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One model to rule them all: identifying priority bat habitats from multi-species habitat suitability models

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Abstract

Bats are important components of global ecosystems, providing essential ecosystem services with substantial economic benefit. Yet North American bat populations have been negatively affected by numerous factors (e.g., disease, habitat loss, wind energy development) with compounding effects. Bats use habitats at a variety of scales, from small, isolated patches to large, contiguous corridors. Landscape-level research is necessary to identify important habitats, patches, and corridors to strategically target management interventions. We created habitat suitability models (HSMs) for hoary bats (*Lasiurus cinereus*), eastern red bats (*L. borealis*), and tri-colored bats (*Perimyotis subflavus*) across Illinois, USA, using species-specific landscape and climate variables. With the 3 models from this study and a previously published HSM for Indiana bats (*Myotis sodalis*), we stacked binary HSMs, thereby identifying priority conservation areas across Illinois. Species exhibited different distributional patterns and habitat preferences across Illinois. Multi-species HSMs highlight high quality habitat (i.e., ecologically important habitat that provides preferred resources for roosting, foraging, and raising young) in southern Illinois and along river riparian areas. This approach identified priority conservation areas mainly following hydrologic zones, which allows managers to strategically target restoration and conservation measures, invest funds in habitat likely to have high

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return-on-investment, and assist with decisions that affect bats (e.g., siting wind turbines, purchasing mitigation lands).

KEYWORDS
bats, eastern red bat, habitat suitability models, hoary bat, Indiana bat, *Lasiurus borealis*, *Lasiurus cinereus*, *Myotis sodalis*, *Perimyotis subflavus*, tri-colored bat

In the midwestern United States, bats provide essential ecosystem services including pest control, disease reduction, and nutrient cycling (Feldhamer et al. 2009, Kunz et al. 2011, Maslo et al. 2022). Agricultural pest reduction specifically has been estimated at $74/0.4 ha, an impact that cannot be understated in this regional agroecosystem where 75% of agriculture in Illinois, USA, is in traditional row crop (e.g., corn and soy; Boyles et al. 2011, Maine and Boyles 2015, Illinois Department of Agriculture 2021). Within this agroecosystem, wind energy is expanding. In 2021, Illinois produced >6,300 megawatts of wind energy, which is estimated to kill bats at a rate of 0.8–8.6 bats/megawatt/year, disproportionately affecting migratory bats (Anderson et al. 1999, Kunz et al. 2007, U.S. Energy Information Administration 2021*a*). In 2022, 75 wind farms are concentrated in the upper half of the state that include >3,500 turbines (Figure S1, available in Supporting Information; Hoen et al. 2018), with expanded capacity in the future a certainty (J. A. Kath, Illinois Department of Conservation, personal communication). In addition, the fungus that causes white-nose syndrome (*Pseudogymnoascus destructans*) has killed 6.7 million bats in North America and is linked to local population extirpations (Frick et al. 2010, 2015; Cheng et al. 2021). Bats in the Midwest are negatively affected in nearly all phases of their annual cycles (i.e., migrating, foraging, hibernating) by these and other issues including habitat loss and climate change, causing population declines and concerns for their persistence into the future (Frick et al. 2020).

Bats use the landscape at a variety of spatial scales, from roosting to foraging to migrating (Ford et al. 2005, Razgour et al. 2011, Bellamy et al. 2013). Some bat species roost within 0.1 km of previous roost sites yet fly up to 2 km away for drinking and foraging (Elmore et al. 2005, Veilleux et al. 2009, Schaefer 2017). Additionally, bats migrate short and long distances (150–1,000 km) between summer roosts and winter hibernacula (Fraser et al. 2012, Weller et al. 2016, Roby et al. 2019). Thus, bat conservation and management decisions must consider multiple scales. Appropriate ecological scales can be quantified via habitat suitability models (HSMs), which test variables across multiple scales (Razgour et al. 2011, Bellamy et al. 2020). This multi-scale approach facilitates variable selection at species-specific scales of importance, based on life history and behavior, and incorporates multiple scales into landscape-wide models (Bellamy et al. 2013, Bellamy and Altringham 2015).

Multi-species (i.e., stacked) HSMs have the potential to identify areas of high importance for those communities across the landscape, facilitating the prioritization of areas with greatest conservation value (Zellmer et al. 2019, Stevens and Conway 2020). Multi-species HSMs can help identify data and information gaps, habitats to protect, and areas of opportunity for adaptive management practices (Guisan et al. 2013). Creating stacked and individual HSMs can help translate field data into models and maps that can support decision making in management and policy (Guisan et al. 2013, Zellmer et al. 2019, Stevens and Conway 2020).

Our objectives were to develop individual HSMs for 3 bat species in Illinois, the eastern red (*Lasiurus borealis*), hoary (*Lasiurus cinereus*), and tri-colored bat (*Perimyotis subflavus*), and to develop a multi-species HSM that includes the 3 species and the previously published HSM for the federally endangered Indiana bat (*Myotis sodalis*; Cable et al. 2021). We chose these 4 species because of their vulnerability to white-nose syndrome (Indiana bat, tri-colored bat) or wind energy development (eastern red bat, hoary bat). Specifically, we asked 3 research questions. What are the main summer use habitats and their characteristics for the eastern red, hoary, and tri-colored bat? Based on these preferences, where would we expect to find them across Illinois? Considering the 4 focal species, where are priority conservation habitats for chiropterans throughout the state? Given that each species our 4 focal species has different life histories, we predicted that the top models for each species would be species-specific based on the different ecological characteristics of each species.

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STUDY AREA

Illinois ranges from 182–365 m in elevation with an area of 149,997 km^2. Illinois is a habitat mosaic in the midwestern United States with 76% of the land classified as agriculture, 12% as forest, 6% as urban, 3% as wetland, and 2% as other (Luman et al. 2004). The northern third of Illinois is dominated by agriculture and an urban-suburban-exurban interface with rolling hills, while the southern third is home to the Shawnee National Forest, which is 113,312 ha of rolling forest and bluffs managed by the United States National Forest Service (Iverson 1988, Luman et al. 2004). The middle third of the state is primarily flat with row crops (corn, soy) and small, isolated fragments of forests, riparian corridors, degraded prairie, and urban areas. Across the state, Illinois forests are primarily composed of hickory (*Carya* spp.)-oak (*Quercus* spp.) deciduous hardwood trees with major riparian zones of predominantly elm (*Ulmus* spp.)-hickory (*Populus* spp.) forests along the Illinois and Mississippi rivers (Illinois Forestry Development Council 2017). Dominant terrestrial fauna for Illinois include white-tailed deer (*Odocoileus virginanus*), squirrel (*Sciurus* spp.), Virginia opossum (*Didelphis virginiana*), red fox (*Vulpes vulpes*), and a robust urban and rural Canada goose (*Branta canadensis*) population. This study used bat acoustic, capture, and mortality occurrence records from 1999–2020. Illinois climate includes typically cold winters (Nov–Feb, average temp = 0–7°C) and hot and humid summers (May–Aug, average temp = 29°C). The average precipitation in Illinois is 121 cm/year in southern Illinois and 81 cm/year in northern Illinois (Changnon et al. 2004).

