrionalis	24.9	41.5	7.4	4.8	14.8	6.6

high habitat suitability in the Northeastern extending through the central United States (Fig. 3A) with patches of suitable habitat in Louisiana (Fig. 3B).

Predicted areas of highly suitable habitat.—For *E. fuscus*, highly suitable habitat was found throughout the United States including the Southwest and the Northeast with patchier areas in the central United States. The most northern part of the United States (Montana, Wyoming, North and South Dakota, and Minnesota) appeared to be less suitable, as well as areas along the coast of the Gulf of Mexico and southern coast of the Atlantic Ocean (Fig. 1A). The results for Louisiana indicated the best habitat suitability to be in the northeastern portion of the state from Claiborne and Webster parishes south into Sabine and Natchitoches and as far east as Caldwell Parish (Fig. 1B). The farther east and south, the less suitable the habitat was for *E. fuscus*, especially closer to the coast.

In the United States, highly suitable habitat for *M. austroriparius* was predicted in the southeastern United States throughout Alabama, Louisiana, and Missouri with large areas in Arkansas, Florida, and Georgia (Fig. 2A). Patchy areas of suitable habitat were predicted in parts of Indiana, Illinois, Kentucky, Missouri, South Carolina, and Tennessee (Fig. 2B). Of the three species in this study, *M. austroriparius* had the greatest amount of suitable habitat in Louisiana, covering most of the state as far north as Union and Moorehouse parishes to the coast. Highest suitability ran west to east through the center of the state with areas in southern and northwestern Louisiana being less suitable.

The ENM for *M. septentrionalis* predicted areas of suitable habitat in the northeastern United States with patchy areas of habitat stretching west into Alabama, Arkansas, Georgia, Iowa, Louisiana, Missouri, Nebraska, and Oklahoma (Fig. 3A). In contrast to the more widespread suitable habitat in Louisiana for *M. austroriparius*, the *M. septentrionalis* ENM revealed patchy, yet connected, areas of suitable habitat (Fig. 3B). One such area included Beauregard, Allen, Evangeline, and St. Landy parishes that connected to an area of suitable habitat in Sabine and Natchitoches parishes, which together correspond to the Kisatchie National Forest. Another area of suitable habitat was identified in the north-central portion of the state in Pointe Coupee, West Feliciana, East Feliciana, St. Helena, East Baton Rouge, Tangipahoa, and St. Tammany parishes. This area includes several managed and preserved forests such as Tunica Hills Wildlife Management Area.

