ASSESSING MULTIPLE DATA SETS FOR HABITAT SUITABILITY MODELING OF
BATS ACROSS ILLINOIS

BY

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THESIS

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ABSTRACT

North American bat populations have been severely and negatively impacted by numerous factors, including habitat loss and fragmentation, disease, and wind energy development. Yet bats provide critical ecosystem services, and are thus a focus of habitat conservation and management. As wide-ranging flyers, bats use habitats at a variety of scales, from small, isolated patches for roosting to large, contiguous corridors for migration. Landscape-level research is necessary to identify critical habitats, patches, and corridors to target management interventions. Habitat suitability models (HSMs) identify high quality habitat by predicting species occurrence at various spatial scales based on occurrence data and environmental variables. Bat occurrence data are mainly collected by mist netting or acoustics. The North American Bat Monitoring Program (NABat), a national monitoring protocol, provides a new data repository for developing HSMs. By combining NABat data with historical data, I can compare model performance by data type, which is essential for effective modeling. In this thesis, I seek to identify where suitable bat habitat is available across the state and compare the impact of different detection methods on HSM.

First, I created Maxent HSMs for three bat species (hoary bat, eastern red bat, and tri-colored bat) across Illinois using species-specific landscape and climate variables. With the three models from this study and a previously published HSM for Indiana bats, I stacked the binary HSMs identifying priority conservation areas across Illinois I found that each species exhibited different distributions and habitat usage across Illinois. Stacking the HSMs highlights shared high-quality bat habitat in southern IL and along riparian areas. Identifying quality conservation areas allows managers to prioritize restoration and conservation and use available funds on the most effective habitat, especially as energy companies look for mitigation lands to purchase.

Secondly, I sought to understand how different data types can influence HSM. I compared the overlap of models created from passive-only, active-only, and combined occurrences to identify the effect of multiple data types and detection bias. Passive data involves sensing the species remotely, while active detection involves handling the animal. For each species, the data type with the highest AUC value was the active-only model. By comparing the niche overlaps of HSMs between data types, I found a high amount of variation with no species having over 45% overlap among models. Passive models showed more suitable habitat in agricultural lands, while active models showed higher suitability in forested land, a reflection of sampling bias. Overall, this emphasizes the need to consider influences of detection and survey biases on modeling, especially when combining multiple data types. Biases from sampling, behavior at time of detection, and species life history intertwine to create striking differences among models. The biases and effects of each detection type should be considered in the final model output, particularly when the goal is to inform management decisions, as one data type may support very different interventions than another.

Lastly, I created HSMs using only data from NABat's acoustic protocol to compare to a model from all occurrences to understand if the data produced by the protocol were sufficient to create a robust HSM. I found that the NABat model was heavily impacted by acoustic data bias and did not create a robust enough model compared to a combined model, arguing for the inclusion of more occurrence records to create a model sufficiently robust enough to inform management decisions. Ultimately, I undertook a rigorous assessment of how various data types perform in the HSM ecosystem and provide recommendations for best practices of developing habitat models for bats using disparate data sources.

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CHAPTER 1: INTRODUCTION

Bats are impacted across North America from white nose syndrome (WNS), wind energy development, and habitat loss and fragmentation, which threatens species both locally and range-wide (Kunz et al. 2007, Farrow and Broders 2011, Frick et al. 2015). Establishing conservation and research that occurs across scales to meet these threats is important for ensuring effective species preservation (Akasaka et al. 2010, Kalda et al. 2015, Bellamy et al. 2020). Due to the difficulty of sampling nocturnal flying mammals, optimizing data collected at local and regional levels for continental scale analyses is the best use of sampling resources (Bellamy et al. 2013, Reichert et al. 2021). Habitat suitability models (HSMs) can merge presence-only data with environmental layers to map suitable habitat across varying spatial scales (Elith et al. 2006, Bellamy et al. 2013, Guisan et al. 2013). With this information, targeted management can be done to maximize return on conservation investment (Rodhouse et al. 2015, Stevens and Conway 2020). Only one species of bat, the Indiana bat, *Myotis sodalis*, (Miller and Allem 1928) has a HSM for Illinois; the other 12 bat species found in Illinois lack HSMs (Cable et al. 2021). To address this gap, three bat species are the focus of this study: the tri-colored bat, *Perimyotis subflavus,* (Cuvier 1832); hoary bat, *Lasiurus cinereus,* (Palisot de Beauvois 1796); and eastern red bat, *Lasiurus borealis,* (Müller 1776). In addition, this study examines the impact of different data types and their biases on large scale HSMs. Lastly, the study will look at the standardized data collection protocol, the North American Bat Monitoring Program (NABat), to see if the data protocol is sufficient to make robust HSMs (Loeb et al. 2015, U.S. Geological Survey 2021).

ECOLOGY & IMPORTANCE OF BATS

Globally, bats are essential components of ecosystems and are threatened by compounding factors of wind development (Kunz et al. 2007, Arnett and Baerwald 2013, Péron et al. 2013), disease (Cryan et al. 2010, Frick et al. 2010, Turner et al. 2011), habitat loss/degradation (Farrow and Broders 2011, Rainho and Palmeirim 2011, Cable et al. 2021), and other factors (Aguiar et al. 2016, Hall et al. 2016, Mendes and De Marco 2018). Bats are the second most diverse mammalian order of mammals and their variety of prey, life history traits, and behavior render them incredibly important components of biodiversity and provide essential ecosystem services from local to global scales (Jones et al. 2009, Kunz et al. 2011, Kasso and Balakrishnan 2013). Among other services, bats pollinate many species of plants, reduce disease vectors and agricultural pests, promote nutrient cycling, and provide billions of dollars in tourism (Jones et al. 2009, Kunz et al. 2011, Kasso and Balakrishnan 2013). Many bat species have experienced severe population declines from disease, habitat loss, and wind energy development, and have become a focus of wildlife conservation and forest management (Kunz et al. 2007, Frick et al. 2015).

Since Illinois is a predominately agricultural habitat mosaic, with cropland covering 75% of the state's total land area, bats likely play an essential role in pest suppression at an estimated value of $74/acre (Luman et al. 2004, Boyles et al. 2011, Illinois Department of Agriculture 2021). However, increasing investments in wind energy, particularly on agricultural lands, compound bat mortalities, particularly threatening migratory bat populations. Wind energy installations negatively impact both habitat connectivity and population viability (Frick et al., 2017; Roscioni et al., 2014). As of 2021, 6,516 megawatts of energy have been installed in Illinois with rapid growth potential (Aldeman et al. 2015, Clean Power Illinois 2021). A Midwest

study found bats are killed at the rate of 0.8-8.6 bats per megawatt per year, though this is considered an underestimate (Anderson et al. 1999, Kunz et al. 2007). Across the United States, an estimated 500,000 bats are killed per year from barometric trauma and blade collisions, and this number is thought to be increasing (Grodsky et al. 2011, Hayes 2013, Smallwood 2020). Without steps taken to mitigate the numbers of bats killed by wind turbines, increasing amounts of wind energy can potentially cause long term damage to bat populations (Arnett and Baerwald 2013, Roscioni et al. 2014, Friedenberg et al. 2021).

In addition to wind energy, WNS, confirmed in Illinois in 2013 (Kath & Froschauer, 2013), is a fungal pathogen that decreased hibernating populations 10-fold nationally, has killed an estimated 6.7 million bats, and has been linked to local population extirpations (Frick et al. 2015, Cheng et al. 2021). WNS dehydrates hibernating bats, causing them to arouse from torpor and burn through essential fat stores before summer, in addition to causing damage to wing tissue (Cryan et al. 2010). Since WNS has taken its toll on bat populations throughout much of the eastern United States, including Illinois, work to rebuild the populations of heavily impacted species with high extinction risk is a conservation imperative (Frick et al. 2015, Hammerson et al. 2017). To mitigate both wind energy and WNS threats, it is critical to manage and conserve habitat resources necessary to maintain populations (Farrow and Broders 2011, Barré et al. 2018, Cheng et al. 2021).

Lastly, habitat loss and fragmentation have a major impact on imperiled bat populations (Farrow and Broders 2011). Across the globe, deforestation, urbanization, and the conversion of contiguous habitat for agriculture and livestock has reduced available habitat for most species (Voigt and Kingston 2016, Barré et al. 2018). Some types of silviculture treatments can be beneficial to bats, including differing thinning treatments across the area and retaining snags.

Some species of bat such as the federally listed Indiana bat rely on shagbark hickory trees for maternity roosts (Carter 2006, Yates and Muzika 2006, Perry et al. 2008). In addition, wind turbines have a 1km buffer of reduced bat activity reducing potential habitat, increasing mortality risk, and fragmenting migration corridors (Cryan 2011, Barré et al. 2018). While underground caves may seem like a safe location from habitat degradation, recreational use of caves during winter may cause bats to arouse from hibernation and burn through fat reserves, reduce survival of young, and reduce thermoregulatory benefits of roosting (Furey and Racey 2016).

While different species of bats have differential home range sizes, all species of bats use habitats on a variety of scales. As volant species, they use resource patches spread across the landscape (Akasaka et al. 2012, Wordley et al. 2015). Some species (e.g. hoary bat) are long-distance migrants, traveling over 1000km, while others (e.g. Indiana bat) are short-distance migrants, traveling approximately 160km from summer roost sites to and from over-wintering hibernacula (Weller et al. 2016, Roby et al. 2019). This dichotomy of both regional and landscape-scale habitat importance emphasizes the need for both protection of migratory corridors and conservation of contiguous habitat across the landscape (Akasaka et al. 2012, Cable et al. 2021). While not all bats migrate, they often forage in different places than they roost, with foraging areas of 50-150 ha (Menzel et al. 2001, Henry et al. 2002, Veilleux et al. 2009). Red bats will travel up to 2.5km from their roost site to forage (Elmore et al. 2005, Walters et al. 2007). At their roost sites, some species of bats often exhibit high roost philopatry. Although they may not use the same roost tree every time, species are known to roost in trees within 50-100m of each other on consecutive nights (Mager and Nelson 2001, Veilleux et al. 2003). Thus, though distances vary for each species, bats use resources on a variety of scales to meet their needs (Bellamy et al. 2020).

Focal Species

The tri-colored bat is a small, short-distance migratory bat found in eastern North America (Fraser et al. 2012). Having one of the longest hibernation periods of bat species, WNS has severely impacted the species, with population losses up to 100% in some hibernacula (Turner et al. 2011). In addition, the species is impacted by wind energy development and as such, has been petitioned for listing under the Endangered Species Act (Kunz et al. 2011, Center for Biological Diversity and Defenders of Wildlife 2016, Endangered and Threatened Wildlife and Plants; 90-Day Findings for Five Species 2017). Tri-colored bats are uncommon to catch via mist-net as the species tends to forage above the trees (Menzel et al. 2005) and prefer partially open habitat, including forest edges and riparian corridors (Amelon et al. 2014), which are often difficult to net effectively. Tri-colored bats prefer to roost in trees, particularly hardwoods such as oaks or pines in a mature forest (Perry and Thill 2007). While regional HSMs have been created, no statewide landscape level models have been published.

The hoary bat is a widespread migratory bat found across North and South America (Cryan 2003, Weller et al. 2016). Due to their migratory behaviors, hoary bats have been severely impacted by wind energy development, comprising an estimated 38% of wind farm mortalities from 2000 to 2011 across North America, the highest proportion among all bat species (Arnett and Baerwald 2013, Weller et al. 2016). Hoary bats usually roost solitarily in trees and are considered foraging generalists (Hayes et al. 2015). As hoary bats are larger and more adapted to foraging in open areas, they often forage above the tree canopy, meaning they are rarely caught in a mist net (Caire et al. 1984, Kalcounis et al. 1999, Menzel et al. 2005).

The eastern red bat is a migratory bat found east of the Rocky Mountains from Canada to Florida (Cryan 2003). A solitary roosting bat, the eastern red bat prefers mature hardwood forests

with substantial foliage and bark roosting opportunities (Mager and Nelson 2001, Limpert et al. 2007, Amelon et al. 2014). They also roost away from development, near openings and edges, typically close to streams (Limpert et al. 2007, O'Keefe et al. 2009). Several habitat studies emphasize the importance of landscape characteristics over plot or microhabitat roost selection for this species, potentially due to their large home ranges and generalist tendencies (Ford et al. 2005, Limpert et al. 2007, O'Keefe et al. 2009, Starbuck et al. 2015). Eastern red bats are known to be clutter adapted, foraging below the tree canopy and allowing for relatively frequent mist netting captures (LaVal and LaVal 1979, Carroll et al. 2002, Menzel et al. 2005).

BAT SURVEYS & THEIR BIASES

Presence and absence data for bat species are commonly acquired through passive (acoustic) monitoring or active (physical) capture (Kuenzi and Morrison 1998, O'Farrell and Gannon 1999, Barnhart and Gillam 2014). Each sampling method has benefits and shortcomings that can influence inferences drawn from the data, ultimately impacting research and management decisions (O'Farrell and Gannon 1999, Hohoff 2016). In addition, each sampling method has different detection probabilities for different species based on their unique natural history, ecology, and biology which creates inherent detection biases (Kuenzi and Morrison 1998, Flaquer et al. 2007, Law et al. 2015, Neece et al. 2019). These biases are important to consider when developing presence-only models as they impact the model's results and interpretation (Barnhart and Gillam 2014, Ford et al. 2016, Hohoff 2016).