METHODS

The 4 species included in this study represent a range of common (eastern red and hoary bat; Feldhamer et al. 2015) to rare species (Indiana and tri-colored bat; Feldhamer et al. 2015) with a variety of roosting (e.g., solitary roosting in foliage [eastern red and hoary] or colonial roosts in snags [Indiana]; Carter and Feldhamer 2005, Limpert et al. 2007, Klug et al. 2012), foraging (e.g., high open space foraging [hoary] or forest edges, gaps, and openings [eastern red, Indiana, and tri-colored]; Loeb and O'Keefe 2003, Walters et al. 2007, Farrow and Broders 2011, Starbuck et al. 2015), and migrating preferences (e.g., long-distance migrants [hoary], regional migrants [Indiana], and hibernators [tri-colored]; Cryan et al. 2004, Fraser et al. 2012, Hayes et al. 2015, Roby et al. 2019) that broadly represent all of Illinois' bat species. Moreover, they are representatives of multiple strategies employed for foraging including cluttered (Indiana), edge (eastern red and tri-colored), and open-spaced foragers (hoary) and all echolocation phonic groupings (low frequency [hoary bat], mid frequency [eastern red bat and tri-colored bat], and high frequency (Indiana bat; Beilke et al. 2021). Body sizes vary across species (average body sizes for tri-colored bat = 5.6 g to hoary bat = 25.7 g) and roosting preferences, ranging from communal roosting in sloughing bark on dead trees [Indiana bat] to solitary roosting in live foliage [eastern red bat]; Feldhamer et al. 2015, Beilke et al. 2021). Thirteen bat species occur in Illinois; however, several species are rare and only found in the extreme southern extent of the state like Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and the eastern small-footed bat (*Myotis leibii*; Feldhamer et al. 2015). While the HSM we produced may not best represent specialized species like Rafinesque's big-eared or gray bat (*Myotis grisescens*), the 4 species chosen are cosmopolitan across the state and represent the most widespread and imperiled species. The range of Illinois' chiropteran biology, ecologies, and life histories are largely captured by these 4 species; therefore, the multi-species HSM we produced represents a viable proxy for the broader chiropteran community.

Occurrence data

We obtained historical capture data via data sharing agreements with the Illinois Department of Natural Resources and the United States Fish and Wildlife Service (USFWS) for mist-netting and summer wind farm mortalities from 1999–2021. Because Illinois Department of Natural Resources primarily maintains records for threatened and

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endangered species, the historical capture data were incomplete for non-listed species. Thus, we contacted Illinois Department of Natural Resources' list of Illinois mist-netting permittees, requesting mist-netting records for the hoary, eastern red, and tri-colored bat between 1999 and 2021. Eight permittees responded, which added to the data from 2015–2019 generated by the Illinois Bat Conservation Program at 46 mist net sites. We derived wind farm mortalities from any publicly available post-construction monitoring reports resulting from federal regulations that require wind energy companies to monitor for bat mortalities at all new installations. We combined windfarm mortality and mist-net records, reducing the number of individual species records to 1 per mist-netting location or turbine site. For all data, we removed sites with low positional or temporal accuracy, or lacking no data associated with captures. All data required a date and global positioning system location associated with each occurrence to be included in the analysis.

Biologists from the Illinois Bat Conservation Program collected state-wide acoustic data using the North American Bat Monitoring Program (NABat) protocol for 20 NABat cells annually since 2016 (Illinois Bat Conservation Program 2021, U.S. Geological Survey [USGS] 2021). The North American Bat Monitoring Program uses a generalized random-tessellation stratified system to create a 10-km × 10-km grid across North America and identify priority cells in each state composed of 4 quadrants (Stevens and Olsen 2004, Larsen et al. 2008, Loeb et al. 2015). We deployed full spectrum ultrasonic recorders, SM4BAT (Wildlife Acoustics, Maynard, MA, USA) with a SMM-U1 or U2 microphone (Wildlife Acoustics) or Pettersson D500x units (Pettersson Elektronik AB, Uppsala, Sweden) in 2–4 quadrants in each generalized random-tessellation stratified cell. We chose sites in each quadrant to represent habitat diversity in each cell. We deployed recorders for a minimum of 4 nights with approved weather (i.e., no rain, temp > 15°C, sustained wind < 12.8 km/hr). We used the same protocol for all years, and sites remained unchanged, with 15 exceptions due to lack of landowner permissions. Data were recorded from 1900 to 0730 each detector night. Biologists from the Illinois Bat Conservation Program also sampled acoustic monitoring sites across Illinois that were surveyed with a similar acoustic protocol as generalized random-tessellation stratified system cells.

Using the NABat protocol (Reichert et al. 2018), we processed all files recorded in the field through Sonobat 4 software (Sonobat, Arcata, CA, USA) using the medium filter to reduce noise files. We ran Kaleidoscope Pro 5.4.0 as the auto-classifier (Wildlife Acoustics). Kaleidoscope is a powerful auto-classifier that, in addition to identification, provides maximum likelihood estimates of species occupancy by night. We considered at or below $\alpha = 0.05$ to be present and above $\alpha = 0.05$ to be absent following standard conservative protocols from NABat and USFWS (Nocera et al. 2019, USFWS and USGS 2019). We did not manually vet these acoustic data because NABat does not require manual vetting for data upload. In 2021, we processed the raw acoustic data from all years to ensure that the classifier's conditions were the same through all analyses.

We combined acoustic and capture data and processed them in R 4.1.2 (R Core Team 2021). To reduce sampling bias and spatial autocorrelation, we removed records within 1 km of each other. We maintained only records from 15 May–15 August to ensure that no records were from migratory periods, per USFWS guidelines (USFWS 2020). After data cleaning and quality control, there were 264 occurrences for eastern red bats (17 from wind turbine fatalities, 159 from mist-netting captures, 88 from acoustic detections), 116 occurrences for hoary bats (9 from wind turbine fatalities, 21 from mist-netting captures, 86 from acoustic detections), and 106 occurrences for tri-colored bats (77 from mist-netting captures, 27 from acoustic detections) established.

Environmental layers

We chose variables based on top models of published HSMs or occupancy models for each of the species creating a list of 25 biologically important and regionally relevant variables (Table 1). We used 16 biologically meaningful land cover variables (Table 1; Cable et al. 2021) created from the Illinois Geospatial Clearing house land cover layer (Illinois Department of Natural Resources et al. 2003). In brief, Cable et al. (2021) resampled the layers to a 0.1-km resolution and simplified to 8 land cover classes (bottomland forest, deciduous forest, coniferous forest, agriculture, grassland, urban, water, other), then used FRAGSTATs (McGarigal et al. 2012) to calculate the number of patches, area, and

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TABLE 1 Variables tested in univariate models of occurrence for the eastern red, hoary, and tri-colored bat, Illinois, USA, 1999–2021.

Variables	Spatial scale (km)	Original resolution (km)	Original data source
Aspect		0.03	U.S. Geological Survey (2018)
Canopy cover		0.03	U.S. Geological Survey (2018)
Elevation		0.03	U.S. Geological Survey (2018)
Distance to roads[a]		0.1	Illinois Department of Transportation (2018)
Distance to water[a]		0.1	U.S. Geological Survey
Existing vegetation height		0.03	U.S. Department of Interior et al. (2013)
Number of patches of agriculture[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Number of patches of forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Number of patches of urban[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Number of patches of water[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Null[a]		0.03	Illinois Department of Natural Resources et al. (2003)
Precipitation (30-yr average of monthly summer precipitation)		0.8	PRISM Climate Group (2021)
Quadratic mean diameter		0.24	U.S. Forest Service (2012)
Stand density index		0.24	U.S. Forest Service (2012)
Solar radiation		1	Solargis (2019)
Area of agriculture[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of bottomland forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of closed canopy deciduous forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of coniferous forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of open canopy deciduous forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of urban[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Area of water[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)

(Continues)

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TABLE 1 (Continued)

Variables	Spatial scale (km)	Original resolution (km)	Original data source
Edge of forest[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Edge of water[a]	0.1, 0.5, 1	0.03	Illinois Department of Natural Resources et al. (2003)
Temperature (30-year average of monthly minimum summer temperature)		0.8	PRISM Climate Group (2021)

[a]Layer was created by Cable et al. (2021).

edge of land cover types relevant to Indiana bat ecology. Each metric was calculated at 3 different scales statewide (0.1 km, 0.5 km, and 1 km) using a moving window analysis to determine the appropriate scale of each land cover variable in predicting suitability for roosting, foraging, and landscape distances (Glasbey and Jones 1997). We chose to test the same spatial scales across all species to maintain consistency as in previously published HSMs and because data are lacking for the foraging distance of some of these species (Bellamy et al. 2013, 2020). Cable et al. (2021) also used ArcMap (Esri, Redlands, CA, USA) to measure the distance to each road and water body from the center of the raster cell. We used only roads with an annual average daily traffic rate of >2 cars/minute and water bodies with area <1 ha (Illinois Department of Transportation 2018, USGS 2020).