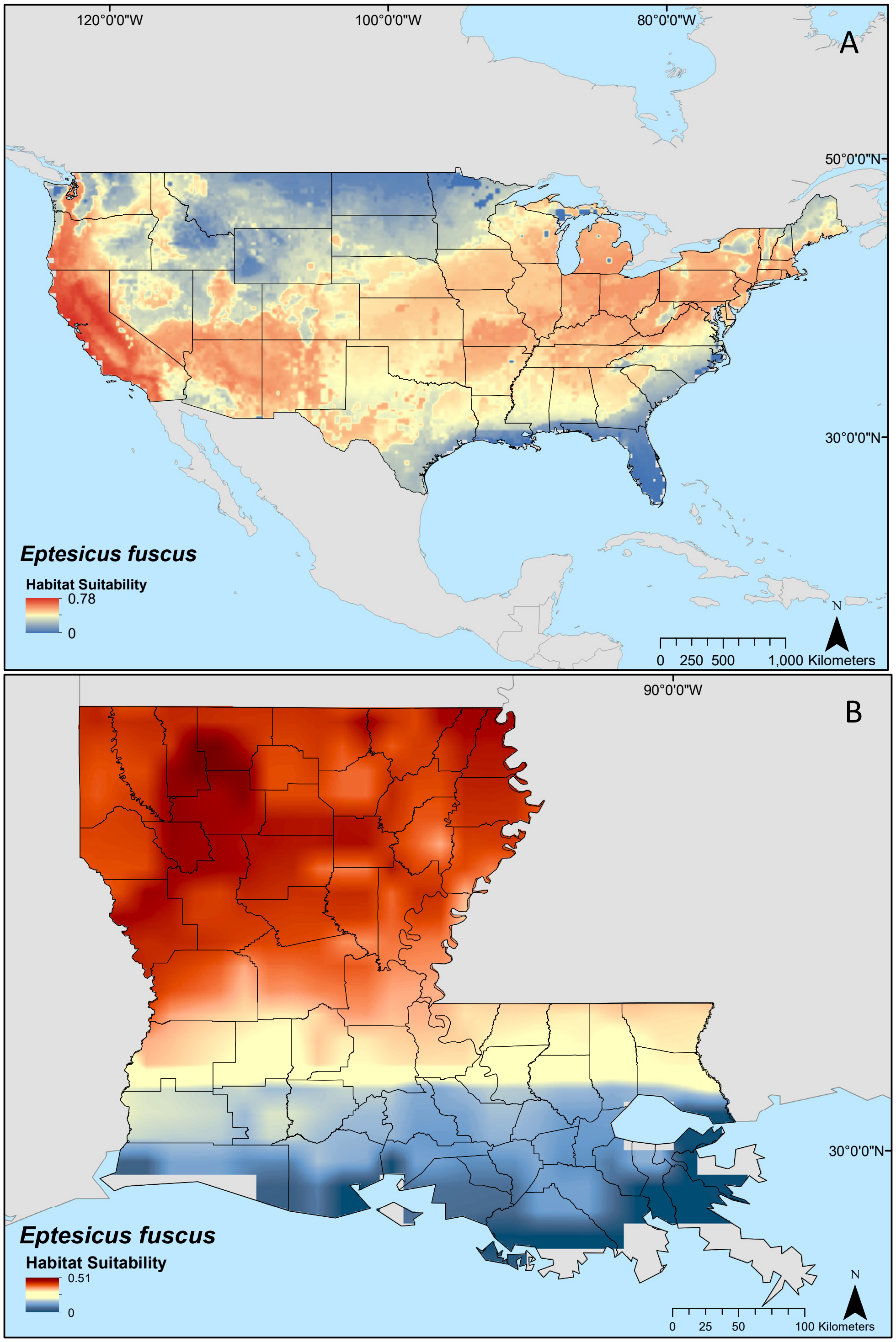

Figure 1. Ecological niche models for *Eptesicus fuscus* in (A) the United States and (B) Louisiana. Warmer colors indicate areas of higher habitat suitability and cooler colors indicate areas of lower habitat suitability. Gray indicates areas of no data. Please note that scales differ.