Acoustics

Bats navigate, forage, and communicate using echolocation calls that are unique to each species and their purpose (Fenton 2003, Knörnschild et al. 2012). These calls can be recorded non-invasively using ultrasonic microphones and detectors to efficiently gather information on species, presence, and overall activity levels (Gorresen et al. 2008, Coleman et al. 2014, Neece et al. 2019). An acoustic detector is quick and easy to set-up and low maintenance once deployed that can be used in a variety of habitats. Several sites can be deployed in a single day and only need servicing every few weeks for an entire summer. Once deployed, acoustic detectors can gather thousands of calls per night and, over time, terabytes of data. With an appropriate sampling design, a network of detectors can effectively survey an area both spatially and temporally (Rodhouse et al. 2011, Froidevaux et al. 2014, Loeb et al. 2015).

Once collected, acoustic data are analyzed with an automatic call identification software. Acoustic data are easier to collect than capture data, but identifying species based on the call alone is difficult to confirm and with potentially high false-positivity rates (Clement et al. 2014, Banner et al. 2018, Rojas et al. 2019). For example, hoary bat calls are distinctively lower frequency (>20khz) compared to other North American bats, while some Myotis species have very similar calls that are more difficult to identify to species, both via call identification software and manually (Barclay et al. 1999, Russo and Voigt 2016). While automated call software is readily accessible to many biologists, variance among software identification is large and changes with classification updates over time (Lemen et al. 2015, Russo and Voigt 2016, Goodwin 2019). Despite these caveats, acoustic detection is an efficient and relatively easy survey technique (Coleman et al. 2014, Neece et al. 2019). Although variation in detection and

discrepancies in species identification remain, acoustic surveys are accessible to non-bat biologists and managers to survey bats in their area (Seguin 2019).

North American Bat Monitoring Protocol

A standardized protocol that creates an even and informed probabilistic survey design is the best way to maximize resources and make proper statistical inferences to inform conservation decision making (Loeb et al. 2015). The North American Bat Monitoring Protocol (NABat) creates a standardized data collection method, allowing for building occupancy and species distribution models in addition to conducting large-scale change analyses (Banner et al. 2019, Rodhouse et al. 2019, Reichert et al. 2021).

NABat seeks to further understand species distributions, populations, and trends, especially in the face of sudden and abrupt declines (Loeb et al., 2015; Reichert et al., 2018). In order to do so, the program establishes a standardized acoustic-only monitoring protocol through a series of spatially balanced and randomized grid cells, generating data across the United States and Canada (Talbert and Reichert 2018). The generalized random-tessellation stratified (GRTS) cells create a prioritized continental grid of 10km x10km squares (Loeb et al. 2015, Talbert and Reichert 2018, Banner et al. 2019). The number of cells that should be surveyed is determined via power analysis which prioritizes the cells (Banner et al. 2019, Reichert et al. 2021). With the ranking of cell importance, it creates flexibility in the implementation of the program while still ensuring random, stratified, and systematic sampling (Talbert and Reichert 2018). If one cell is unavailable for surveying, other cells of similar importance can be substituted (Loeb et al. 2015).

Each GRTS cell is further broken into four quadrants surveyed annually with two to four stationary points in different quadrants and a mobile transect throughout the entire GRTS cell

(Loeb et al. 2015). The stationary points are placed in habitats representative of the cell's habitat diversity, including public and private lands with landowner permission (Loeb et al. 2015, Seguin 2019). The stationary detectors are deployed for at least four nights in the summer, with the potential for spring and fall surveys (Loeb et al. 2015). The 25-48 km mobile transect is driven twice during the summer with an acoustic detector elevated on a pole outside of a vehicle (Loeb et al. 2015). While stationary points cannot estimate abundance, mobile transects better estimate abundance by maintaining a driving speed of 32kph, which is faster than bats can fly (Seguin 2019). Mobile transects also survey a larger area of land and diversity of habitat types, although a species bias has been found from the recordings (Loeb et al. 2015, Braun de Torrez et al. 2017, Fisher-Phelps et al. 2017). NABat also encourages surveys of private lands with landowner permission, which may otherwise have been a roadblock to surveying (Seguin 2019). With the combination of spatial and temporal diversity through multiple acoustic survey types across multiple years, NABat establishes a rigorous acoustic survey.

A benefit of the NABat protocol is the accessibility of the program to local and regional agencies that may otherwise have been prohibitive. The NABat data collection, while organized by a state or federal agency, can be implemented by community scientists (Seguin 2019). This brings both an educational aspect to the public, but also reduces the work load for biologists (Neece et al. 2019, Seguin 2019, Rodhouse et al. 2021). In addition, most of the acoustic equipment is re-used each year, yielding a higher start-up investment, but low annual maintenance cost (Seguin 2019). After data are collected, acoustic processing is completed through automatic call identification software, before being uploaded to an online database (Loeb et al. 2015, Reichert et al. 2018). This removes the need for an acoustics expert to manually review the calls, reducing process time (Nocera et al. 2019). While this program

provides data and information to the local biologist, it also provides data benefits on a larger scope as part of the program. Collaborative monitoring in NABat across the United States increases the amount of data collected while spreading out the responsibility for data collection (Neece et al. 2019, Reichert et al. 2021).

Many U.S. states and Canadian provinces have already implemented this survey protocol, while others are in the planning stages (Reichert et al., 2021). Every state has surveyed at least some of the GRTS cells (U.S. Geological Survey, 2021). The Illinois Bat Conservation Program has implemented 20 GRTS cells across the state since 2016, with 10 additional GRTS being added in 2022 (Illinois Bat Conservation Program, 2021). In Nebraska, 35 GRTS cells were implemented in 2017 with 12 being covered by community scientists. (Seguin 2019). In South Carolina, 20-25 GRTS cells between 2015-2016 were surveyed and 35-38 priority GRTS cells had a mobile transect (Neece et al. 2019). NABat generates terabytes of landscape scale data through a standardized acoustic protocol that uses unbiased habitat selection. Utilizing these data to create HSMs can be a way for states to gain information for their bat species with little additional field work or expenses.

Captures

Alternatively, physical capture (i.e. mist-netting) can definitively identify species in hand but can be invasive, time and labor intensive and, thus, expensive, while producing low amounts of data compared to acoustics (Kuenzi and Morrison 1998, Winhold and Kurta 2008, Clement et al. 2014). Mist netting is a common technique for bird and bat surveys that involves placing a fine net across a flyway to catch animals flying through. A mist netting operation needs a skilled, experienced, permitted, and rabies vaccinated crew to remove bats from the net (U.S. Fish & Wildlife Service 2020). In addition to the field work of mist-netting, all gear must be

decontaminated following the U.S. Fish and Wildlife service WNS protocol to ensure the fungus that causes WNS is not passed between sites (U.S. Fish & Wildlife Service 2020). However, once the bat is in hand, morphological measurements can usually confidently identify the bat down to species. In addition, taking a tissue sample (guano, hair, wing punch) can confirm species via genetic analysis (Walker et al. 2016, 2019, Guan et al. 2020).

The effectiveness of mist netting changes across a bat's life cycle and decreases with repeated nights of mist-netting (MacCarthy et al. 2006, Weller and Lee 2007, Winhold and Kurta 2008). Fully sampling multiple habitats in an area can take weeks of netting. In addition, mist-netting can be more difficult in some habitats (Carroll et al. 2002). Without surrounding vegetation or structures to funnel bats into the net, bats can easily sense the net and avoid capture (Carroll et al. 2002, MacCarthy et al. 2006, Geluso and Geluso 2012). It is also possible to capture zero bats for a night of mist netting as bats can avoid the net, bounce out of the net, and even free themselves before they are removed (MacCarthy et al. 2006). Of utmost importance. mist-netting involves capture and handling of the bats which always creates a small, but present risk of injury or death to the bat (U.S. Fish & Wildlife Service 2020).

Another method of physical capture is carcass counts from wind farm mortalities, which has been used in previous HSMs and population modeling (Péron et al. 2013, Roscioni et al. 2014). Migratory bats (e.g. hoary bats and eastern red bats) are disproportionally affected by wind farms as they follow their migration routes, while some species are rarely or never found at wind farms (Kunz et al. 2007, Cryan 2011). Wind farms can only represent one spatial location as they are permanent fixtures on the landscape. Additionally, it can be difficult to obtain carcass data from wind farms as they do not generally share their mortality data.

Biases

Every survey method has its own data quality and species detection biases (Gu and Swihart 2004, Yamaura et al. 2016, Braun de Torrez et al. 2017). Recognizing bias and how it will impact model results is essential to proper model interpretation (Barnhart and Gillam 2016, Ford et al. 2016, Hohoff 2016). Most bat HSMs use data from various methods of capture and monitoring efforts (mist netting, telemetry, historic captures, etc.), with mist-netting being the more prevalent choice, although some studies have used both (Weber and Sparks 2013). In a local scale model predicting presence of northern long-eared bats, *Myotis septentrionalis,* (Trouessart 1897), unique detection types had a number of different variables with varying predictive fits (Ford et al. 2016). In a state-wide HSM, the difference in model predictions between an acoustic and capture HSM varied greatly among species (Barnhart and Gillam 2014). While many papers have investigated detection bias in occupancy models even in bats, few papers have looked at the effects of detection bias in HSMs (Gorresen et al. 2008, Hohoff 2016, Rojas et al. 2019).

While acoustic monitoring is an incredibly efficient monitoring tool, there are detection and quality biases among species, detector brand, and habitat type (Adams et al. 2012, Frick 2013, O'Keefe et al. 2014). Varying call frequencies and distances can cause differences in recording between detector brands (Waters and Walsh 1994, Adams et al. 2012). In addition, louder low-frequency calls are more detectable than higher frequency calls which more rapidly attenuate due to the structure of the sound wave (Lawrence and Simmons 1982, Adams et al. 2012). Vegetation and environmental conditions also change detection probability, as both dense foliage and inclement weather reducing detections (Egebjerg and Lee 1999, O'Keefe 2009, Neece et al. 2019).

There are species biases in mist-netting as well. Bats that forage above the tree canopy, higher in the sky, or in open habitats (e.g. hoary bat) are more difficult to catch than those that forage lower in the tree canopy (Caire et al. 1984, Kalcounis et al. 1999, Menzel et al. 2005). When cross-checked with cameras, mist-netting only caught 3.2% of bats in the airspace, and efficacy decreases over time as bats remember net locations (Larsen et al. 2007).

HABITAT SUITABILITY MODELING

One commonly used tool for identifying high quality habitat for targeted conservation efforts are HSMs, which produce spatial predictions of suitability across various scales based on occurrence data and environmental/ecological variables (Hirzel et al. 2006, Pearson et al. 2007). Globally, HSMs have been used across a broad array of taxa, a variety of geographic scales, and in varied ecological contexts to understand resource use, species occurrence, and habitat preferences (Boyce and McDonald 1999, Guisan and Zimmermann 2000, Hirzel et al. 2006). Accordingly, HSMs can provide essential species-specific information for federal, state, local and private land management decisions, policy planning, and conservation interventions both under current conditions as well as under future climate and land use scenarios (Gorresen et al. 2005, Razgour et al. 2011, Bellamy et al. 2013). HSMs can operate at multiple scales to pinpoint relevant ranges based on the species' ecology and life history traits (Razgour et al. 2011, Zellmer et al. 2019, Bellamy et al. 2020).

As wide-ranging fliers, bats forage and roost in a variety of habitats, including from small, isolated patches to large, contiguous corridors. On a landscape scale, species of migratory tree bats do fly 200-2000 km between summer and winter habitats (Cryan et al. 2004, Neubaum

et al. 2006, Krauel et al. 2018). Landscape connectivity is important to ensure safe migratory routes are preserved for long-distance and regional migrants. On a smaller scale, roosting and foraging resources are important on scales ranging from 100m to 1km (Veilleux et al. 2003, 2009, Cable et al. 2021). Many species forage around 2 km from roosting sites and once at the foraging site, stand-level features influence prey assemblage (Henry et al. 2002, Dodd et al. 2012, Bellamy et al. 2013, Cable et al. 2021). Habitat features vary in the scale of importance for different bat species (Bellamy et al. 2013). As such, they can be impacted by habitat changes at all scales (Ford et al. 2005, Razgour et al. 2011, Bellamy et al. 2013). Consequently, landscape scale research is necessary to identify essential habitat patches and corridors used by multiple bat species to strategically target conservation actions (Bellamy et al. 2013, Bellamy and Altringham 2015, Zellmer et al. 2019). Looking for cost-effective ways to implement landscape-level habitat conservation is important for statewide management decisions.

For many landscape-scale HSMs, environmental variables includ 19 climate variables from the WorldClim Bioclimatic database, with historical datasets available at a small-scale resolution (Soto-Centeno et al. 2015, Fick and Hijmans 2017, Torres-Morales et al. 2019). Smaller scale HSMs for bats often focus on forest stand scales,aand assess roost tree suitability. In these instances, forest stand metrics (e.g. diameter at breast height (DBH), tree species composition, percent canopy cover, etc.) are often cross validated in the field. Land-use and elevation are also often incorporated into HSMs based on publicly available national datasets. While most HSMs are utilized for identifying habitat and species distributions, bat HSMs can also be utilized to identify disease and virus emergences (Escobar and Craft 2016, Deka and Morshed 2018).

Additionally, there are several algorithms that can be utilized to create HSMs such as generalized linear models, ecological niche factor analysis, and ensemble modeling. The most popular approach is maximum entropy modeling, which is primarily used through the program MaxEnt with a user-friendly graphical interface (Phillips et al. 2006, 2021). MaxEnt estimates a species distribution across geographic space and can be created with presence-only data (Phillips et al. 2006). The probability distribution is estimated by finding the density of the covariates at presence sites and comparing them to the density of covariates across study area to find the relative habitat suitability at locations (Elith et al. 2011, Merow et al. 2013). The maximum entropy, or optimal probability distribution, is calculated by comparing habitat preferences found with presence location compared to a null model that the species does not prefer any habitat type (Elith et al. 2011). When compared to other types of modeling, MaxEnt preforms well with presence-only data (Elith et al. 2006, Phillips et al. 2006).