We also considered 9 additional variables (Table 1). Many of these variables were forest stand structure or topographical landscape metrics gathered from publicly available geographic information system layers and resampled in ArcGIS for 0.1-km resolution to match layers (Cable et al. 2021). We took temperature and precipitation layers from a 30-year normal and averaged across May–August to represent the summer average (PRISM Climate Group 2021).

Modeling

For all variables, we created single-predictor models for each bat species in MaxEnt version 3.4.4 (Phillips et al. 2006, 2021) to select the optimal spatial scale for variables and chose the top 15 variables for each species by area under the curve test (AUC_{test}) scores to minimize over-parameterization. For univariate models, we used the default parameters with 20 replicates, and 10% random test percentage (Phillips et al. 2021). Using AUC_{test} scores, we determined the best spatial scale for each species for each land cover variable. We ranked the top scaled land cover variables among the non-scaled variables, selecting the top 15 variables for each species with $AUC_{test} > 0.5$. We carried the top 15 variables for each species through subsequent analyses. To be as rigorous as possible, we included this approach to ensure that we created the models in a quantitative way, and that we were not biased by biological perceptions for data-deficient species in choosing variables. In addition, these models are computationally intensive; thus, by limiting our analyses to quantitatively meaningful variables, we reduced computational time. Given the ranges in AUC_{test} values across species, ranking and retaining 15 variables based on AUC_{test} values reduced the potential for over-fitting in our models and allowed us to choose the best species-specific spatial scale for each variable.

Using the combined species-specific variables, we tested differing regularization multipliers ranging from 1–12 using the same default parameters of 20 replicates and 10% as a random test percentage. We used the regularization multiplier with the top AUC_{test} score in subsequent analyses. A larger regularization multiplier puts a higher penalty on more complex models, thus reducing overfitting (Elith et al. 2011).

For each species, we created a set of candidate models based on available literature and ecologically relevant hypotheses. If the exact variable used in the literature was not in the top 15 variables for each species, we chose

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proxies based on the available variables (e.g., if the top model in the literature had basal area, we substituted stand density index; U.S. Forest Service 2012). We created a correlation matrix in ArcMap for the 15 variables for each species, removed highly correlated variables (>0.7), and maintained the variable with the higher AUC_{test} value. After a literature review, we created ≥23 models for each species, using all variables in multiple combinations, using each variable at least twice to maintain evenness (Tables S2, S3, S4, available in Supporting Information). We ran all models in MaxEnt using presence-only data, top regularization multiplier, 20 replicates, 10% of data points withheld for testing from the dataset by MaxEnt, and 5,000 maximum iterations. For pseudo-absence points, MaxEnt randomly sampled 10,000 background points across the state via bootstrapping.

Model analysis

We evaluated models via AUC_{test} scores and ranked them using Akaike's Information Criterion for small sample size (AIC_c) using raw outputs and LAMBDAS files in EMNTools (Bozdogan 1987, Warren et al. 2010). The AUC_{test} scores predict the discriminatory ability of the model to tell occurrence points from background points with a score 0.5 indicating that the model is no better than random chance and a score of 1 indicating perfect discriminatory ability (Jiménez-Valverde 2012). We used the following function in the raster calculator in ArcGIS to convert models from raw to log format, standardizing the suitability scale from 0 to 1 (Hammond et al. 2016):

$$logistic = (raw \times e^{entropy})/(1 + raw \times e^{entropy}).$$

We combined top models (i.e., AIC_c weight > 0.01) in ArcGIS using the weighted sum function proportionally according to AIC_c weights, creating a final model for each species. To create binary models, we used an omission threshold for each species by omitting the lowest 10% of suitability scores for true presences in the test datasets (Hovick et al. 2015). To calculate variable importance of the candidate set, we added the AIC_c weight of each model that contained each variable. For any variable with a weight of 1, we created response curves based off the values provided by MaxEnt.

Based on the 3 HSMs created above and the existing HSM for Indiana bats (Cable et al. 2021), we created a stacked HSM for the 4 species across Illinois. For the final binary model for each species, we summed the 4 binary models determined by the 10% omission rate across the state with equal weights. This created a raster layer with integers from 0–4 where, for example, a value of 2 would indicate suitable habitat for 2 species.

RESULTS

The best spatial scale for each variable differed among species, indicating the importance of habitats at different scales and reflecting species' biology and ecology (Table S1, available in Supporting Information). For the eastern red bat, 2 variables were optimal at 1 km, 2 variables at 0.5 km, and 5 variables at 0.1 km. For the hoary bat, 5 variables were optimal at 1 km, 0 variables at 0.5 km, and 9 variables at 0.1 km. For the tri-colored bat, 5 variables were optimal at 1 km, 7 variables at 0.5 km, and 2 variables at 0.1 km.

Across all species, 9 of the top 15 variables were consistent but at different spatial scales (Table 2). The hoary bat had the most distinctive set of variables, with 5 variables exclusive to the species, whereas eastern red bat and tri-colored bat did not have any unique variables, although the spatial scales on some variables differed. Eastern red bats and tri-colored bats had more variables associated with forest structure and density, while the hoary bat had more variables related to landscape openness (Table 2).

The top model for the eastern red bat was composed of elevation, area of agriculture in 0.1 km, area of forest in 0.1 km, area of water in 1 km, edge of forest in 0.1 km, and edge of water in 1 km (Table 3). This model had just over half of the AIC_c weight (0.51), with the next top model having 0.37 of the AIC_c weight. The second model was

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TABLE 2 Univariate model results ranked by discriminant ability of the area under the curve test (AUC_{test}) values based on occurrence points for the eastern red, hoary, and tri-colored bat across Illinois, USA, 1999–2021. We used the top 15 variables in subsequent multivariate models.

Rank	Eastern red	AUC_{test}	Hoary	AUC_{test}	Tri-colored	AUC_{test}
1	Area of agriculture in 0.1 km	0.7231	Area of agriculture in 0.1 km	0.6376	Distance to roads	0.9056
2	Area of forest in 0.1 km	0.7206	Distance to roads	0.6172	Stand density index	0.8071
3	Existing vegetation height	0.7193	Area of urban in 0.1 km	0.6038	Area of bottomland forest in 1 km	0.8033
4	Stand density index	0.7169	Distance to water	0.5968	Area of forest in 0.5 km	0.7980
5	Number of patches of forest in 0.1 km	0.7016	Number of patches of forest in 0.1 km	0.5871	Existing vegetation height	0.7959
6	Quadratic mean diameter	0.6999	Area of water in 1 km	0.5860	Area of agriculture in 0.5 km	0.7858
7	Canopy cover	0.6985	Solar radiation	0.5819	Elevation	0.7721
8	Edge of forest in 0.1 km	0.6967	Existing vegetation height	0.5812	Quadratic mean diameter	0.7719
9	Area of bottomland forest in 1 km	0.6548	Area of forest in 0.1 km	0.5790	Canopy cover	0.7678
10	Edge of water in 1 km	0.6470	Edge of forest in 0.1 km	0.5741	Area of water in 0.5 km	0.7620
11	Elevation	0.6434	Stand density index	0.5730	Temperature	0.7502
12	Area of water in 1 km	0.6412	Aspect	0.5700	Edge of forest in 0.5 km	0.7444
13	Number of patches of water in 1 km	0.6355	Number of patches of urban in 0.1 km	0.5611	Number of patches of forest in 0.1 km	0.7362
14	Temperature	0.6258	Area of open canopy deciduous forest in 1 km	0.5568	Number of patches of water in 0.5 km	0.7313
15	Distance to water	0.6243	Area of bottomland forest in 0.1 km	0.5554	Edge of water in 0.5 km	0.7134
16	Number of patches of agriculture in 0.5 km	0.6186	Edge of water in 1 km	0.5509	Area of closed canopy deciduous forest in 1 km	0.7124

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TABLE 2 (Continued)