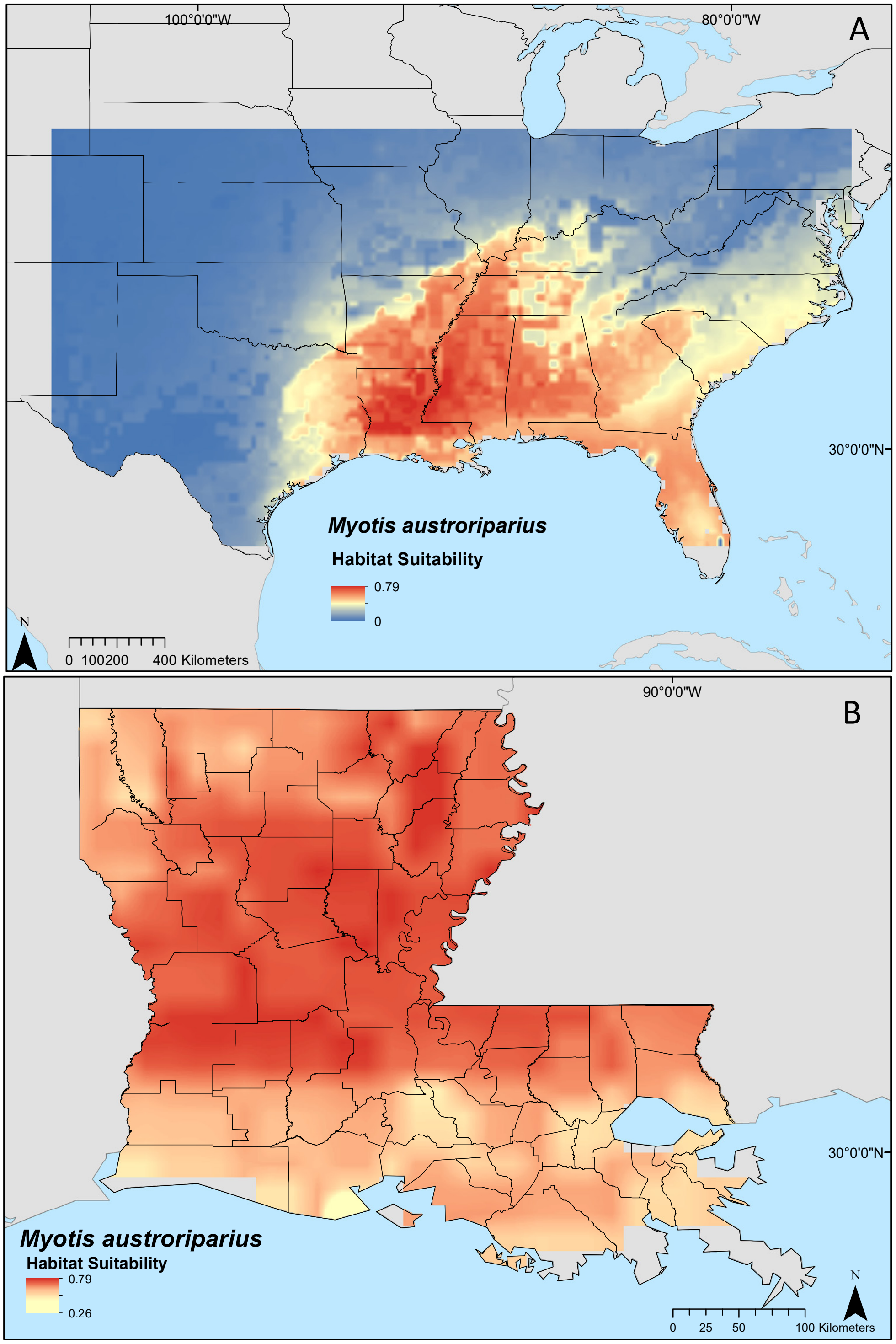

Figure 2. Ecological niche model for *Myotis austroriparius* in (A) the United States and (B) Louisiana. Warmer colors indicate areas of higher habitat suitability and cooler colors indicate areas of lower habitat suitability. Gray indicates areas of no data. Please note that scales differ.

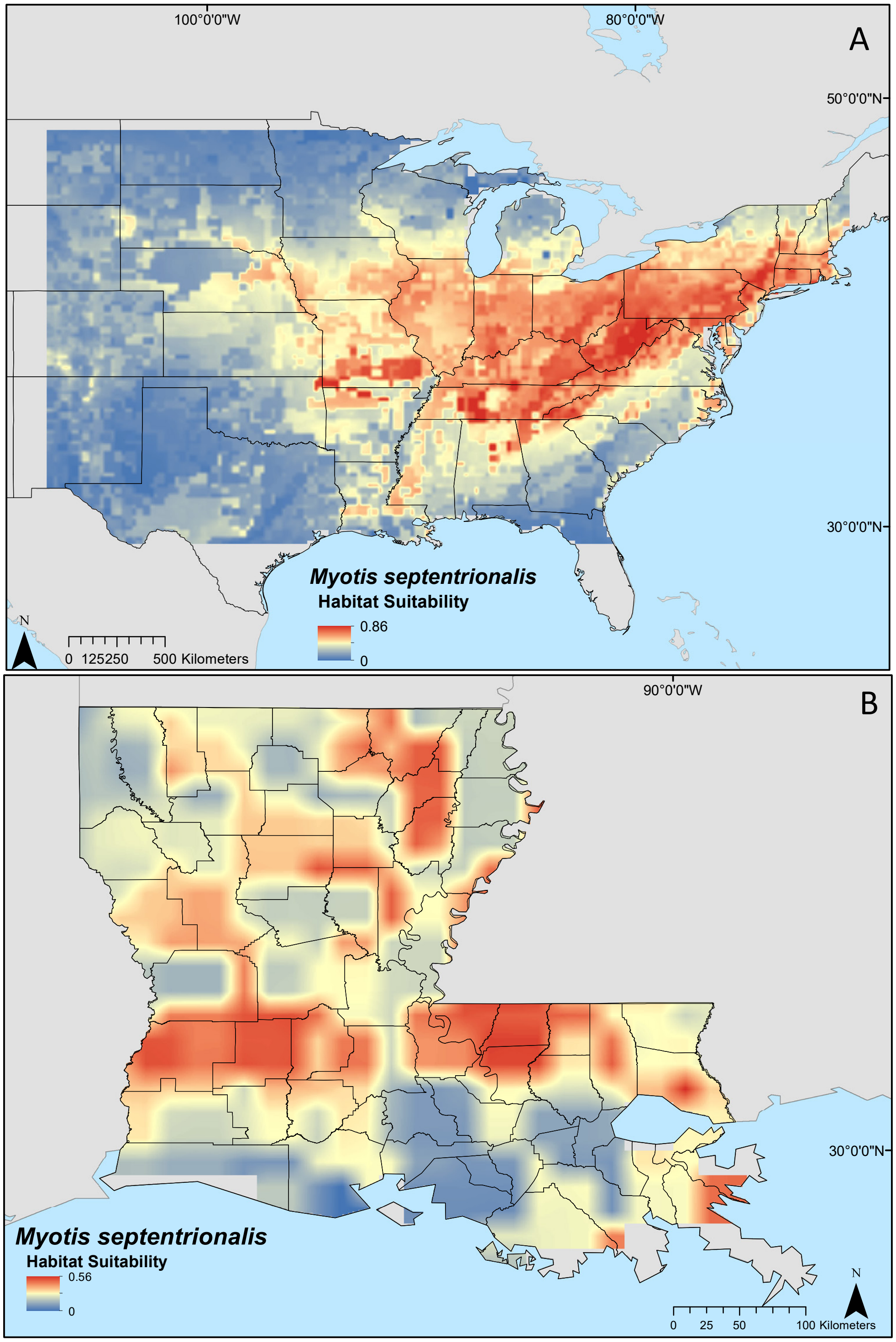

Figure 3. Ecological niche model *Myotis septentrionalis* in (A) the United States and (B) Louisiana. Warmer colors indicate areas of higher habitat suitability and cooler colors indicate areas of lower habitat suitability. Gray indicates areas of no data. Please note that scales differ.