Modeling habitat suitability for bats is particularly useful as they are nocturnal, utilize large home ranges, and are difficult, if not impossible, to identify in flight (Greaves et al. 2006). Without HSMs, it becomes much more difficult to assess which habitats are critical targets to increase connectivity, to develop data-driven conservation plans, and predict future habitat needs caused by climate change and anthropogenic development (Razgour et al. 2011, Aguiar et al. 2016, Zellmer et al. 2019). HSMs are frequently used in bat conservation, but comparisons of acoustic data versus physical capture data are few and often suffer from low sample size, limited geographic scope, and/or other factors, limiting their broad applicability (Barnhart and Gillam 2014, Ford et al. 2016). Finding the optimal data type necessary for creating a sufficient HSM is important for agencies to be able to focus their sampling.

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CHAPTER 2: ONE MODEL TO RULE THEM ALL: IDENTIFYING PRIORITY BAT HABITATS FROM MULTI-SPECIES HABITAT SUITABILITY MODELS

ABSTRACT

Bats are critical components of global ecosystems, providing essential ecosystem services with substantial economic benefit. Yet, North American bat populations have been severely and negatively impacted by myriad of factors (e.g. disease, wind energy development) with compounding effects. Given the above, bats are a focus of intense conservation and management. As wide-ranging flyers, bats utilize habitats at a variety of scales, from small, isolated patches to large, contiguous corridors. Landscape-level research is necessary to identify critical habitats, patches, and corridors to strategically target management interventions. Habitat suitability models (HSMs) identify high quality habitat by predicting species occurrence at various spatial scales based on occurrence data and environmental variables. Using species-specific landscape and climate variables, I created HSMs for three bat species (hoary bat, eastern red bat, and tri-colored bat) across Illinois. With the three models from this study and a previously published HSM for Indiana bats, I stacked binary HSMs, thereby identifying priority conservation areas across Illinois. I found that species exhibited different distributional patterns and habitat preferences across Illinois. Multi-species HSMs highlight high quality habitat in southern Illinois and along big river riparian areas. This approach identified priority conservation areas, which allows managers to strategically target restoration and conservation measures, invest funds in habitat likely to have high return-on-investment, and inform decisions like siting wind turbines or purchasing mitigation lands.

INTRODUCTION

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 per acre, an impact which cannot be understated in this regional agroecosystem where 75% of Illinois is traditional row crop (Boyles et al. 2011, Maine and Boyles 2015, Illinois Department of Agriculture 2021). Within this agroecosystem, wind energy is expanding. In 2021, Illinois produced over 6,300 megawatts of wind energy, which is estimated to kill bats at a rate of 0.8-8.6 bats/megawatt/year, disproportionately impacting migratory bats (Anderson et al. 1999, Kunz et al. 2007, U.S. Energy Information Administration 2021*a*). In addition, the fungus, *Pseudogymnoascus destructans*, causes a disease called white-nose syndrome (WNS) which is estimated to have 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 impacted in nearly all phases of their annual cycles by these many issues (i.e. migrating, foraging, and hibernating), causing population declines and concerns for their persistence into the future.

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 both short and long-distances (150-1000 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 these multiple scales. Appropriate ecological scales can be quantified via habitat

suitability models (HSMs), which tests variables across multiple scales (Razgour et al. 2011, Bellamy et al. 2020). This facilitates variable selection at species-specific scales of importance, informed by life history and behavior, and incorporating multiple scales into landscape-wide models (Bellamy et al. 2013, Bellamy and Altringham 2015).

Multi-species (or "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). Cost-effective approaches for landscape-level habitat conservation are important for statewide management decisions. 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 both stacked and individual HSMs can help translate field data into models and maps that can inform decision making in management and policy (Guisan et al. 2013, Zellmer et al. 2019, Stevens and Conway 2020).

The goal of this study was two-fold. First, I sought to develop individual HSMs for three Illinois bat species: the eastern red (*Lasiurus borealis*), hoary (*Lasiurus cinereus*), and tri-colored bat (*Perimyotis subflavus*) using landscape and climatic variables believed to be important to each species. Second, to develop a multi-species HSM that includes the three focal bats and the federally endangered Indiana bat (*Myotis sodalis*). I chose these species due to their vulnerability to white-nose syndrome (Indiana bat and tri-colored bat) or wind energy development (eastern red bat and hoary bat). Specifically, I sought to answer the following research questions: 1) What are the main summer use habitats and their characteristics for the eastern red, hoary, and tri-colored bat? 2) Based on these preferences, where would I expect to find them across Illinois? 3) Considering these four focal species, where are priority conservation habitats for chiropterans

throughout the state? Ultimately, these models provide actionable information for Illinois state biologists and land mangers by providing landscape-level habitat information for approximately one-third of Illinois' thirteen bat species. While these models explicitly predict suitability in Illinois, finding important habitat characteristics of these species can promote species conservation across all bat populations, especially in Midwestern states in similar habitat mosaics and with shared existing threats.

METHODS

Study Area

Illinois is a habitat mosaic 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 thirds of Illinois is dominated by agriculture and an urban/suburban/exurban interface, while the southern third is home to the Shawnee National Forest; 280,000 acres of forest managed by the U.S. National Forest Service (Iverson 1988, Luman et al. 2004, Rey 2004). The middle third of the state is primarily row crops (corn and soy) with small, isolated forest fragments, riparian corridors, degraded prairie, and urban areas. Across the state, Illinois forests are primarily composed of hardwood deciduous trees with major riparian zones along the Illinois and Mississippi rivers.

Study Species

Midwestern bat species exhibit a diversity of life history characteristics. The eastern red bat, *Lasiurus borealis* (Müller 1776) is a common generalist forager that primarily roosts solitarily in foliage and tree bark (Limpert et al. 2007, Perry et al. 2007). Their longer, narrow wings are adapted for fast flying over long distances and foraging in forest gaps, edges, and openings (Walters et al. 2007, Amelon et al. 2014, Starbuck et al. 2015). The hoary bat, *Lasiurus*

cinereus (Palisot de Beauvois 1796), migrates long-distances (>1000 km) and primarily forages in open spaces, both behaviors linked with high wind-turbine mortality (Hayes et al. 2015, Weller et al. 2016, Friedenberg et al. 2021). The tri-colored bat, *Perimyotis subflavus* (Cuvier 1832) has the longest hibernation period in Illinois, contributing to devastating population losses from white-nose syndrome and prompting its candidacy for listing under the U.S. Endangered Species Act (ESA) (Turner et al. 2011, Center for Biological Diversity and Defenders of Wildlife 2016, Cheng et al. 2021). They most often roost in live or dead foliage in mature forest stands and forage above the trees and in partially open habitat and riparian areas (Veilleux et al. 2003, Kalcounis-Rüppell et al. 2005, Farrow and Broders 2011). There is not much known about their migration ecology, however they may be long distance migrants (Fraser et al. 2012). Lastly, the Indiana bat (*Myotis sodalis)* (Miller and Allen 1928), listed as "endangered" under the ESA, is a regional migrant, with the longest recorded distance traveled of 575km. This species forms large maternity colonies, typically in snag roosts during the summer (Carter and Feldhamer 2005, Hammond et al. 2016, Roby et al. 2019). In Illinois, these maternity roosts occur in cottonwood-elm bottomlands or oak-hickory uplands (Carter and Feldhamer 2005, Carter 2006, Schroder et al. 2017). Given its endangered status, the Indiana bat has a greater body of published literature devoted to it, including a state-wide HSM for Illinois (Cable et al. 2021). These four species represent common to rare species that rely on both open and forested interior and edge habitats for roosting and foraging.

Occurrence Data

Historic capture data was acquired via data sharing agreements with the Illinois Department of Natural Resources (IDNR) and the U.S. Fish and Wildlife Service for both mist-netting and summer wind farm mortalities from 1999-2021. Since IDNR primarily maintains

records for threatened and endangered species, the historic capture data was incomplete for non-listed species. Thus, I contacted IDNR's list of Illinois mist-netting permittees, requesting mist-netting records for the three focal species between 1999-2021. Eight permittees responded which added to the data from 2015-2019 generated by the Illinois Bat Conservation Program (IBCP) at 46 mist net sites. I combined windfarm mortality and mist-net records, reducing the number of individual records to one per mist-netting location or turbine site. For all data, I removed sites with low positional or temporal accuracy, or lacking no data associated with captures.

IBCP collected 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 2021). Song Meter SM4BAT Full Spectrum Ultrasonic Recorders or Pettersson D500x were deployed in 2-4 quadrants in each GRTS cell with a SMM-U1 or U2 microphone (Pettersson Elektronik AB, Wildlife Acoustics). IBCP typically chose sites in each quadrant to represent habitat diversity in each cell. I deployed recorders for a minimum of four good weather nights (i.e. no rain, temperature > 60 degrees, sustained wind < 8 mph). I used the same protocol for all years, and sites remained largely unchanged, with some exceptions due to landowner permissions or personnel changes. Data were recorded from 19:00 to 7:30 each night. IBCP also sampled acoustic monitoring sites across Illinois that were surveyed with a similar acoustic protocol as GRTS cells. These data are considered presence-only as survey effort at each site (i.e. four nights) is insufficient to determine absence (Moreno and Halffter 2000, Skalak et al. 2012).

Using the NABat protocol (Reichert et al. 2018) I processed all files recorded in the field through Sonobat 4 software (Arcata, CA) using the medium filter to reduce noise files (Szewczak 2010). I ran Kaleidoscope Pro 5.4.0 as the auto-classifier (Kaleidoscope Pro n.d.).

Kaleidoscope is a powerful auto-classifier that, in addition to identification, provides maximum likelihood estimates of species occupancy by night. I considered below $\alpha = 0.05$ to be present and above $\alpha = 0.05$ to be absent following standard conservative protocols (Nocera et al. 2019, U.S. Fish & Wildlife Service and U.S. Geological Survey 2019). These acoustic data were not manually vetted since NABat does not require manual vetting for data upload. All data was processed in 2021 to ensure that the classifier's conditions were the same through all analyses.

Acoustic and capture data were combined and processed in R 4.1.2 (R Core Team 2021). To reduce spatial autocorrelation, I removed records within 1 km of each other. Records were also temporally restricted from May 15th - Aug 15th to ensure that no records were from migratory periods, per U.S. Fish and Wildlife Guidelines (U.S. Fish & Wildlife Service 2020). After data cleaning and quality control, there were 264 occurrences for eastern red bats (17 from wind turbines, 159 from mist-netting, and 88 from acoustics), 116 occurrences for hoary bats (9 from wind turbines, 21 from mist-netting, and 86 from acoustics), and 106 occurrences for tri-colored bats (77 from mist-netting, and 27 from acoustics) established.

Environmental Layers

I used 16 landcover variables (Table 1) (per Cable et al. 2020) created from the Illinois Geospatial Clearing house land cover layer (Illinois Department of Natural Resources et al. 2003). Cable et al. (2020) used Fragstats (McGarigal and Marks 1995) to calculate the number of patches, total area, and total edge of land cover types relevant to Indiana bat ecology. Each metric was calculated at three different scales statewide (0.1km, 0.5km, and 1km) to determine the appropriate scale of each landcover variable in predicting suitability for roosting, foraging, and landscape distances. I chose to keep the same spatial scales across all species to maintain consistency.

Nine additional variables were also considered based on top models of published

chiropteran HSMs or occupancy models (Table 1). Many of these variables were forest stand

structure or topographical landscape metrics, gathered from publicly available GIS layers and

resampled in ArcGIS for 0.1km resolution to match layers (Cable et al. 2020). Both temperature

and precipitation layers were taken from a 30-year normal and averaged across May-Aug to

represent the summer average (PRISM Climate Group 2021).

Modeling

For all variables, I created single-predictor models for each bat species in MaxEnt v3.4.4

(Phillips et al. 2006, 2021) to select the optimal spatial scale for variables and chose the top 15

variables for each species by AUC_{test} scores to minimize over-parameterization. For univariate

models, I used the default parameters with 20 replicates, and 10% random test percentage

(Phillips et al. 2021). Using AUC_{test} scores, I determined the best spatial scale for each species

for each landcover variable. I ranked the top scaled landcover variables among the non-scaled

variables, selecting the top 15 variables for each species with AUC_{test} >0.5. The top 15 variables

for each species were carried through subsequent analyses.

Using the combined species-specific variables, I tested differing regularization

multipliers ranging from 1-12 using the same default parameters of 20 replicates and 10% as a

random test percentage. The regularization multiplier with the top AUC_{test} score was used 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, I 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, proxies were chosen based on the available variables (e.g., if the top

model in the literature had basal area, stand density index was substituted (U.S. Forest Service

2012)). A correlation matrix was created in ArcGIS for the 15 variables for each species and

highly correlated variables (>0.7) were removed maintaining the variable with the higher AUC_{test}

value. After a literature review for each species, at least 23 models were created for each species,

utilizing all variables in multiple combinations and used each variable at least twice (Table A.2,

A.3, A.4). All models were run in MaxEnt using presence-only data, top regularization

multiplier, 20 replicates, 10% of datapoints withheld for testing from the dataset by Maxent, and

5000 maximum iterations. For pseudo-absence points, MaxEnt randomly 10,000 sampled

background points across the state via bootstrapping.

Model Comparison

Models were evaluated via AUC_{test} scores and ranked by AICc scores using raw outputs

and LAMBDAS files in EMNTools (Bozdogan 1987, Warren et al. 2010, Warren and Seifert

2011). 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). I 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):

$$logistic = (raw * e^{entropy})/(1 + raw * e^{entropy})$$

Top models (i.e. AICc weight> 0.01) were combined in ArcGIS using the "weighted sum"

function proportionally according to AICc weights, creating a final model for each species. To

create binary models, I created a threshold of omission for each species based on the bottom 10%

of suitability scores for true presences in the test datasets (Hovick et al. 2015). To calculate variable importance of the candidate set, I added the AICc weight value of each model that contained each variable. For any variable with a weight of 1, I created response curves based off the values provided by Maxent.