Rank	Eastern red	AUC_{test}	Hoary	AUC_{test}	Tri-colored	AUC_{test}
17	Area of closed canopy deciduous forest in 1 km	0.6126	Temperature	0.5501	Area of open canopy deciduous forest in 1 km	0.6996
18	Distance to roads	0.6110	Area of closed canopy deciduous forest in 0.1 km	0.5447	Number of patches of agriculture in 1 km	0.6993
19	Solar radiation	0.6039	Precipitation	0.5421	Solar radiation	0.6782
20	Area of open canopy deciduous forest in 1 km	0.5914	Canopy cover	0.5418	Precipitation	0.6563
21	Precipitation	0.5723	Number of patches of agriculture in 1 km	0.5271	Distance to water	0.6370
22	Aspect	0.5719	Quadratic mean diameter	0.5261	Area of coniferous forest in 0.5 km	0.6255
23	Area of coniferous forest in 1 km	0.5475	Number of patches of water in 0.1 km	0.5259	Aspect	0.5804
24	Null	0.5388	Elevation	0.5244	Number of patches of urban in 1 km	0.5566
25	Area of urban in 0.1 km	0.5278	Area of coniferous forest in 1 km	0.5136	Area of urban in 0.1 km	0.5504
26	Number of patches of urban in 0.5 km	0.5200	Null	0.4507	Null	0.5279

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TABLE 3 Top multivariate models of habitat suitability for the eastern red, hoary, and tri-colored bat ranked by the Akaike's Information Criterion for small sample size (AIC_c) across Illinois, 1999–2021. We present values for the area under the curve test (AUC_{test}), which show each model's discriminant ability. The difference between the top AIC_c value and that model's AIC_c value is the ΔAIC_c. The AIC_c w_i is the model's weight. Only models with AIC_c weight are shown in this table. All models are shown in Supporting Information.

Model	Rationale	Variables	AUC_{test}	AIC_c	ΔAIC_c	AIC_c w_i
Eastern red bat						
Amelon et al. (2014)	Access to water, high prey availability, and commuting by topographic features	Elevation + area of agriculture in 0.1 km + area of forest in 0.1 km + area of water in 1 km + edge of forest in 0.1 km + edge of water in 1 km	0.7837	8,423.76	0.00	0.52
Limpert et al. (2007)	Preferred roosting habitat and foraging habitat in riparian zones	Canopy cover + distance to water + quadratic mean diameter + area of agriculture in 0.1 km + area of bottomland forest in 1 km + area of forest in 0.1 km + area of water in 1 km + temperature	0.7927	8,424.40	0.64	0.37
Global model		Elevation + distance to water + existing vegetation height + quadratic mean diameter + area of agriculture in 0.1 km + area of bottomland forest in 1 km + area of forest in 0.1 km + area of water in 1 km + edge of forest in 0.1 km + edge of water in 1 km	0.7922	8,426.83	3.07	0.11
Hoary bat						
Land use history bias	Where most historical human impact has occurred	Distance to roads + area of agriculture in 0.1 km + area of urban in 0.1 km	0.7444	3,742.44	0.00	1.00
Tri-colored bat						
O'Keefe (2009)	Minimize commuting costs as a smaller bat and prefer riparian zones for roosting and minimizing foraging costs	Canopy cover + elevation + distance to roads + number of patches of forest in 0.1 km + edge of forest in 0.5 km + edge of water in 0.5 km	0.8832	3,261.34	0.00	0.56
O'Keefe (2009)	Minimize commuting costs as a smaller bat and prefer riparian zones for roosting and minimizing foraging costs	Canopy cover + elevation + distance to roads + edge of forest in 0.5 km + edge of water in 0.5 km	0.8704	3,261.81	0.47	0.44

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composed of canopy cover, distance to water, quadratic mean diameter (a measure of average tree diameter), area of agriculture in 0.1 km, area of bottomland forest in 1 km, area of forest in 0.1 km, area of water in 1 km, and temperature. Finally, the global model (AIC_c weight of 0.11) was composed of existing vegetation height, elevation, distance to water, quadratic mean diameter, area of agriculture in 0.1 km, area of bottomland forest in 1 km, area of forest in 0.1 km, area of water in 1 km, edge of forest in 0.1 km, and edge of water in 1 km. After averaging all 3 of

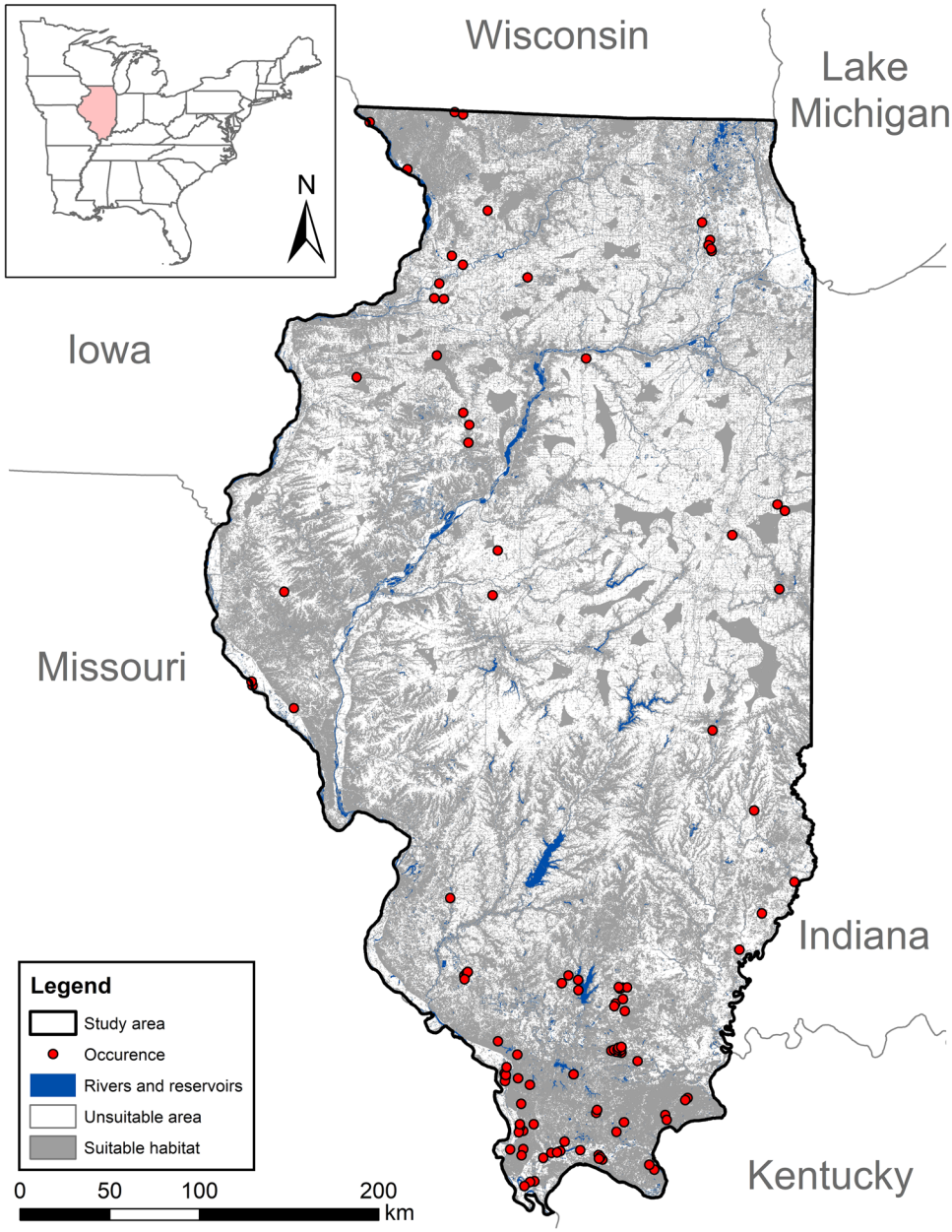


FIGURE 1 Habitat suitability model for the eastern red bat with occurrences across Illinois, USA, 1999–2021. Suitable areas are indicated in gray and each red circle indicates an occurrence point. Habitat for eastern red bats is evenly distributed across the state with large tracts of agricultural land and forested areas deemed suitable.