DISCUSSION

In response to numerous threats to plants and wildlife, Louisiana Department of Wildlife and Fisheries outlined its Wildlife Action Plan (WAP) to identify key areas of research that would support monitoring and conservation of many at-risk species in Louisiana (Holcomb et al. 2015). The project discussed herein addressed several research needs described in the WAP, including identification of areas of suitable habitat for bats in Louisiana such as *E. fuscus*, *M. austroriparius*, and the federally-listed threatened species *M. septentrionalis*. Using occurrences across the continental United States, ecological niche models were generated to determine areas of highly suitable habitat for each of these species within the United States and Louisiana.

Hoffman and Chauhan (2020) recently published ENMs for *E. fuscus* and *M. septentrionalis* in Louisiana. Although the Hoffman and Chauhan (2020) models were similar to those presented herein, there were several differences. For example, this study identified suitable habitat in northeastern Louisiana in Franklin, Richland, and Moorehouse parishes for *M. septentrionalis*, but did not find similarly suitable habitat for *E. fuscus* in the north-central portion of the state. These disparities could be due to differences in methodologies, as the previous study included land cover from 1992–1993 Advanced Very High-Resolution Radiometer data, whereas the model herein used 2014 NACP soil data. Although bats may not respond directly to soil composition itself, they do respond to forest type, vegetation, and other factors that are directly affected by soil conditions. Additionally, principle components were used in this study to reduce multicollinearity for the 19 Bioclim variables and ClimMond radiation and soil moisture variables. Moreover, this study included occurrence data from across the United States and environmental data throughout the domain of each species. Regional and local factors both affect where species can exist, therefore using occurrence data from larger spatial scale provides valuable insights into understanding species ecology. Additionally, determining suitable habitat throughout the domain of a species helps guide conservation decisions when using a broader perspective.

Despite these methodological differences, the ENMs in this study were quite similar to those produced in the earlier study (Hoffman and Chauhan 2020). Indeed, ENMs of Hoffman and Chauhan (2020) and those presented here are based on complementary data sets and analyses. As a result, they provide complementary predictions of distributions of these bats in the state. Areas of agreement likely provide quite robust predictions of probability of occurrence. Where they disagree point to areas of need for ground-truthing and additional efforts to characterize presence and absence.

Studies based on occurrence data depend on biological surveys and therefore are intrinsically limited by where these surveys took place. As more fieldwork is completed, more occurrence data will be available to increase the robustness and accuracy of future distribution models. Consequently, research projects such as this one can direct field biologists as to where to focus future efforts in areas that have not been as thoroughly sampled. Thus, fieldwork and modeling can work in tandem to increase our knowledge of species of interest. Moreover, ENM research also depends on available environmental data. More detailed and precise environmental layers, such as climate variables and soil data, increase the accuracy and precision of ENMs. For example, the coastline for Louisiana for our ENMs was limited by the resolution of the radiation and soil moisture data and was not as detailed as the other environmental data. Regardless, we conclude that including radiation and soil moisture data improved our ENMs.

In Louisiana specifically, there is a large amount of suitable habitat throughout the state for *M. austroriparius*, whereas highly suitable habitat for *E. fuscus* and *M. septentrionalis* is more patchy in distribution. The Kisatchie National Forest (Calcasieue–Vernon Unit, northern Catahoula, Kisatchie, and Winn districts) appears to provide suitable habitat for both species, and other highly suitable areas for *M. septentrionalis* include the Tunica Hills Wildlife Management Area. These areas should be given top conservation priority not only for *M. septentrionalis*, but for other bat species as well. Louisiana may provide bats with a vital refuge from white-nose syndrome, as neither the disease nor the fungus have thus far been detected in the state (Limon et al. 2019). Identifying areas of high probability of occurrence aids implementation of programs to protect at-risk species from extinction. This research contributes to the knowledge of bat distributions in Louisiana as well as across the United States. Moreover, these models provide valuable information for conservation strategies by revealing areas where the federally threatened species *M. septentrionalis* may occur, based on habitat suitability, but that have not yet been thoroughly sampled.

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