Based on the three HSMs created above and the existing HSM for Indiana bats (Cable et al. 2020), I created a stacked HSM for the four species across Illinois. With the final binary model for each species, I summed the four models across the state with equal weights. This created a raster layer with integers from 0-4 where a value of 2 indicated suitable habitat for two species.

RESULTS

The best spatial scale for each variable varied among species, indicating the importance of habitats at different scales and reflective of species' biology/ecology (Table A.1). For the eastern red bat, seven variables were optimal at 1km, two variables at 0.5km, and five variables at 0.1km. For the hoary bat, five variables were optimal at 1km, zero variables at 0.5km, and nine variables at 0.1km. For the tri-colored bat, five variables were optimal at 1km, seven variables at 0.5km, and two variables at 0.1km.

Across all species, nine 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 five variables exclusive to the species, whereas eastern red bat and tri-colored bat only had one unique variable each (distance to road for the tri-colored bat versus distance to water for the eastern red bat), although the spatial scales on some variables differed. Both eastern red bat and tri-colored bat

had more variables associated with forest structure and density, while the hoary bat had more variables related to landscape openness.

The top model for the eastern red bat was composed of elevation, total area of agriculture in 0.1km, total area of forest in 0.1km, total area of water in 1km, total edge of forest in 0.1km, and total edge of water in 1km (Table 3). This model had just over half of the AICc weight (0.51), with the next top model having 0.37 of the AICc weight. The second model was comprised of canopy cover, distance to water, quadratic mean diameter, total area of agriculture in 0.1km, total area of bottomland forest in 1km, total area of forest in 0.1km, and total area of water in 1km. Finally, the global model (AICc weight of 0.11) was composed of existing vegetation height, elevation, distance to water, quadratic mean diameter, total area of agriculture in 0.1km, total area of bottomland forest in 1km, total area of forest in 0.1km, total area of water in 1km, total edge of forest in 0.1km, and total edge of water in 1km. After averaging all three of the top models, the total 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, as well as contiguous sections of agricultural land in central Illinois (Fig. 1). Variable response curves reveal (Table A.5) that eastern red bat's most suitable habitat is composed of less agriculture at 100m (30%) and more forest area at 100m (40%) than state average, while the amount of water in 100m (< 10%) is approximately the state average.

The top model for hoary bats was an ecologically relevant hypothesis modeling current and historic human use. Top variables recovered were distance to road, total area of agriculture in 0.1km, and the total area of urban land cover in 0.1km (Table 3). This model had all AICc weight and an AUC_{test} value of 0.74, ensuring that all three variables had an importance of 1 (Table A.5). It 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 (Fig. 1). Suitable hoary bat habitat was found slightly farther from roads than average, with less total agricultural area than average (50%) and more urban land cover (50%) than average.

Two tri-colored bat models contained all AICc weight, with the top model composed of canopy cover, elevation, distance to roads, number of patches of forest at 0.1km, total edge of forest at 0.5km and total edge of water at 0.5km (Table 3). The second model removed number of patches of forest at 0.1km (AICc of 3262). Both models had AUC values over 0.87, indicative of a good fit to the data. The model recovered a scant 27.96% of the state as suitable habitat (Fig. 1), composed of much higher canopy cover (75%), lower elevation (200m), higher total forest edge (22%), further distance from roads (12,000m) , and lower total edge of water (50%) than the Illinois average.

The final summed (multi-species) raster revealed most suitable habitat in the southern extent of Illinois, comprised largely of the Shawnee National Forest and following hydrologic features northward (Fig. 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.

DISCUSSION

Single-species HSMs

Each HSM for the eastern red bat, hoary bat, and tri-colored bat largely comport with habitat preferences and suitable habitats in other parts of the species' ranges, however this is among the first landscape-scale HSMs for most of these species (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 landcover variables were important at the (0.1km) foraging and roosting scale, while water variables were important at the landscape (1km) scale. This indicates that red bats choose suitable areas with available roost sites. As eastern red bats are known to fly ~2km from roosts to foraging locations, the importance of water is reflected at landscape scale (Elmore et al. 2005, Walters et al. 2007). Stand structure and density variables (e.g. existing vegetation height and 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 suitable habitat is distributed along big rivers, as well as the agriculturally dominated central "corn desert" 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 landcover as suitable habitat.

As a high-flying, open area forager, suitable hoary bat habitat differed from 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 landcover and less on forests. In addition, univariate AUC values were lower overall (AUC > 0.65,) and the top model had with an AUC value less than 0.8 (AUC = 0.75), 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 chooses pseudo-absence points. Most occurrences (both acoustic and wind turbine mortalities) are from open row crop agricultural areas which are areas similar to background areas, and reflective of the broad landcover of the state. The optimal spatial scale (0.1km) 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, total area of agriculture, and total area of urban landcover reflect the open landcover preference of hoary bat.

While using both urban and agriculture as suitable habitat 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. Large tracts of once suitable agricultural habitat area are being developed with 1,100 additional 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 south-east), from the agroecosystem of the Midwest to the open desert in the Southwest to offshore developments on both coasts for a total production of 338 billion kilowatt-hours nationally (U.S. Energy Information Administration 2021*a*, *b*). The hoary bat occurs in every state and country in North America and thus this source-sink dynamic could be seen across almost the entirety of its range, where hoary bats find suitable habitat, but are

killed by wind turbines (Pulliam 1988, Hayes et al. 2015). While the hoary bat is not currently

being considered for listing, substantial concern of the effect of the long-term impacts of

increased wind energy development on the population viability of the species exists (Frick et al.

2017, Friedenberg et al. 2021, Wieringa et al. 2021).

Both the eastern red and hoary bat are habitat generalists, but 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 have been shown to be important for foraging and roosting (Menzel et al. 2005, Perry and

Thill 2007, O'Keefe 2009). Important roosting variables, such as tree height, tree size and

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 0.5km which may indicate that fine-scale features are more

predictive of where they'll 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 as well as total edges of water and forest, which has been thought to minimize

commuting benefits (O'Keefe 2009). In these models, distance from roads and increasing forest

edges and canopy cover indicate 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 River) 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 are

worrisome and should be considered during the listing of the tri-colored bat under the U.S. ESA if forested habitat is being converted to agriculture across the state.

While the creation of a HSM for the Indiana bat was done under Cable et al. (2020), the modeling methods paralleled this paper. With some additional forest metrics tested herein, the only other difference was that Cable et al. (2020) 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. The HSM for the Indiana bat is not shown in this thesis, however the top model for this species was the "Goldilocks" model with total area of forest in 0.5km, total area of agriculture in 0.5km, total area of water in 0.5km, elevation, distance to hibernacula, and total area of urban in 0.5km with 30% of the state as suitable habitat. Across the state, suitable habitat was found in places of low elevation forested riparian floodplains, often leaving snags preferred for roosting. Suitable habitat closely followed riparian zones along the Illinois and Mississippi Rivers with most of the suitable habitat confined to the bottom third of the state.

Multi-species HSM

The multi-species HSM represents core habitat for nearly one-third of Illinois' bat species, two of which are either federally listed, or under consideration for listing. Additionally, these four 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). Total area or edge of water, agriculture, and forest had a variable importance of one for at least three of the four focal species. In addition, the forested southern third of the state and the riparian areas along big rivers represent core bat habitat. Much of these

highly suitable riparian habitats for three and four species remains connected through the river system, thus maintenance of this connectivity is critical (Cable et al. 2021). Riparian habitat has been shown as 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 agriculturally dominated parts of the state as well as the top third, there remains pockets of suitable habitat for two species. As a representative sample of Illinois bats, this model stands as a baseline for change based on potential environmental impact of climate change or urbanization (Arumoogum et al. 2019, Stevens and Conway 2020).

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. Three of our focal species are tree-obligate bats leading to a greater emphasis on forested habitat, which potentially skews the model away from the hoary bat which roosts in trees but prefers foraging in open habitat. 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 habitats overlap for all species but areas suitable for three of the species may be sub-optimal for hoary bats. As rare forest obligates, the habitat-limiting HSM's were the tri-colored bat and Indiana bat (Farrow and Broders 2011, Cox 2019, Cable et al. 2021). Restricting management and conservation decisions to suitable habitats with range-restricted species will ignore suitable 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 suitable habitat for

more species neglects potential bat habitat across the state, especially in core habitat of the hoary bat, which may be essential as wind energy develops.

While HSMs give a landscape scale view of suitable habitat, they don't incorporate biotic factors that may be limiting to some species like competition and predation (Freeman and Mason 2015). In addition, these models only define suitable habitat for general summer use. Modeling migration corridors for both long- and short-distance migrants may find additional areas of important suitable habitat as well as ideal maternity habitat during the summer (Hayes et al. 2015, Gottwald et al. 2017, Wieringa et al. 2021). Stacked multi-species HSMs may also over-predict species richness across a landscape, however a stacked HSM outperforms a joint HSM, which uses combines species occurrences in one model run. Thus, this can still be used for consideration of considering habitat conservation and management decisions (Mateo et al. 2012, Del Toro et al. 2019, Zurell et al. 2020).

Management Implications

Our multi-species HSM reveals core habitat by creating a landscape-level model based on suitable habitat at smaller scales. As such, suitable areas should be a target for restoration, enhancement, and/or protection, particularly in and adjacent to areas of contiguous habitat. Much of the suitable 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). Multi-species HSMs have been used to inform reserve networks and biodiversity reserves for other species (Buchanan et al. 2011, Cooper-Bohannon et al. 2016, Stevens and Conway 2020). With identified core habitat for all four bat species, land protection in the public trust is imperative to maintain sufficient habitat and prevent loss and degradation (Buchanan et al. 2011, Cooper-Bohannon et al. 2016). In addition, best forestry management practices for bats, including

maintaining snags for tree roosting species, removal of invasive forest plants, and maintaining water quality, should be prioritized in core habitats (Leput 2004, O'Keefe 2009, Welch and Leppanen 2017). Highlighting these areas provides wildlife managers the ability to advocate for bat-friendly management on their lands.

In this mosaic system, patches of unsuitable habitat are often adjacent to or surrounded by suitable habitat, and thus remain important for these volant species. Unsuitable areas, in this context, could therefore be targets for land acquisitions as a part of remediation efforts, and restored into prairie and/or forest habitat, thereby increasing overall suitable habitat areas and increasing habitat continuity (Starbuck et al. 2015, Barré et al. 2018, Sandoval-Herrera et al. 2020). Cable et al. (2020) identified priority areas within 125km of Indiana bat hibernacula that could be key areas for habitat restoration and limiting wind turbine siting. Beyond the value in guiding land acquisitions and restoration efforts, these same results can inform where to limit siting of wind turbines and monitoring water quality for contamination to increase and improve habitat suitability (Starbuck et al. 2015, Barré et al. 2018, Sandoval-Herrera et al. 2020). Ultimately, prioritizing restoration funds in unsuitable areas should expand suitable habitat and maximize return-on-investment by merging with established suitable habitat. This is especially relevant as wind energy companies often buy land as mitigation for wind turbine mortalities (Smallwood 2013, Roscioni et al. 2014). HSMs can inform both potential areas to avoid for wind turbine development as well as highly impactful habitat mitigation sites for multiple species, including endangered or migratory species (Santos et al. 2013, Roscioni et al. 2014).

In contrast to the above, wind energy development in 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 suitable habitat has been linked to decreases in wind-turbine mortalities (Santos et al. 2013, Vanausdall et al. 2018). Our results reveal considerable unsuitable habitat in the eastern-central part of the state. Given this, our HSM should be considered when deciding where to site wind turbines, ideally siting new developments away from identified core habitat areas in the east-central region. In addition, HSMs for spring and fall migrations should be modeled and considered. If new wind energy development must be placed in or adjacent to suitable habitat, especially for multiple species, increased mitigation directed towards habitat restoration (as above) should be considered to offset losses, and adaptive management, like curtailing turbines when wind speed is over 7km/h or during migration season should be considered (Arnett et al. 2011, Roscioni et al. 2014, Smallwood and Bell 2020).

ETHICS STATEMENT

Mist-netting and bat handling occurred under IACUC Protocol 16074 and IRB UIUC IBC-18.1 which was approved by the University of Illinois Committee and all appropriate state (Illinois 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]).

TABLES AND FIGURES

Table 1. Variables tested in univariate models for the eastern red, hoary, and tri-colored bat.

Variables	Spatial scale (km)	Original data source	Creator
Aspect	0.1	(U.S. Geological Survey 2018)	Gaulke
Canopy Cover	0.1	(U.S. Geological Survey 2018)	Gaulke
Elevation	0.1	(U.S. Geological Survey 2018)	Gaulke
Distance to Roads	0.1	(Illinois Department of Transportation 2018)	(Cable et al. 2021)
Distance to Water	0.1	(U.S. Geological Survey n.d.)	(Cable et al. 2021)
Existing Vegetation Height	0.1	(U.S. Department of Interior et al. 2013)	Gaulke
Number of Patches of Agriculture	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Urban	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Water	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Null	0.1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Precipitation (30-year average of monthly summer precipitation)	0.1	(PRISM Climate Group 2021)	Gaulke
Quadratic Mean Diameter	0.1	(U.S. Forest Service 2012)	Gaulke
Stand Density Index	0.1	(U.S. Forest Service 2012)	Gaulke
Solar Radiation	0.1	(Solargis 2019)	Gaulke

Table 1 (cont.).

Total Area of Agriculture	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Bottomland Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Closed Canopy Deciduous Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Coniferous Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Open Canopy Deciduous Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Urban	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Water	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Forest	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Water	0.1, 0.5, 1	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Temperature (30-year average of monthly minimum summer temperature)	0.1	(PRISM Climate Group 2021)	Gaulke

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 collected from 1999-2021. The top 15 variables were used in subsequent multivariate models.