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the top models, the amount of suitable habitat for the eastern red bat in Illinois was 52%, distributed evenly across the state, with areas both in the southern forests, and contiguous sections of agricultural land in central Illinois (Figure 1). Variable response curves reveal that eastern red bat's most suitable habitat is composed of less agriculture within 0.1 km (40%) and more forest area within 0.1 km (45%) than the state average, while the amount of water within 0.1 km (12%) is approximately the state average (Figure 2A).

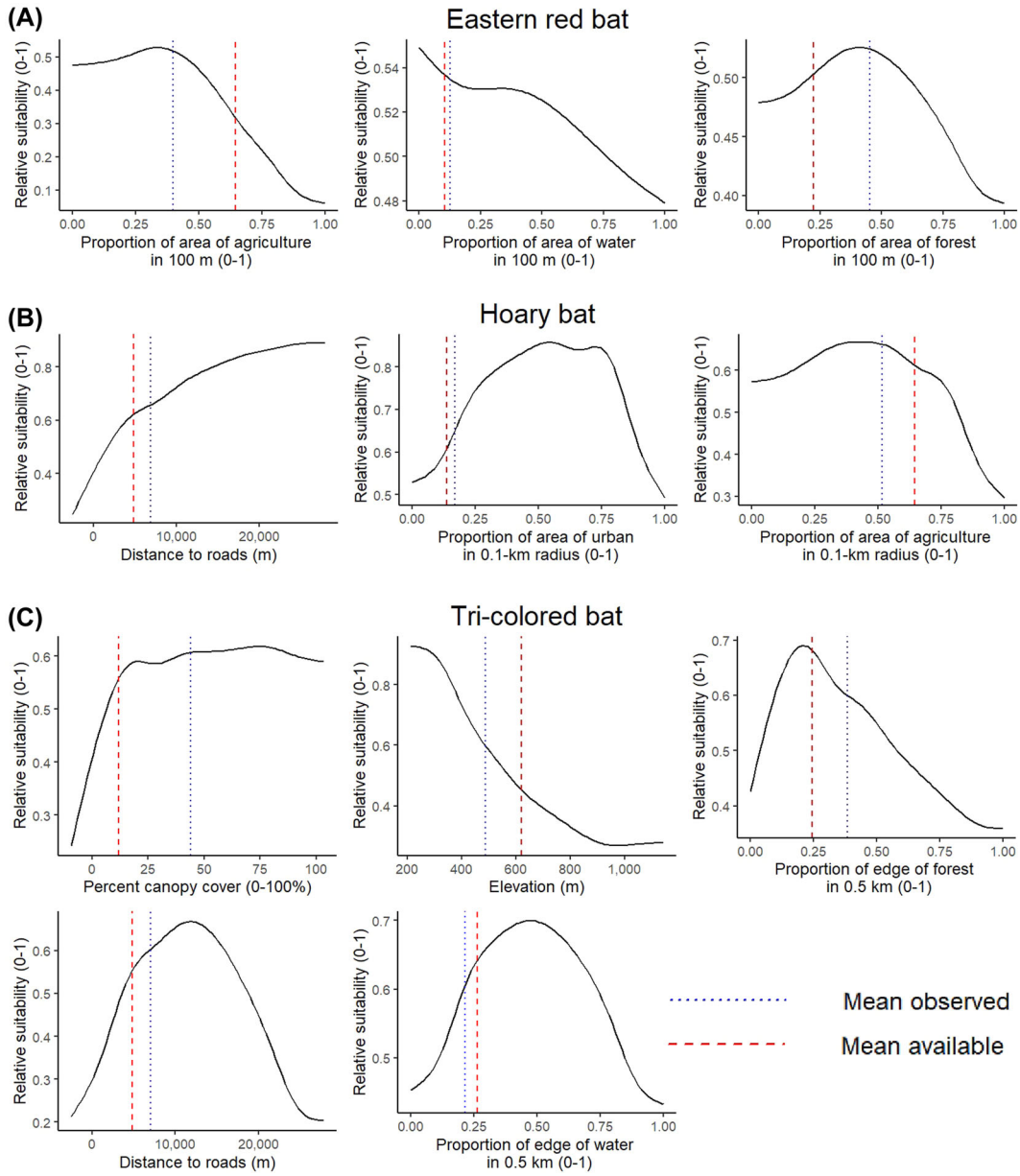


FIGURE 2 MaxEnt response curves for the A) eastern red bat, B) hoary bat, and C) tri-colored bat across Illinois, USA, 1999–2021, showing the relative suitability (0–1) to each variable that had an importance of 1. Land cover variables are scaled for a proportion from 0–1. Dotted blue lines indicate the average of observed occurrences for that species and the dashed red line indicates the average across Illinois.

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The top model for hoary bats was an ecologically relevant hypothesis modeling current and historical anthropogenic landscape use with the top variables recovered were distance to road, area of agriculture in 0.1 km, and the area of urban land cover in 0.1 km (Table 3). This model had all AIC_c weight, an AUC_{test} value of 0.74, and all 3 variables had an importance of 1 (Table S5, available in Supporting Information). The model predicted 58.45% of the state to be suitable habitat, including large tracts of agricultural areas in central Illinois with slightly more along the western side of the Illinois river, and much of the state's southern forests (Figure 3). Suitable hoary bat habitat

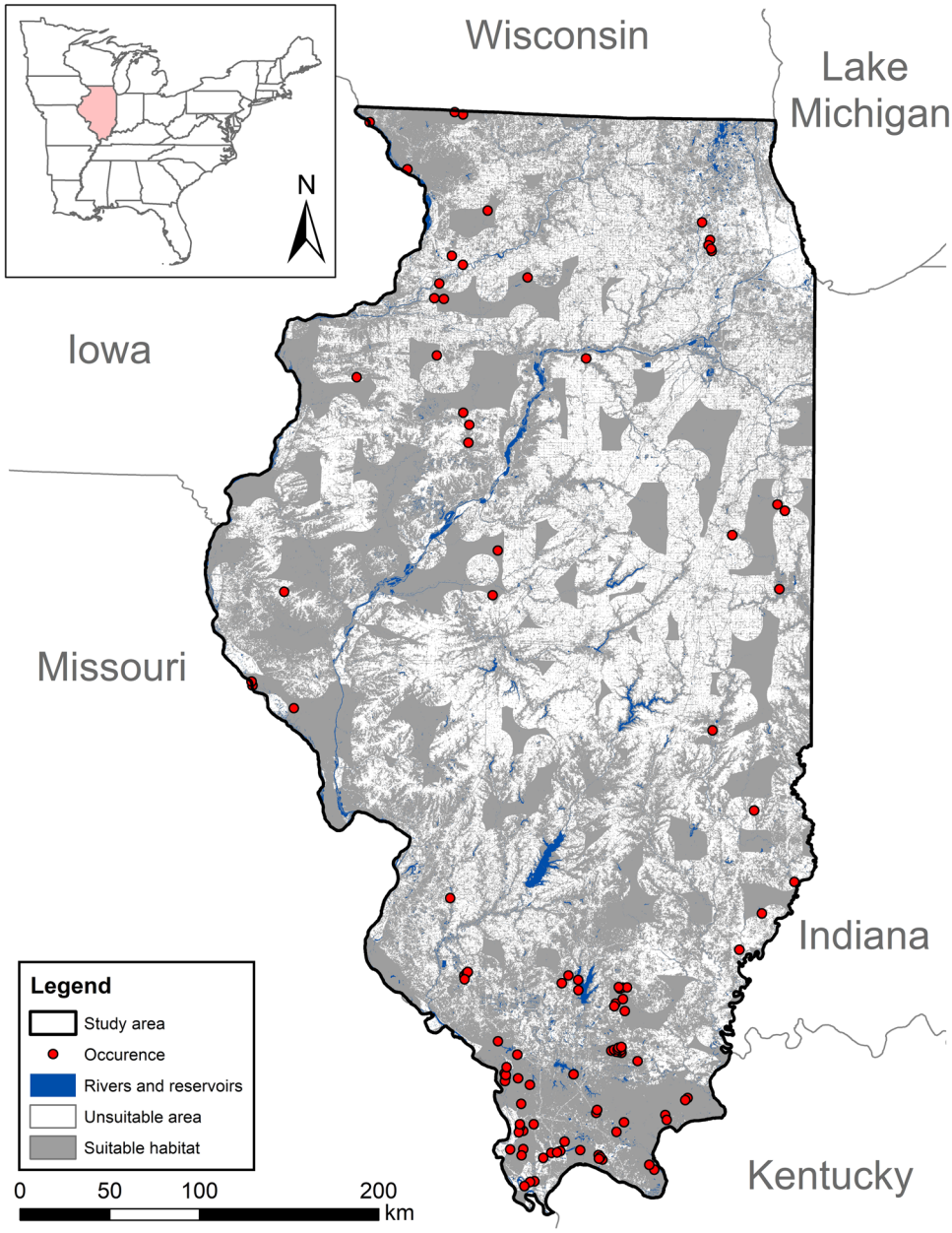


FIGURE 3 Habitat suitability model for the hoary bat with occurrences across Illinois, USA, 1999–2021. Suitable areas are indicated in gray and each red circle indicates an occurrence point. The hoary bat's habitat is seen in large contiguous patches of agricultural land in the middle of the state with additional suitable forests.

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was slightly farther from roads than average, with less agricultural area than average (52%) and more urban land cover (17%) than average (Figure 2B).

Two tri-colored bat models contained all AIC_c weight, with the top model composed of canopy cover, elevation, distance to roads, number of patches of forest within 0.1 km, edge of forest within 0.5 km, and edge of water within 0.5 km (Table 3). The second model did not include number of patches of forest within 0.1 km (ΔAIC_c of 0.4658). Both

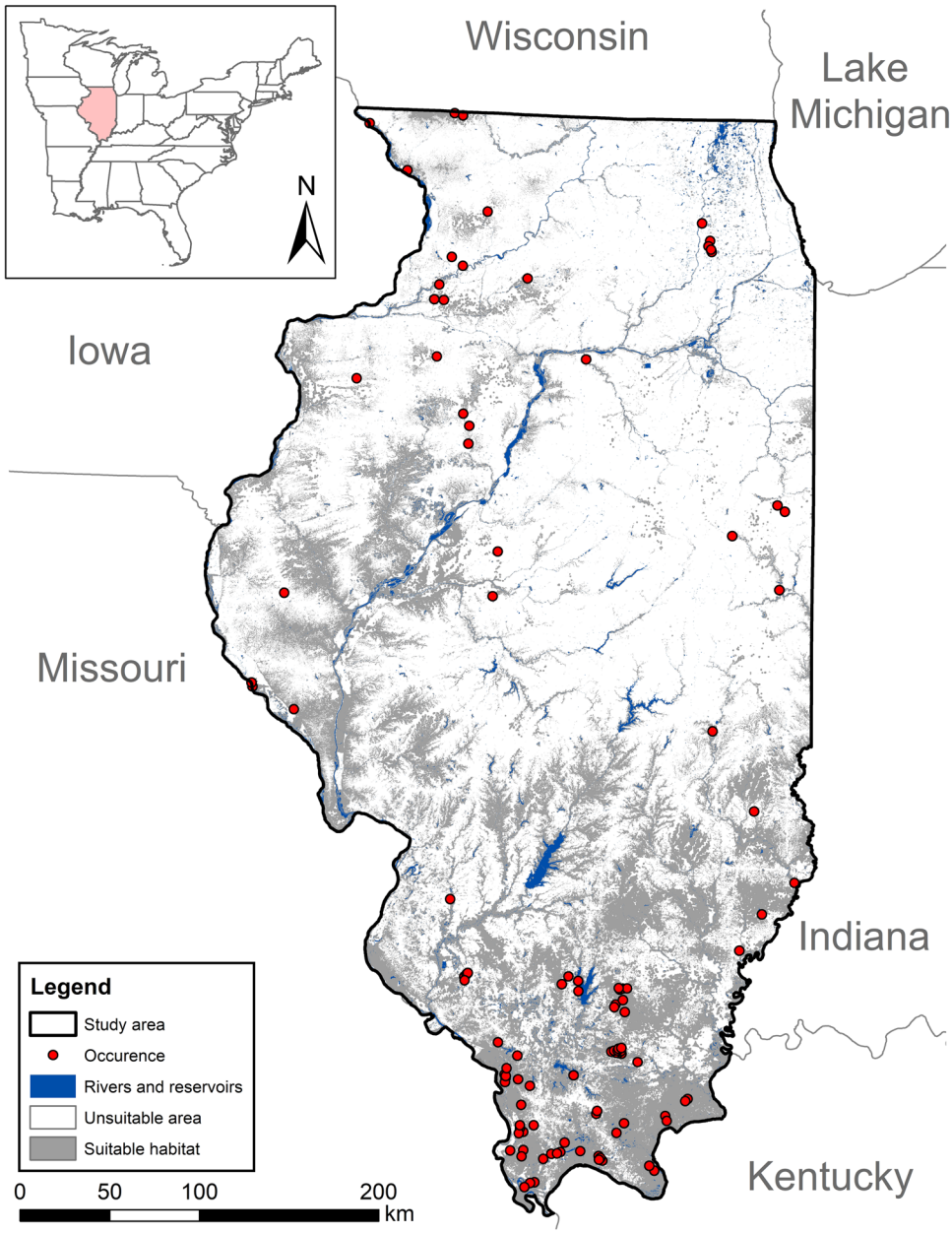


FIGURE 4 Habitat suitability model for the tri-colored bat with occurrences across Illinois, USA, 1999–2021. Suitable areas are indicated in gray and each red circle indicates an occurrence point. The tri-colored bat has the smallest distribution of habitat compared to other species tested following the riparian corridors but mostly in the forested southern third of Illinois.

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models had AUC values >0.87, indicative of a good fit to the data. The model recovered a scant 27.96% of the state as suitable habitat (Figure 4), which had much higher canopy cover (44%), lower elevation (488 m), higher forest edge (38%), farther distance from roads (7 km), and lower edge of water (21%) than the Illinois average (Figure 2C).

The HSM for the Indiana bat is provided by Cable et al. (2021). The top model for Indiana bat was the Goldilocks model with area of forest in 0.5 km, area of agriculture in 0.5 km, area of water in 0.5 km, elevation, distance to hibernacula, and area of urban in 0.5 km with 30% of the state as suitable habitat.