Rank	Eastern red	AUC	Hoary	AUC	Tri-colored	AUC
1	Total area of ag in 0.1km	0.7231	Total area of ag in 0.1km	0.6376	Distance to roads	0.9056
2	Total area of forest in 0.1km	0.7206	Distance to roads	0.6172	Stand density index	0.8071
3	Existing vegetation height	0.7193	Total area of urban in 0.1km	0.6038	Total area of bottomland forest in 1km	0.8033
4	Stand density index	0.7169	Distance to water	0.5968	Total area of forest in 0.5km	0.798
5	Number of patches of forest in 0.1km	0.7016	Number of patches of forest in 0.1km	0.5871	Existing vegetation height	0.7959
6	Quadratic mean diameter	0.6999	Total area of water in 1km	0.586	Total area of ag in 0.5km	0.7858
7	Canopy cover	0.6985	Solar radiation	0.5819	Elevation	0.7721
8	Total edge of forest in 0.1km	0.6967	Existing vegetation height	0.5812	Quadratic mean diameter	0.7719
9	Total area of bottomland forest in 1km	0.6548	Total area of forest in 0.1km	0.579	Canopy cover	0.7678
10	Total edge of water in 1km	0.647	Total edge of forest in 0.1km	0.5741	Total area of water in 0.5km	0.762
11	Elevation	0.6434	Stand density index	0.573	Temperature	0.7502
12	Total area of water in 1km	0.6412	Aspect	0.57	Total edge of forest in 0.5km	0.7444
13	Number of patches of water in 1km	0.6355	Number of patches of urban in 0.1km	0.5611	Number of patches of forest in 0.1km	0.7362
14	Temperature	0.6258	Total area of open canopy deciduous forest in 1km	0.5568	Number of patches of water in 0.5km	0.7313
15	Distance to water	0.6243	Total area of bottomland forest in 0.1km	0.5554	Total edge of water in 0.5km	0.7134
16	Number of patches of agriculture in 0.5km	0.6186	Total edge of water in 1km	0.5509	Total area of closed canopy deciduous forest in 1km	0.7124

Table 2 (cont.).

17	Total area of closed canopy deciduous forest in 1km	0.6126	Temperature	0.5501	Total area of open canopy deciduous forest in 1km	0.6996
18	Distance to roads	0.611	Total area of closed canopy deciduous forest in 0.1km	0.5447	Number of patches of agriculture in 1km	0.6993
19	Solar radiation	0.6039	Precipitation	0.5421	Solar radiation	0.6782
20	Total area of open canopy deciduous forest in 1km	0.5914	Canopy cover	0.5418	Precipitation	0.6563
21	Precipitation	0.5723	Number of patches of agriculture in 1km	0.5271	Distance to water	0.637
22	Aspect	0.5719	Quadratic mean diameter	0.5261	Total area of coniferous forest in 0.5km	0.6255
23	Total area of coniferous forest in 1km	0.5475	Number of patches of water in 0.1km	0.5259	Aspect	0.5804
24	Null	0.5388	Elevation	0.5244	Number of patches of urban in 1km	0.5566
25	Total area of urban in 0.1km	0.5278	Total area of coniferous forest in 1km	0.5136	Total area of urban in 0.1km	0.5504
26	Number of patches of urban in 0.5km	0.52	Null	0.4507	Null	0.5279

Table 3. Top multivariate models for the eastern red, hoary, and tri-colored bat ranked by the AICc values based on occurrence points from 1999-2021 across Illinois. AUC$_{test}$ values show model's goodness-of-fit. AICc values is Akaike's Information Criterion for small sample size which ranks the model selection. The difference between the top AICc value and that model's AICc value is the ΔAICc. The AIC$_c$ w$_i$ is the models' weight. Only models with AICc weight are shown in this table. All models are shown in the Appendix.

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 + total area of ag in 0.1km + total area of forest in 0.1km + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km	0.7837	8423.76	0	0.5151
(Limpert et al. 2007)	Preferred roosting habitat and foraging habitat in riparian zones	canopy cover + distance to water + quadratic mean diameter + total area of ag in 0.1km + total area of bottomland forest in 1km + total area of forest in 0.1km + total area of water in 1km + temperature	0.7927	8424.4	0.6417	0.3737
Global Model		elevation + distance to water + existing vegetation height + quadratic mean diameter + total area of ag in 0.1km + total area of bottomland forest in 1km + total area of forest in 0.1km + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km	0.7922	8426.83	3.0681	0.1111
Hoary bat						
Land Use History Bias	Where most historical human impact has occurred	distance to roads + total area of ag in 0.1km + total area of urban in 0.1km	0.7444	3742.44	0	1
Tri-colored bat						

Table 3 (cont.).

(O'Keefe 2009)	Minimize commuting costs as a smaller bat and prefer riparian habitats for roosting and maximizing foraging costs	canopy cover + elevation + distance to roads + number of patches of forest in 0.1kmm + total edge of forest in 0.5km + total edge of water in 0.5km	0.8832	3261.34	0	0.56
(O'Keefe 2009)	Minimize commuting costs as a smaller bat and prefer riparian habitats for roosting and maximizing foraging costs	canopy cover + elevation + distance to roads + total edge of forest in 0.5km + total edge of water in 0.5km	0.8704	3261.8	0.4658	0.44
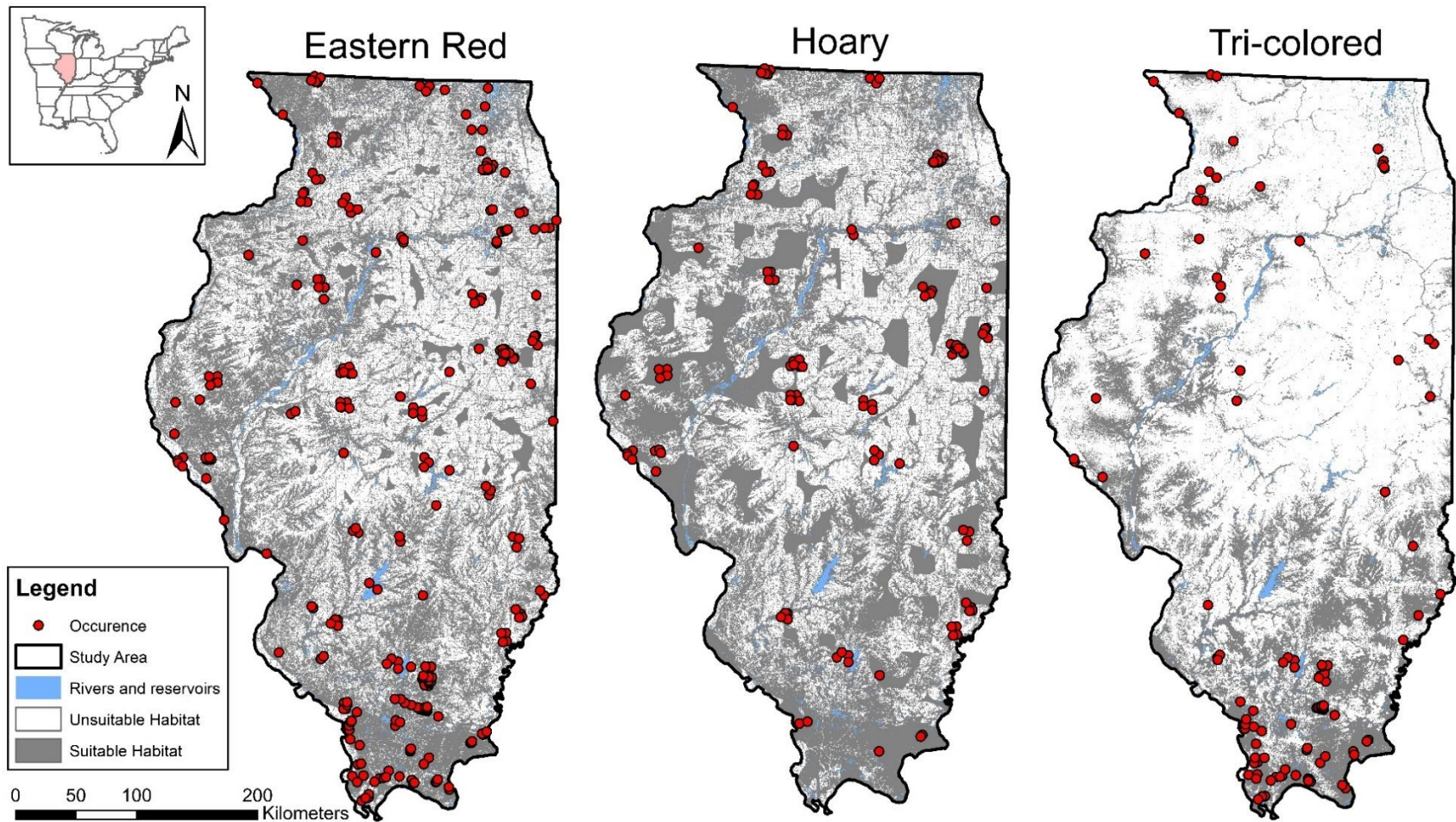
Figure 1. HSMs for the eastern red bat, hoary bat, and tri-colored bat with occurrences from 1999-2021 across Illinois. Suitable areas are indicated in gray while each red circle indicates an occurrence point. Suitable habitat for eastern red bats is evenly distributed across the state with large tracts of agricultural land and forested areas deemed suitable. The hoary bat's suitable habitat is seen in large contiguous patches of agricultural land in the middle of the state with additional suitable forested habitat. The tri-colored bat has the smallest distribution of suitable habitat following the riparian corridors, but mostly in the forested southern third of Illinois.
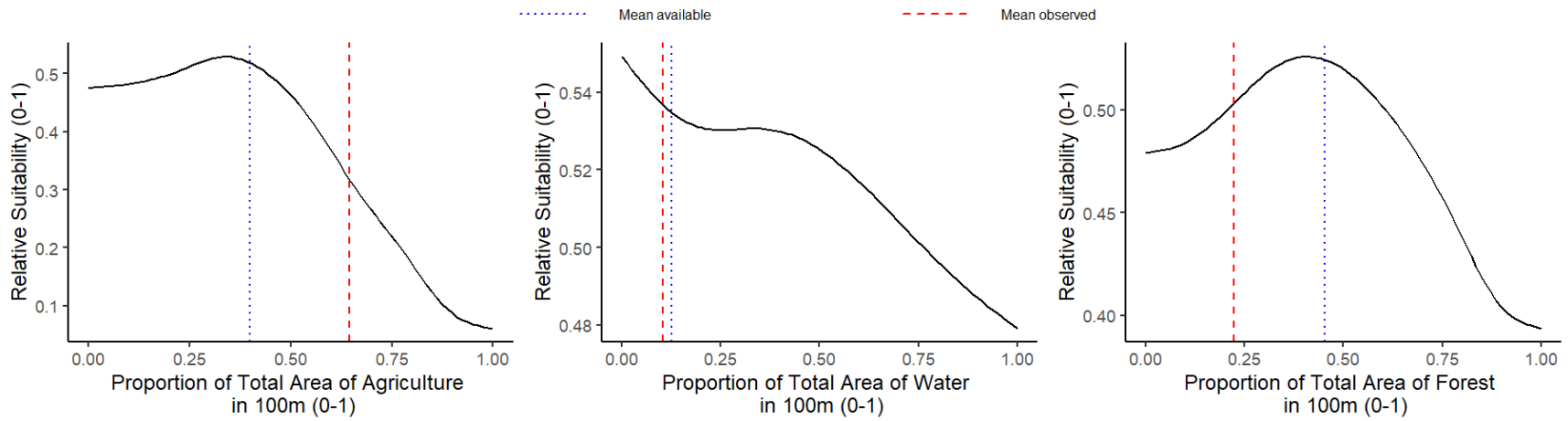
Figure 2. Maxent response curves for the eastern red bat showing the relative suitability (0-1) to each variable that had an importance of 1. All three variables are scaled for a proportion from 0-1. Dotted blue lines indicate the average of suitable eastern red bat habitat while the dashed red line indicates the average across Illinois.
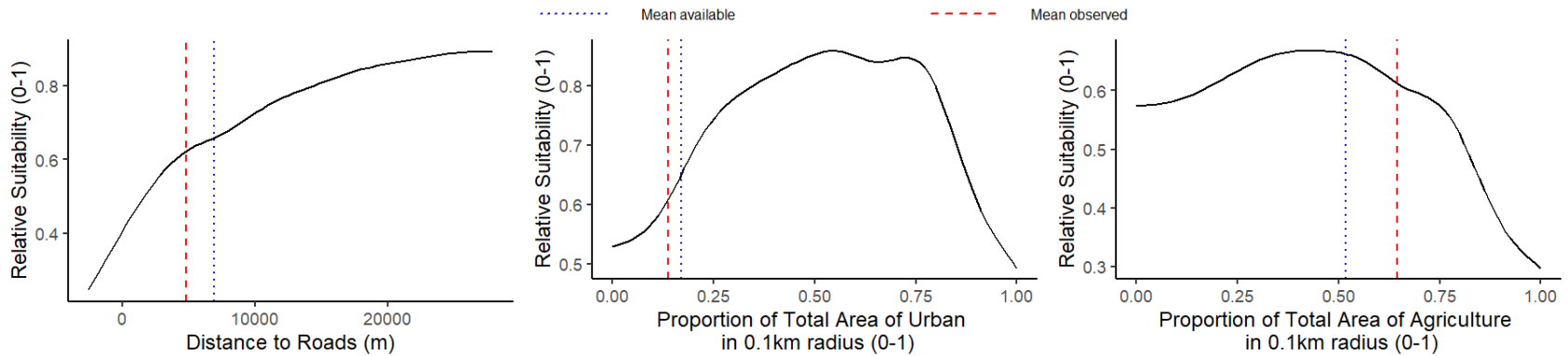
Figure 3. Maxent response curves for the hoary bat showing the relative suitability (0-1) to each variable that had an importance of 1. The two landcover variables are scaled for a proportion from 0-1. Dotted blue lines indicate the average of suitable hoary bat habitat while the dashed red line indicates the average across Illinois.
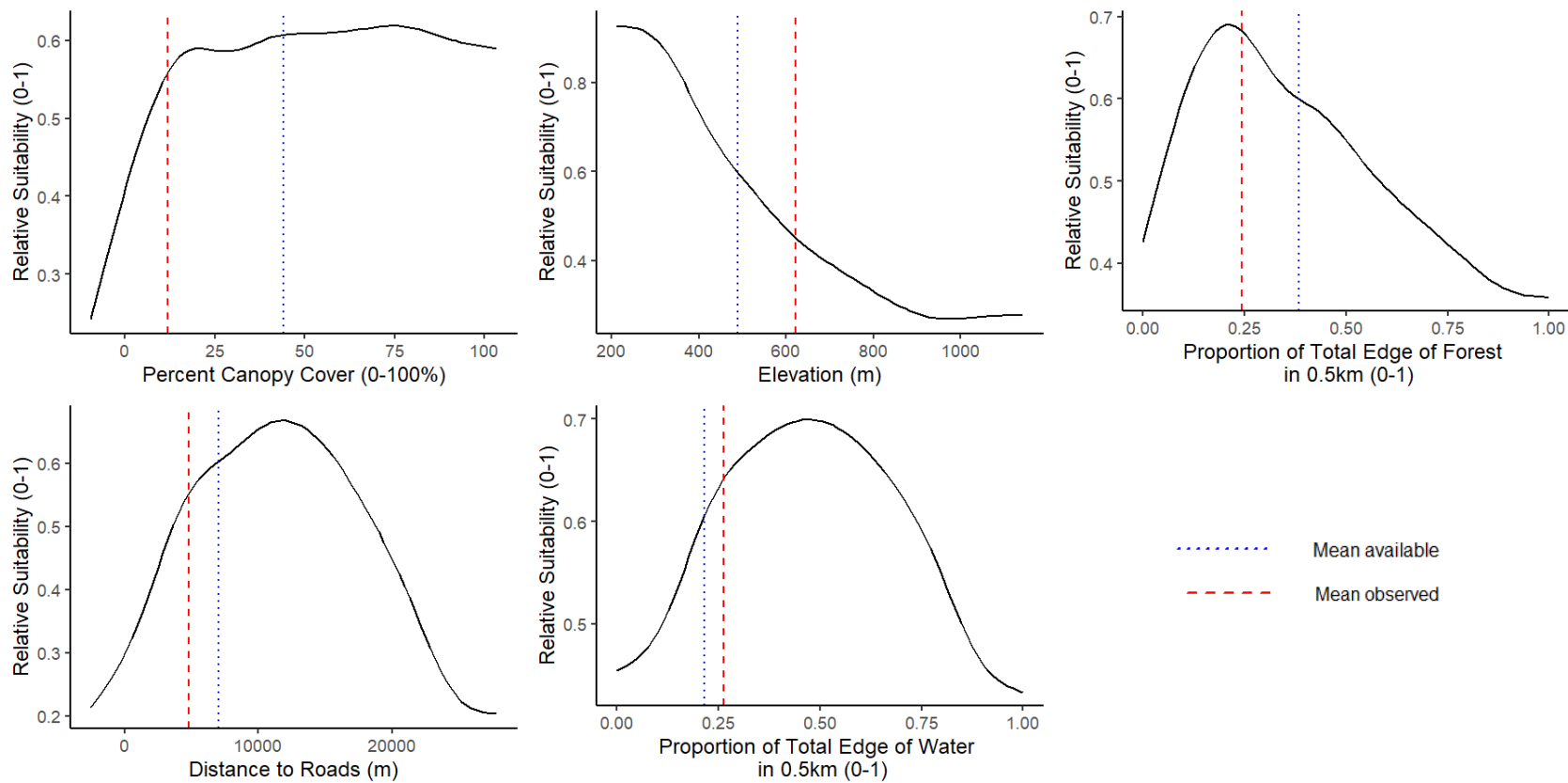
Figure 4. Maxent response curves for the tri-colored bat showing the relative suitability (0-1) to each variable that had an importance of 1. The two landcover variables (total edge of forest and total edge of water) are scaled for a proportion from 0-1. Dotted blue lines indicate the average of suitable tri-colored bat habitat while the dashed red line indicates the average across Illinois.
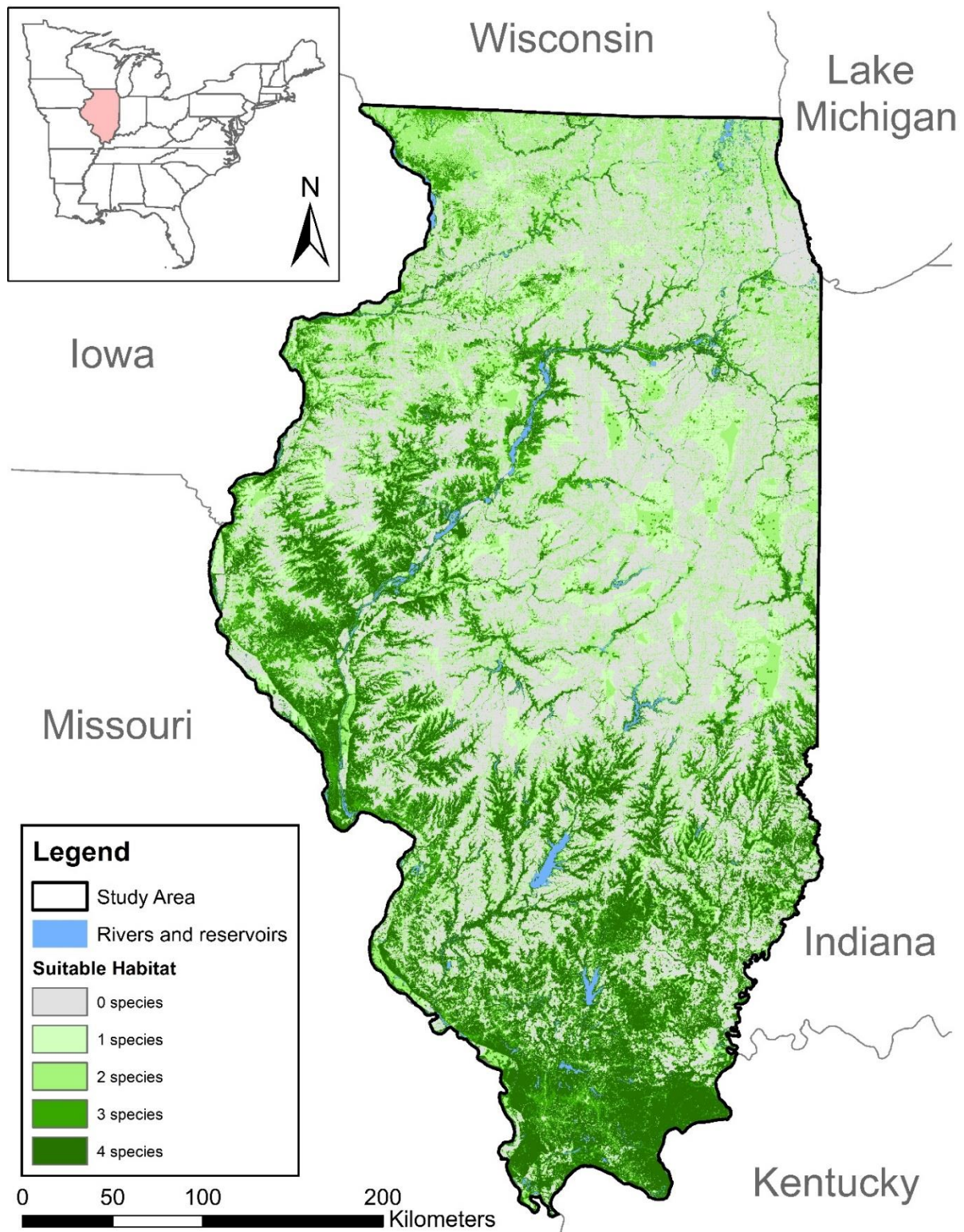
Figure 5. Stacked HSM from the eastern red, hoary, tri-colored, and Indiana bat binary habitat suitability maps based on occurrences from 1999-2021 across Illinois.

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CHAPTER 3: SAMPLING METHODOLOGY INFLUENCES HABITAT SUITABILITY MODELING FOR CHIROPTERAN SPECIES

ABSTRACT

Technological advances increase opportunities for novel wildlife survey methods using both passive and active surveys. With an increase in detection methods, many organizations and agencies are creating habitat suitability models (HSMs) to identify critical habitats and prioritize conservation measures. However, multiple occurrence data types (passive vs. active) are being utilized to create these HSMs with little understanding of how inherent biases related to different data types might impact HSM efficacy. Here I sought to understand how different data types can influence HSMs using three bat species (eastern red, hoary, and tri-colored bat). I compared the overlap of models created from passive-only, active-only, and combined occurrences to identify the effect of multiple data types and detection bias. For each species, the best performing models were always active-only. By comparing the niche overlaps of HSMs between data types, I found a high amount of variation with no species having over 45% overlap between the models. Passive models showed more suitable habitat in agricultural lands, while active models showed higher suitability in forested land, a reflection of sampling bias. Overall, this emphasizes the need to consider influences of detection and survey biases on modeling, especially when combining multiple data types. Biases from sampling, behavior at time of detection, and species life history intertwine to create striking differences among models. These biases and concomitant of each detection type should be considered in the final model output, particularly when the goal is to inform management decisions, as one data type may support very different management strategies than another.

INTRODUCTION

Emerging technologies afford new opportunities for monitoring wildlife via passive or active detection. Passive detection involves minimally invasive methods, often with no contact with the animal, and includes tracking prints in snow or soil, listening or recording calls, or camera trapping (Clare et al. 2017, Coxen et al. 2017, Sugai et al. 2019). In the age of genetics, additional opportunities for passive detection are created through environmental DNA (eDNA) and fecal sampling (Beckmann et al. 2015, Carraro et al. 2018, Hashemzadeh Segherloo et al. 2021). Active detection involves the direct capture and subsequent handling of individuals of species of interest (Praca et al. 2009, Hohoff 2016, Coxen et al. 2017). These different detection methodologies occur across all types of wildlife; large carnivores can be passively detected via camera traps or actively captured (Kabir et al. 2017, Bai et al. 2018, Watts et al. 2019), birds can be surveyed passively through acoustic monitoring, or actively via mist-netting (Coxen et al. 2017, Hallman 2018, Neice and McRae 2021), and for fish, electrofishing is the traditional active sampling while passive sampling via fyke nets is common (Rogers et al. 2003, Ruetz et al. 2007, Mehdi et al. 2021). More broadly, eDNA now allows for passive sampling of most vertebrates compared to more traditional active sampling (Harper et al. 2019, Leempoel et al. 2020, Moss et al. 2022).

Passive and active detection each have their own benefits and shortcomings. Particularly for cryptic species, passive detection can be more efficient, easier to deploy, and may yield substantially more occurrences at larger temporal and spatial scales (Hohoff 2016, Clare et al. 2017, Coxen et al. 2017). While passive detection may have a greater chance of species misidentification (ex. a misidentified acoustic call or fuzzy camera trap photo), active detection can often be time-consuming, expensive, stresses organisms, and creates a mortality risk

(Coleman et al. 2014, Russo and Voigt 2016, Clare et al. 2017). Additionally, active sampling is frequently limited to one/few capture sites per trapping period, often with accessibility constraints, and is dependent on species phenology (Coleman et al. 2014, Zwart et al. 2014, Rounsville et al. 2022). In addition, for the extensive effort that some active capture methods require, few to zero individuals can be captured (Flaquer et al. 2007, Bai et al. 2018). Different data collection methods creates detection biases that can impact future modeling (Flaquer et al. 2007, Clare et al. 2017, Risch et al. 2021). As each data type is biased, careful consideration of the purpose and sampling design to account for biases of each detection type is critical (Barnhart and Gillam 2014, Ford et al. 2016, Risch et al. 2021).

Most occurrence data collected are utilized in modeling distributions, habitat associations, or population trends, and combining multiple sampling methods in the same model introduces detection biases (Graves et al. 2012, Banner et al. 2018, Hallman 2018). When conducting species distribution modeling, HSMs are affected by the occurrence data supplied (Gu and Swihart 2004, Barnes et al. 2014, Barnhart and Gillam 2014). Passive acoustic and eDNA data are increasing in use in HSMs for multiple taxa, including fish, birds, and bats (Cox 2019, Hedley et al. 2020, Hashemzadeh Segherloo et al. 2021). Omitting imperfect detection and false positives can impact model precision and accuracy (Banner et al. 2018, Louvrier et al. 2019, Rojas et al. 2019). Combining data sets may greatly increase the number of occurrences for cryptic species as well as introducing greater species misidentification and imperfect detection (Miller et al. 2011, Clare et al. 2017, Louvrier et al. 2019).