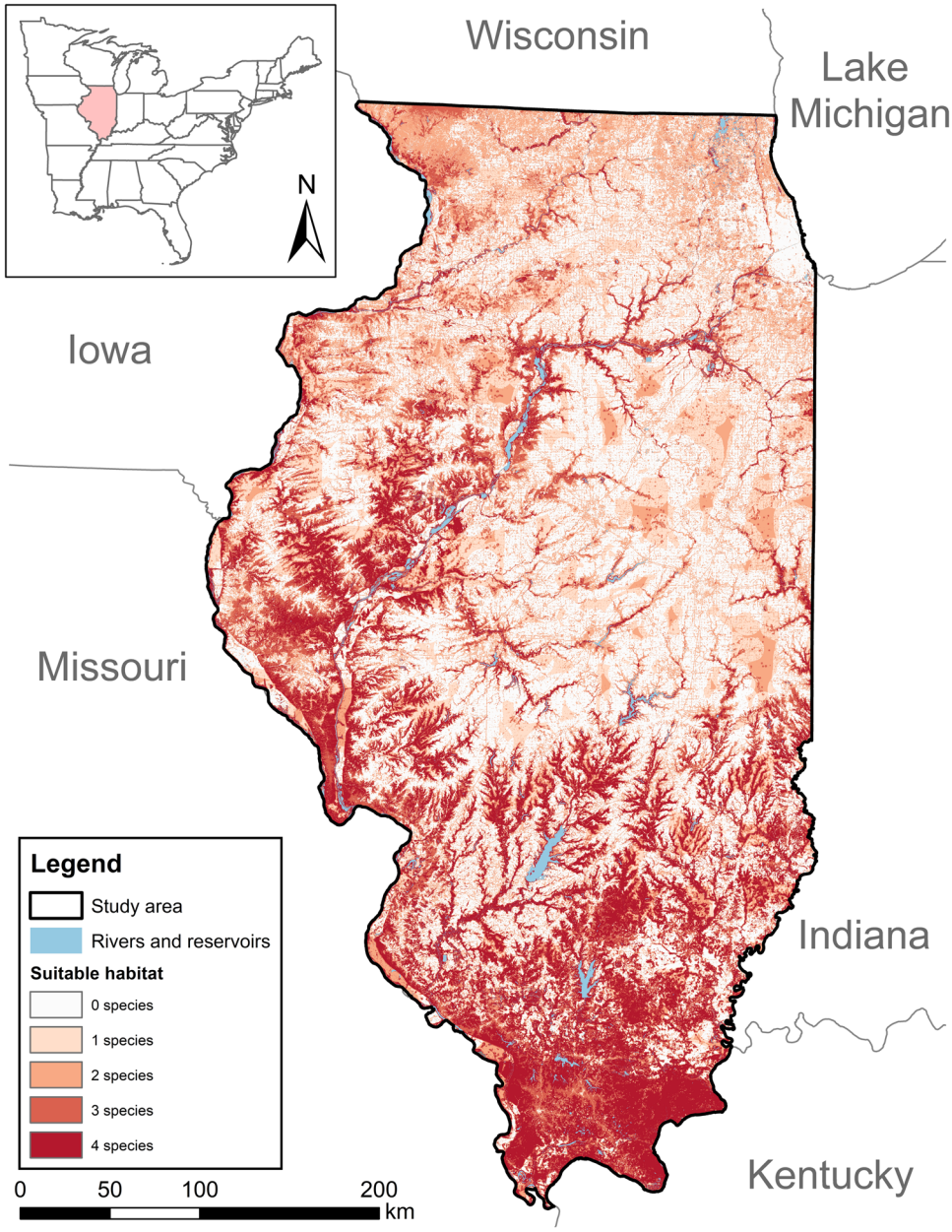


FIGURE 5 Stacked habitat suitability model from the eastern red, hoary, tri-colored, and Indiana bat binary habitat suitability maps based on occurrences across Illinois, USA, 1999–2021. Value of 2 indicates the habitat is suitable for 2 species of bat.

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The final summed (multi-species) raster of binarized suitable habitat for individual species revealed most suitable habitat in the southern third of Illinois, composed largely of the Shawnee National Forest and following hydrologic features northward (Figure 5). Suitable habitat in the rest of the state closely follows the Illinois River and other riparian zones. Eighteen percent of the state was considered suitable habitat for all 4 species, 13% was suitable for 3 species, 23% was suitable for 2 species, 12% was suitable for 1 species, and 34% of the state was unsuitable. Suitable habitat can be considered as areas that bats would use during some point in their ecological cycle (i.e., foraging, roosting, commuting).

DISCUSSION

Single-species HSMs

Each HSM for the eastern red bat, hoary bat, and tri-colored bat largely comported with habitat preferences in other parts of the species' ranges (O'Keefe 2009, Veilleux et al. 2009, Amelon et al. 2014). Eastern red bats, generalist foragers, prefer edge habitats and un-cluttered forests for foraging, commuting, and roosting (Ford et al. 2005, Amelon et al. 2014). Within the top eastern red bat variables, many of the land cover variables were important at the foraging and roosting scale (0.1 km), while water variables were important at the landscape scale (1 km). This indicates that eastern red bats choose suitable areas with available roost sites. As eastern red bats can fly 2 km from roosts to foraging locations, the importance of water is reflected at landscape scales (1 km; Elmore et al. 2005, Walters et al. 2007). Stand structure and density variables (e.g., existing vegetation height, stand density index) also remained high in univariate model rankings, indicative of selection for navigable forested areas and potential roost sites. Throughout Illinois, eastern red bat habitat is distributed along big rivers, and the agriculturally dominated central corn region. Large amounts of the state (52%), including agriculture and forests, deemed suitable reinforces the eastern red bat's generalist tendencies and its ability to use multiple types of land cover as habitat.

As a high-flying, open area forager, hoary bat habitat differed from that of forest-adapted eastern red and tri-colored bats (Ford et al. 2005, Menzel et al. 2005, Veilleux et al. 2009). Important variables focused more on open land cover and less on forests. In addition, univariate AUC values were lower overall compared to other species (AUC < 0.65) and the top multivariate model had with an AUC value of 0.74, suggesting that the variables tested may not predict hoary bat habitat particularly well. This may also be because hoary bat's generalist tendencies lower the algorithm's discriminant ability to discern presence locations from background pseudoabsence points. The AUC values may be highest at the smallest scale, as the coarser scales around occurrences are less discriminable from the background when MaxEnt samples pseudo-absence points. Most occurrences (acoustic, wind turbine mortalities) are from open row crop agricultural areas, which are areas similar to background areas, and reflective of the broad land cover of the state. The optimal spatial scale (0.1 km) suggests local (roost) habitat importance, contrary to the regional (1 km) expectations of high-altitude, long-distance fliers (Ford et al. 2005, Menzel et al. 2005, Weller et al. 2016). Overall, the importance of variables including distance to road, area of agriculture, and area of urban land cover reflect the open land cover preference of hoary bat.

While using urban and agricultural land cover is beneficial in response to forest loss and agricultural conversion for the generalist nature of the hoary bat, much of Illinois' agroecosystem is experiencing rapid wind energy development (Aldeman et al. 2015, U.S. Energy Information Administration 2021*a*). Large tracts of once suitable agricultural areas are being developed, with 1,100 megawatts of energy already under construction or in advanced development across the state, in addition to the 6,300 megawatts already implemented (U.S. Energy Information Administration 2021*a*). Although Illinois is the fifth highest wind-energy producer, this trend is seen across almost the entire United States (except for the Southeast; U.S. Energy Information Administration 2021*a*, *b*). The hoary bat occurs in every state and country and most provinces in North America and thus this source-sink dynamic could be seen across almost the entirety of its range, where hoary bats find habitat but are killed by wind turbines (Pulliam

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1988, Hayes et al. 2015). While the hoary bat is not currently being considered for listing, concerns of the effects of the long-term impacts of increased wind energy development on the population viability of the species exist (Frick et al. 2017, Friedenberg and Frick 2021, Wieringa et al. 2021). The limited number of wind turbines used in this study reflects the limited available mortality information, not the limited number of mortalities as has been reported by others (Frick et al. 2017, Friedenberg and Frick 2021, Wieringa et al. 2021). Wind energy companies are reticent to report the number of mortalities occurring, nor are they required to do so, beyond federally listed species (J. A. Kath, personal communication). As such, our wind-farm mortality numbers likely represent a vast undercount of actual mortalities.

The tri-colored bat's status as a riparian specialist is reflected in our modeling (Ford et al. 2005, Menzel et al. 2005, Cox 2019). More than half of the top variables were forest land cover or stand structure metrics, which are important for foraging and roosting (Menzel et al. 2005, Perry and Thill 2007, O'Keefe 2009). Important roosting variables, such as vegetation height, tree diameter, and stand density, were in the top 10 variables; however, they were not included in the top multivariate model, indicating that while roost presence is important, it may not be the primary factor for habitat selection (Perry and Thill 2007, Schaefer 2017). In addition, the most frequent scale of importance by the tri-colored bat was 0.5 km, which may indicate that fine-scale features (0.1–0.5 km) are more predictive of where they will be found and that that they are choosing areas to roost and forage based on habitat availability in the more immediate area (O'Keefe 2009, Schaefer 2017). Several variables reflected the importance of edges for the tri-colored bat, including the number of patches of forest and edges of water and forest, which minimizes commuting costs (O'Keefe 2009). In these models, distance from roads and increasing forest edges and canopy cover reflect the tri-colored's size and affinity for foraging and roosting in structured forests with available water and openings. Suitable habitat is tightly concentrated around riparian (i.e., Illinois and Mississippi rivers) corridors and the forested southern third of the state. As an apparent forest obligate, habitat loss and degradation would have a stronger impact on the tri-colored bat (Farrow and Broders 2011, Schaefer 2017). These results should be considered during the listing of the tri-colored bat under the United States Endangered Species Act if forests are being converted to agriculture across the state.