While the impact of multiple detection types has been studied for occupancy modeling, there has been little research on landscape-level effects of multiple data types on habitat modeling, particularly for chiropteran species (Clement et al. 2014, Banner et al. 2018, Rojas et

al. 2019). Common detection methods for bats includes passive detection (acoustics) or active (mist-netting or wind turbine mortalities) (Barnhart and Gillam 2014, Ford et al. 2016, Hohoff 2016). Varying life histories and behaviors among species result in differential detection probabilities among sampling methods (O'Farrell and Gannon 1999, Flaquer et al. 2007, Hohoff 2016). For example, high-flying bats (e.g. hoary bat) are rarely caught in mist-nets but are frequently detected by acoustic monitoring (O'Farrell and Gannon 1999, Menzel et al. 2005). Unfortunately, North American bat populations are threatened by pesticide use, wind-energy development, white-nose syndrome, and habitat loss and as such landscape-level research is necessary to identify critical habitats, patches, and corridors to target management interventions (Bellamy et al. 2013, Rodhouse et al. 2019, Sandoval-Herrera et al. 2020, Cheng et al. 2021).

Using two different data types and mindful of their biases, I tested if data type (combined, passive, or active) impacts HSMs for three focal bat species (*Lasiurus borealis*, *Lasiurus cinereus*, *Perimyotis subflavus*). My research questions were: (1) Does sampling type result in differences in HSMs? (2) Do differences in species' ecology result in differential HSMs derived from different sampling type? I hypothesize that the consistency across models from different data types will vary by species and their life history traits, i.e. that species that have larger disparities between passive and active detection will have greater model inconsistency.

METHODS

Study Area

Illinois is a habitat mosaic 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 thirds of Illinois

is dominated by agriculture and an urban/suburban/exurban interface, while the southern third is home to the Shawnee National Forest; 280,000 acres of protected forest managed by the U.S. National Forest Service (Iverson 1988, Luman et al. 2004, Rey 2004). The middle third of the state is primarily row crops (corn and soy) with small, isolated forest fragments, riparian corridors, degraded prairie, and urban areas. Across the state, Illinois forests are primarily composed of hardwood deciduous trees with major riparian zones along the Illinois and Mississippi rivers.

Study Species

There are diverse life history traits across Midwestern bat species. The eastern red bat, *Lasiurus borealis* (Müller 1776) is a common generalist forager that primarily roosts solitarily in foliage and tree bark (Limpert et al. 2007, Perry et al. 2007). Their longer, narrow wings are adapted for fast flying over long distances and foraging in forest gaps, edges, and openings (Walters et al. 2007, Amelon et al. 2014, Starbuck et al. 2015). The hoary bat, *Lasiurus cinereus* (Palisot de Beauvois 1796), migrates long-distances and primarily forages in open spaces, both behaviors linked with high wind-turbine mortality (Hayes et al. 2015, Weller et al. 2016, Friedenberg et al. 2021). The tri-colored bat, *Perimyotis subflavus* (Cuvier 1832) has the longest hibernation time in Illinois, contributing to devastating losses from white-nose syndrome and prompting its candidacy for listing under the U.S. Endangered Species Act (ESA) (Turner et al. 2011, Center for Biological Diversity and Defenders of Wildlife 2016, Cheng et al. 2021). They are foliage roosters choosing mature stands and forage above the trees and in partially open habitat (Veilleux et al. 2003, O'Keefe 2009, Farrow and Broders 2011).

Active Detection Data

Historic capture data was acquired via a data sharing agreement with the Illinois Department of Natural Resources (IDNR) and the U.S. Fish and Wildlife Service for both mist-netting and summer wind farm mortalities from 1999-2021. Since IDNR primarily maintains records for threatened and endangered species, the historic capture data was incomplete for non-listed species. Thus, I contacted IDNR's list of Illinois mist-netting permittees requesting mist-netting records for the three focal species between 1999-2021. Eight additional sources responded augmenting 46 mist net sites from 2015-2019 generated by the Illinois Bat Conservation Program (IBCP). I combined windfarm mortality and mist-net records, reducing the number of individual records to one per site. For all data, I removed sites with low positional or temporal accuracy, or no data associated with captures.

Passive Detection Data

Acoustic data were collected by IBCP, following the NABat protocol for 20 NABat GRTS cells surveyed annually since 2016 (Illinois Bat Conservation Program 2021, U.S. Geological Survey 2021). A Song Meter SM4+ detector was deployed in 2-4 of the quadrants in each GRTS cell with a SMM-U1 or U2 microphone (Wildlife Acoustics). Sites in each quadrant were chosen to represent habitat diversity in each cell. Monitors were deployed for a minimum of four good weather nights (i.e. no rain, temperatures > 60 degrees, and sustained wind < 8 mph). The same protocol was used for all years, and sites remained largely unchanged, with some exceptions due to landowner permissions or personnel changes. Data were recorded from 19:00 to 7:30 each night. IBCP also generated acoustic monitoring sites across Illinois that were surveyed with a similar acoustic protocol as the GRTS cells. These data are considered presence-

only; the survey effort at some sites (i.e. four nights) was insufficient to determine absence (Moreno and Halffter 2000, Skalak et al. 2012).

I used the NABat protocol to process the acoustic data (Reichert et al., 2018). Specifically, I processed all files recorded in the field through Sonobat 4 (Arcata, CA) using the medium filter to reduce noise files (Szewczak 2010). Due to time and data storage constraints, I ran Kaleidoscope Pro 5.4.0 as the auto-identifier (Kaleidoscope Pro n.d.). Kaleidoscope is a powerful auto-classifier that, in addition to identification, provides maximum likelihood estimates of species occupancy. I considered below $\alpha = 0.05$ to be present and above $\alpha = 0.05$ to be absent following standard conservative protocols (Nocera et al. 2019, U.S. Fish & Wildlife Service and U.S. Geological Survey 2019). These acoustic data were not manually vetted since NABat does not require manual vetting for their data upload. All data was re-processed in 2021 to ensure that the classifier's conditions were the same through all analyses.

Data Cleaning

Active and passive data were combined and processed in R 4.1.2 (R Core Team 2021). To reduce spatial autocorrelation, I removed records within 1 km of each other. Records were also temporally restricted from May 15 - Aug 15 to ensure that no records were from migration time periods following the U.S. Fish and Wildlife Guidelines (U.S. Fish & Wildlife Service 2020). After data cleaning and quality control, there were 264 occurrences for eastern red bats, 116 occurrences for hoary bats, and 106 occurrences for tri-colored bats spread across Illinois.

Environmental Layers

I used sixteen landcover variables (Table 4) (per Cable, 2020) created from the Illinois Geospatial Clearing house land cover layer (Illinois Department of Natural Resources et al.

2003). Cable et al (2020) used parallel methods to create a statewide HSM for the Indiana bat (*Myotis sodalis*). Cable used Fragstats (McGarigal and Marks 1995) to find the number of patches of four landcover types, total area of eight landcover types, and total edge of two landcover types. Each metric was calculated at three different scales state-wide (0.1km, 0.5km, and 1km) representing roosting, foraging, and landscape distances.

An additional nine variables were also considered based on the top models of published chiropteran HSMs or occupancy models (Table 4). Many of these variables were forest stand structure metrics or topographical landscape metrics, gathered from publicly available GIS layers and resampled in ArcGIS for 100m resolution to match layers (Esri Inc. 2021). Both temperature and precipitation layers were taken from a 30-year normal and averaged across May-Aug to represent the summer average (PRISM Climate Group 2021).

Modeling

For all variables, I created single-predictor models in MaxEnt v3.4.4 using both data types to optimize spatial scale for variables and chose the top 15 variables for each species by AUC_{test} scores (Phillips et al. 2006, 2021). For univariate models, I used the default parameters with 20 replicates, and 10% random test percentage (Phillips et al. 2021). Using AUC_{test} scores, I determined the best spatial scale for each species for each landcover variable. I ranked the top scaled landcover variables among the non-scaled variables, selecting the top 15 variables for each species with $AUC_{test} > 0.5$. The top 15 variables for each species were carried on throughout the analysis. A correlation matrix was created in ArcGIS for the fifteen variables for each species and highly correlated variables (>0.7) were removed based on their univariate rank. With the remaining non-correlated variables, a global model was created for each species.

Using the global model, I tested differing regularization multipliers ranging from 1-12 using the same default parameters of 20 replicates and 10% as a random test percentage. The regularization multiplier with the top AUC$_{test}$ scores was carried out through the rest of the analysis. Each species had three models run with the same global model for each data set: passive-only occurrences, active-only occurrences, and combined passive and active detections. This yielded nine models across all species. All models were identically run in MaxEnt using presence-only data, the top regularization multiplier, 20 replicates, 10% of datapoints withheld for testing from the dataset, and 5000 maximum iterations. For pseudo-absence points, MaxEnt randomly sampled 10,000 background points across the state using bootstrapping.

Model Analysis

Model goodness-of-fit was assessed via AUC$_{test}$ scores and omission rates. 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). The dataset from the opposite data types was used to test the omission rate. I 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).

$$logistic = (raw * e^{entropy})/(1 + raw * e^{entropy})$$

To create binary models, I created a threshold of omission for each species based on the bottom 10% of suitability scores for true presences in the test datasets (Hovick et al. 2015). For a comparison of the binary models, I ran a niche overlap function in ENMTools, using the

Schoener's D value to calculate niche equivalence by the proportion of shared pixels between the two models (Schoener 1968, Warren et al. 2010).

RESULTS

There was a range in the number of occurrences for each detection type among species (Table 6). Hoary bats, high-flying open foragers, had almost three times as many passive detections (n = 86) than active detections (n = 30), whereas tri-colored bat, a declining forest obligate, passive detections (n=27) were much less frequent than active detections (n = 77). The eastern red bat, a forest generalist, has the highest number of occurrences (n=264) with a third of them being passive (n=88) and two-thirds being active (n=176).

Suitable habitat for both tri-colored and eastern red bats was dominated by forest-related variables, while hoary bat was dominated by open variables. (Table 5). Specifically, elevation, distance to water, existing vegetation height, quadratic mean diameter, total area of agriculture in 100m, total area of bottomland forest in 1km, total area of forest in 100m, total area of water in 1km, total edge of forest in 100m, and total edge of water in 1km defined core eastern red bat habitat (Table 6). Similarly, the global model for the tri-colored bat included elevation, distance to roads, existing vegetation height, number of patches of forest in 100m, number of patches of water in 500m, quadratic mean diameter, stand density index, total area of agriculture in 500m, total area of bottomland forest in 1km, and total area of water in 500m. By contrast, the hoary bat global model included aspect, distance to roads, distance to water, existing vegetation height, number of patches of forest in 100m, stand density index, solar radiation, total area of agriculture

in 100m, total area of bottomland forest in 100m, total area of open canopy deciduous forest in 1km, total area of urban in 100m, and total area of water in 1km.

Model outputs differed greatly between data types, however active detection recovered the highest AUCs for all species. For eastern red bat, active detection had the highest AUC (0.86), highest number of occurrences and projected the most conservative HSM (Table 6). Only 32.6% of the state was considered suitable habitat compared to 43.3% with passive detection and 50.9% with a combined dataset. The omission rate between the two data types (53-54%) was high for the eastern red bat. The active HSM recovers suitable habitat in southern IL and following the forested riparian areas and major river corridors, while the passive HSM revealed most suitable habitat near the Chicago region and in large contiguous agricultural patches in the central western part of the state (Fig. 6). The combined model merges these agricultural patches with forested/riparian suitability but predicts Chicago as unsuitable habitat.

For hoary bats, the active model had the highest AUC value (0.84) and the most conservative HSM with only 25% of the state as suitable habitat (Table 6). While the combined and passive models had AUC values very close to the active model (0.80 and 0.82 respectively), the amount of modeled suitable habitat nearly doubled, with 47% of the state comprised of suitable habitat in both models. While the number of active detections was one third of the overall number of detections, the omission rate of the active model was high at 72% of passive occurrences being modeled in unsuitable habitat. The passive model had a lower omission rate of 46.7% which is still impractically high.

The hoary bat's active HSM reveals small suitable patches distributed across north-western Illinois with a large habitat patch in the southern forests (Fig. 7). In addition, major roads, highways, and waterways stand out in this model as unsuitable habitat. The passive HSM

recovers much larger-scale, evenly distributed and contiguous patches, particularly in agricultural areas. The southern third of the state include more fine-scale suitable habitat, but the influence of roads and waterways are less pronounced than in the active model. The combined detection model includes both the larger-scale patches and greater distribution of the passive detection model with the smaller scale suitability of the active model.

The top model for the tri-colored bat was the active model with a high AUC value of 0.9212 and 19.8% of the state modeled as suitable habitat (Table 6). The passive model yielded the lowest AUC value of 0.75 with 33% of the state as suitable habitat while the combined model had an AUC value of 0.85 with 28.3% of the state as suitable habitat. Both omission rates of the tri-colored bat were impractically high with over 61% of occurrences omitted in the passive model and over 78% of passive occurrences omitted in the active model.

The tri-colored bat's HSMs are dissimilar in predicted suitable habitat (Fig. 8). The active HSM confines the suitable habitat to forested and major riparian zones throughout the state, but particularly in and around Shawnee National Forest. Conversely the passive model reveals no obvious forest association and an even distribution throughout the state, with a slight increase in suitable habitat in the northern third. The wide distribution from the passive model is not reflected in the combined model in areas of dense agriculture.

Comparing niche overlap values for different model types showed a maximum of 45% (range: 22-45%) overlap between active and passive detection types across all species (Table 7), indicative of substantial disparity between the two data types among species. In fact, >50% of the entire state of Illinois was modeled differently when active and passive models were compared. Comparing passive detection to combined detection resulted in a higher degree of overlap (range: 48-83%) as well as active detection to the combined (range: 43-63%). For all

species, the data type with larger sample size had greater overlap with the combined model. This is expected as the larger sample size would have a higher influence on the distribution.