While the creation of an HSM for the Indiana bat was done by Cable et al. (2021), the modeling methods paralleled this paper. With some additional forest metrics tested herein, the only other difference was that Cable et al. (2021) only allowed linear and quadratic models from MaxEnt and did not include acoustics in their occurrence records. While this prevents direct comparison of suitability values between the HSMs, both models are created with similar enough methods to build a multi-species HSM. Across the state, habitat for the Indiana bat was in places of low elevation forested riparian floodplains, often leaving snags preferred for roosting (Cable et al. 2022). Indiana bat habitat closely followed riparian zones along the Illinois and Mississippi rivers with most of the habitat confined to the bottom third of the state.

Multi-species HSM

The multi-species HSM represents higher quality habitat (i.e., areas with ecologically important habitat that provides more of species' preferred resources for roosting, foraging, and raising young) for nearly a third of Illinois' bat species, 2 of which are either federally listed, or under consideration for listing. Additionally, these 4 species represent a range of ecologies and natural histories, ostensibly acting as a representative sample for categories of Illinois bats imperiled by disease and wind energy (Feldhamer et al. 2015). Area or edge of water, agriculture, and forest had a variable importance of 1 for at least 3 of the 4 species. In addition, the forested southern third of the state and the riparian areas along big rivers represent higher quality bat habitat. Much of these highly suitable riparian areas remain connected through the river system; thus, maintenance of this connectivity is important (Cable et al. 2021). Riparian areas are important for creating snag roosting habitat from flooding, water accessibility for drinking, and higher insect availability (Carter 2006, Scott et al. 2010, Akasaka et al. 2012). Throughout the

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agriculturally dominated parts of the state and the more urban-suburban-exurban northern third, there remains pockets of habitat for 2 species. As a representative sample of Illinois bats, this model stands as a baseline for change based on the potential environmental impacts of climate change or urbanization (Arumoogum et al. 2019, Stevens and Conway 2020). Because these HSMs are confined to summer, migration paths are not modeled. Pinpointing suitable habitat for summer is important for maintaining healthy bat populations through supporting reproduction, recovering from white-nose syndrome, and restoring energy and fat reserves after hibernation and migration.

While the multi-species HSM represents a landscape-level approach to chiropteran habitat in Illinois, combining HSMs loses some nuance associated with single-species HSMs. Multi-species HSMs provide a broad perspective of suitable habitat for the chiropteran community, and thus may be valuable in supporting the siting of wind energy development. In contrast, single-species HSMs provide additional nuance, and thus may be more useful for identifying areas for land acquisitions and habitat restoration, enhancement, or protection. Three of our species are tree-obligate bats leading to a greater emphasis on forests, which potentially skews the model away from the hoary bat, which roosts in trees but prefers foraging in open areas. Eastern red and hoary bats are both habitat generalists, but eastern red bats are considered forest generalists, while hoary bats are considered open generalists (Ford et al. 2005, Menzel et al. 2005). Our models reveal some suitable habitat overlaps for all species, but areas suitable for 3 of the species may be suboptimal for hoary bats. The habitat-limiting HSMs were those for the rare forest obligates: tri-colored bat and Indiana bat (Farrow and Broders 2011, Cox 2019, Cable et al. 2021). Restricting management and conservation decisions to habitats of range-restricted species will ignore habitat for more common species, especially in the highly agricultural areas where common bats provide ecosystem services in the form of agricultural pest reduction (Cooper-Bohannon et al. 2016, Stevens and Conway 2020). Focusing only on southern Illinois because of the greater habitat for more species neglects potential bat habitat across the state, especially in higher quality habitat for the hoary bat, which may be essential as wind energy development continues (J. A. Kath, personal communication).

While HSMs give a landscape-scale view of suitable habitat, they do not incorporate biotic factors that may be limiting to some species like competition and predation (Freeman and Mason 2015). In addition, the models in this study only define suitable habitat for general summer use. Modeling migration corridors for both long- and short-distance migrants and modeling ideal maternity habitat through female-only models during summer may find additional areas of habitat (Hayes et al. 2015, Gottwald et al. 2017, Wieringa et al. 2021). Lastly, testing the same variable distances for all 3 species (0.1 km, 0.5 km, 1 km), although beneficial for maintaining consistency in the analysis and with previously published HSMs (Bellamy et al. 2013), may be too small for larger ranges in species-specific variation in habitat usage. Stacked multi-species HSMs may also over-predict species richness across a landscape; however, a stacked HSM outperforms a joint HSM in model performance, which uses combined species occurrences in 1 model run and would likely erase many of the non-generalist species needs when combined with the generalist species (Zurell et al. 2020). Thus, a stacked HSM can still be used for consideration of habitat conservation and management decisions (Mateo et al. 2012, Del Toro et al. 2019, Zurell et al. 2020).

Our multi-species HSM reveals habitat for multiple species by creating a landscape-level model. As such, suitable areas should be a target for restoration, enhancement, or protection, particularly in, and adjacent to, areas of contiguous habitat. Much of the habitat along riparian zones remains contiguous, and maintaining this connectivity is important for migration, foraging, and roosting (Ford et al. 2005, Cable et al. 2021). Patches of unsuitable areas are often adjacent to or surrounded by habitat, and thus remain important for these volant species. Multi-species HSMs have been used to support decision making for reserve networks and biodiversity reserves for other species (Buchanan et al. 2011, Cooper-Bohannon et al. 2016, Stevens and Conway 2020).

Given that we included 2 of the species most affected by wind turbines and broadly representing the ecology and diversity of Illinois chiropteran community, our multi-species HSM is a valuable proxy. This is especially relevant as wind energy companies often buy land as mitigation for wind turbine mortalities. Wind energy development in

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the Midwest continues apace, and the siting of new wind energy development is predicted to have profound impacts on migratory bat species (Santos et al. 2013, Roscioni et al. 2014, Vanausdall et al. 2018). Both the number and location of turbines on the landscape is important in reducing mortalities (Roscioni et al. 2014, Hayes et al. 2015). Specifically, increased distance from bat habitat has been linked to decreases in wind-turbine mortalities (Santos et al. 2013, Vanausdall et al. 2018). In addition, HSMs for spring and fall migrations should be modeled and considered. Given this, our HSM should be considered when deciding where to site wind turbines, ideally siting new developments away from identified important habitat areas.

MANAGEMENT IMPLICATIONS

With identified habitat for all 4 bat species, land protection in the public trust is imperative to maintain sufficient habitat and prevent loss and degradation. Highlighting habitat provides wildlife managers the ability to advocate for bat-friendly management on their lands. Unsuitable areas could be targets for land acquisitions as a part of remediation efforts, and restored into prairie or forest, thereby increasing overall habitat and increasing habitat continuity. Beyond the value in guiding land acquisitions and restoration efforts, these results can be used when determining where to limit siting of wind turbines and monitoring water quality for contamination to increase and improve habitat suitability. The HSMs developed in this study can help determine potential areas to avoid for wind turbine development and identify habitat mitigation sites for multiple species, including endangered or migratory species.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Mist-netting and bat handling occurred under the Institutional Animal Care and Use Committee protocol 16074 and IRB UIUC IBC-18.1, which was approved by the University of Illinois Committee and all appropriate state (IL permits SS16-045, 16-056, SS17-041, 17-024, 17-069, SS18-041) and federal research permits (USFWS Recovery Permit TE11170C [A.B. Cable] and TE182436-3-7 [Illinois Natural History Survey]).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available in Dryad.

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