DISCUSSION

As technological advances have introduced efficiencies and opportunities for measuring and monitoring biodiversity, understanding the trade-offs and biases compared to more conventional, active sampling approaches is critical to ensure the quality of conclusions made from this analysis (Barnhart 2014, Ford et al. 2016, Clare et al. 2017). As eDNA, acoustic monitoring, camera trapping and other passive methods are deployed at scale, researchers must be confident in the data to ultimately inform management decisions. Here I compared passive and active sampling for bats. Across all species, the difference in HSMs between passive and active was striking with no more than 45% overlap between the models, indicating that sampling bias between data types influences HSMs, with important implications for how they inform management decisions (Table 7). For each species, the active model recovered the highest AUC_{Test} value and the most conservative amount of suitable habitat, independent of how many occurrences there were for that data type (Table 6). This indicates that active data may create the most robust HSM for chiropteran species on a landscape scale, even for species that are more difficult to capture, contradicting previous studies (Barnhart and Gillam 2014, Ford et al. 2016). Overall, this emphasizes that considerations should be made regarding the influence of data type on HSMs in three key ways: the sampling bias, biological bias during detection, and the species bias from their life history and ecology.

Sampling Bias

Hallmarks of sampling bias for each data type are visible in the models as efficacy of different detection types varies between locations (Gu and Swihart 2004, Zwart et al. 2014, Fisher-Phelps et al. 2017). For effective mist-netting for chiropteran and bird species, nets need to be placed in flyways and corridors that funnel animals into the net (O'Farrell and Gannon 1999, MacCarthy et al. 2006, Geluso and Geluso 2012). Forests and riparian zones provide these 'funnels,' and consequently are frequent netting sites (Geluso and Geluso 2012, Coleman et al. 2014). As such, mist-net derived occurrences are necessarily distributed primarily in riparian and forested zones and lacking in residential and open fields such as prairie or row crop agriculture. This creates a sampling bias with higher numbers of active occurrences within forested and riparian zones, which is reflected in our active models and illustrated by the majority of suitable habitat falling along Illinois' big rivers. This may be the reason for active data having the lowest percentage of the state as suitable for all focal species, as only 12% of Illinois is forested (Luman et al. 2004). This bias may diminish with increasing cell size and landcover type homogenizes.

Conversely, passive data are easily collected, including in urban environments, open fields, row agriculture, forests, and riparian habitats. While distance to detection of acoustics and camera trapping are impacted by vegetation, other passive methods such as eDNA and fecal sampling are less impacted by land cover type (O'Keefe et al. 2014, Leempoel et al. 2020, Moll et al. 2020). As such, passive sampling was distributed more broadly in our study and evenly throughout the landscape, though with a critical disparity in Illinois' southern forests. This is manifest in greater distribution of suitable habitat, not strictly confined to forested areas as in the active models. This may reflect, to a degree, the habitat proclivities of generalist species (e.g. eastern red and hoary bat), which has been supported by previous habitat modeling (Menzel et

al. 2005, Vanausdall et al. 2018, Wieringa et al. 2021). For specialists, such as the tri-colored bat, the passive model does not reflect their forest requirements, potentially because of a lack of sampling in the predominantly forested region of the state (Farrow and Broders 2011, Schaefer 2017, Cox 2019).

In addition to landcover type, sampling bias can occur in other ways. Both types of sampling are typically completed closer to roads than not, although some of the roads used for conventional (i.e. mist net) active sampling may be unmaintained rural roads or roads closed to public use on protected lands. Many species such as mesocarnivores, bears, and some species of bats (eastern red and tri-colored) use roads as linear openings for foraging and commuting (Mace et al. 1996, Hein et al. 2009, Barja and List 2015). However, both data types may have been under sampled in undisturbed natural areas further from roads.

Biological Bias on Modeling

Previous studies on using multiple data types for chiropteran HSMs found a significant difference among data types as well as among species. Ford et al (2016) modeled a HSM for the northern long eared bat (*Myotis septentrionalis*) (Trouessart 1897) at a local scale and strongly recommended against combining three data types, (i.e. acoustics, mist-netting, and roost locations), as it masked ecological trends of roosting vs. foraging (Ford et al. 2016). While this model was at a local scale and using an additional data type (roost sites), their concerns about defining the model objective and using data to reflect that model objective remain true for all model analyses. Including roosting locations constricts occurrence locations to suitable roosting habitat and may sway the model from a generalist model to a more ecologically specific one, ostensibly limiting the inferential efficacy of a general, landscape-level model.

Our model created a general summer use HSM from passive and active sampling, as both types of detection utilized are evidence of general bat use on the landscape. For bats and for many other species, it can often be unclear what the animal is doing when it is detected either passively or actively (e.g. migrating, looking for a mate, foraging, or commuting to and from dens, drinking, and/or foraging locations) (Ford et al. 2016). Even using a single data type leaves uncertainty as to what, biologically or ecologically speaking, the species are doing at time of detection, and as such these models reflect broad habitat associations. Without a clear association of the animal's biological context at each occurrence, incorporating multiple detection types can generalize the ecological utility of the model which the utility of depends on the goal of the model. For other species, where occurrence type may reflect a specific biological need (e.g. roosting or nesting locations, or a species that vocalizes only during mating season), this may not be the case. In these contexts, utilizing that data type would result in a specific ecologically focused HSM.

Species Bias

Barnhart and Gilliam (2014) modeled landscape scale HSMs for six species of bats in North Dakota with paired passive and active sampling at 17 sites total. They found that the best data type was species-specific, and suggested researchers should carefully consider the life history and ecology of each species to select appropriate sampling methods for optimizing HSMs, even if that meant combining data sets (Barnhart and Gillam 2014). I used a larger occurrence data set with over 100 sites for each species, giving better representation of a landscape-scale sampling protocol and, as a result, recover different trends than Barnhart and Gilliam (2014). The difference between our findings and their results may be attributed to different genera, as none of our focal species were *Myotis,* which were the only species in which

passive did better than active in Barnhart and Gillam (2014). I echo their findings that species life history and ecology should be strongly considered when building a sampling design and creating HSMs, as the impact of detection differences varied between our three focal species.

One example of the impact of species ecology is the potential difference in the number of occurrences between common species that are easily detected and cryptic species, as increasing sample size has been shown to improve model performance (Hirzel and Guisan 2002). For cryptic species that are hard to detect with one method, I can increase HSM robustness by using multiple methods and increasing sample size (Hohoff 2016, Clare et al. 2017, Coxen et al. 2017). Another example is the difference in detection between developmental stages of species (Smith et al. 2006, Pirtle et al. 2019, Moss et al. 2022). For example, in amphibians the efficacy of using eDNA in occupancy modeling decreased as amphibians metamorphosed, underperforming conventional, active sampling (Moss et al. 2022). For bats, altricial pups do not fly and thus cannot be detected via conventional mist-netting or acoustics (Kunz and Hood 2000). Species life history plays an important role in detection and the best data type may fluctuate among species as well as across species life stages.

A major drawback of passive sampling that was unaccounted for in this study were false-positives, which may be particularly important for eastern red and tri-colored bat. False-positive and false-negative rates in acoustics vary by species and are lower for species with distinctive call shapes and frequencies (e.g. hoary bat) and higher for species with similar calls (e.g. *Myotis*) (Clement et al. 2014, Russo and Voigt 2016, Rojas et al. 2019). While manual vetting may reduce false positive rates, subjectivity among various call ID software and specialists remains (Russo and Voigt 2016). This extends beyond acoustics to include misidentification of feces, incorrect track identification, and blurry camera trap photos, where genetic analyses provides

confidence for some detection methods (Clare et al. 2017, Louvrier et al. 2019, Guan et al. 2020). For species with high false identification rates, occupancy models have now begun incorporating false-positive parameterizations, thus improving model estimation (Miller et al. 2011, Clement et al. 2014, Rojas et al. 2019). Incorrect species identification may contribute to poor model performance for passive sampling data. Therefore, accounting for false positives and negatives is a critical consideration in modeling exercises leveraging these data types.

Management Considerations

From a management perspective, the difference between models is striking and cause for careful consideration when using to inform decision making. Such HSMs are often utilized in management interventions and conservation planning, including setting restoration objectives, purchasing land for protection, identifying potential areas to improve connectivity, or siting future wind energy developments (Vanausdall et al. 2018, Stevens and Conway 2020, Cable et al. 2021). Additionally, HSMs are frequently used to predict the potential effects of climate change on species distributions (Davis et al. 2015, Razgour et al. 2016, Coxen et al. 2017). Comparing HSMs based on different data types or combined data sets that are heavily skewed towards one data type over another, may highlight differences that are due to sampling bias and detection probabilities, rather than true climate impacts. Thus, different management decisions might be made based on passive vs. active HSMs. Caution is warranted when comparing HSMs, and model biases must be considered when drawing inferences, especially when used in a management context. While this study focuses on bats, passive and active detections are a common difference in surveying many species leading to the broad applicability of this study. The three factors discussed; sampling bias, behavior at time of detection, and species life history,

are inextricably linked. As such, consideration of each will create more biologically relevant and robust models.

TABLES AND FIGURES

Table 4. Variables tested in univariate models. The X in variable name represents the scales at which it was tested.

Variables	Spatial Scale (km)	Variable Name	Original Data Source	Creator
Aspect	0.1	aspect	(U.S. Geological Survey 2018)	Gaulke
Canopy Cover	0.1	canopy_cover	(U.S. Geological Survey 2018)	Gaulke
DEM	0.1	dem	(U.S. Geological Survey 2018)	Gaulke
Distance to Roads	0.1	dist_roads	(Illinois Department of Transportation 2018)	(Cable et al. 2021)
Distance to Water	0.1	dist_water	(U.S. Geological Survey n.d.)	(Cable et al. 2021)
Existing Vegetation Height	0.1	evh	(U.S. Department of Interior et al. 2013)	Gaulke
Number of Patches of Agriculture	0.1, 0.5, 1	np_ag_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Forest	0.1, 0.5, 1	np_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Urban	0.1, 0.5, 1	np_urb_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Water	0.1, 0.5, 1	np_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Null	0.1	null	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Precipitation (30-year average of monthly summer precipitation)	0.1	precip	(PRISM Climate Group 2021)	Gaulke
Quadratic Mean Diameter	0.1	qmd	(U.S. Forest Service 2012)	Gaulke

Table 4 (cont.).

Stand Density Index	0.1	sdi	(U.S. Forest Service 2012)	Gaulke
Solar Radiation	0.1	solar_rad	(Solargis 2019)	Gaulke
Total Area of Agriculture	0.1, 0.5, 1	ta_ag_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Bottomland Forest	0.1, 0.5, 1	ta_bot_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Closed Canopy Deciduous Forest	0.1, 0.5, 1	ta_ccd_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Coniferous Forest	0.1, 0.5, 1	ta_conif_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Forest	0.1, 0.5, 1	ta_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Open Canopy Deciduous Forest	0.1, 0.5, 1	ta_ocd_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Urban	0.1, 0.5, 1	ta_urb_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Water	0.1, 0.5, 1	ta_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Forest	0.1, 0.5, 1	te_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Water	0.1, 0.5, 1	te_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Temperature (30-year average of monthly minimum summer temperature)	0.1	temp	(PRISM Climate Group 2021)	Gaulke

Table 5. Univariate model results ranked by AUC$_{test}$ values. The top 15 variables were used in the multivariate models.

Rank	Eastern red	AUC	Hoary	AUC	Tri-colored	AUC
1	ta_ag_100	0.7231	ta_ag_100	0.6376	dist_roads	0.9056
2	ta_for_100	0.7206	dist_roads	0.6172	sdi	0.8071
3	evh	0.7193	ta_urb_100	0.6038	ta_bot_1km	0.8033
4	sdi	0.7169	dist_water	0.5968	ta_for_500	0.798
5	np_for_100	0.7016	np_for_100	0.5871	evh	0.7959
6	qmd	0.6999	ta_water_1km	0.586	ta_ag_500	0.7858
7	canopy_cover	0.6985	solar_rad	0.5819	dem	0.7721
8	te_for_100	0.6967	evh	0.5812	qmd	0.7719
9	ta_bot_1km	0.6548	ta_for_100	0.579	canopy_cover	0.7678
10	te_water_1k	0.647	te_for_100	0.5741	ta_water_500	0.762
11	dem	0.6434	sdi	0.573	temp	0.7502
12	ta_water_1km	0.6412	aspect	0.57	te_for_500	0.7444
13	np_water_1km	0.6355	np_urb_100	0.5611	np_for_100	0.7362
14	temp	0.6258	ta_ocd_1km	0.5568	np_wat_500	0.7313
15	dist_water	0.6243	ta_bot_100	0.5554	te_water_500	0.7134
16	np_ag_500	0.6186	te_water_1k	0.5509	ta_ccd_1km	0.7124
17	ta_ccd_1km	0.6126	temp	0.5501	ta_ocd_1km	0.6996
18	dist_roads	0.611	ta_ccd_100	0.5447	np_ag_1km	0.6993
19	solar_rad	0.6039	precip	0.5421	solar_rad	0.6782
20	ta_ocd_1km	0.5914	canopy_cover	0.5418	precip	0.6563
21	precip	0.5723	np_ag_1km	0.5271	dist_water	0.637
22	aspect	0.5719	qmd	0.5261	ta_conif_500	0.6255
23	ta_conif_1km	0.5475	np_wat_100	0.5259	aspect	0.5804
24	null_	0.5388	dem	0.5244	np_urb_1km	0.5566
25	ta_urb_100	0.5278	ta_conif_1km	0.5136	ta_urb_100	0.5504
26	np_urb_500	0.52	null_	0.4507	null_	0.5279

Table 6. Global model ran for each species and each data type. AUC$_{test}$ values show model's goodness-of-fit. The percent of suitable habitat is the percent of Illinois that has been found as suitable after the binary threshold. The omission rate is the percent of opposite data type points modeled in unsuitable habitat in the binary model with the number of occurrences omitted in parentheses- i.e. the active data type's omission rate is the percent of passive occurrences that were omitted.

Global Model Variables	Data Type	Total Number of Occurrences	AUC$_{Test}$ Value	% Suitable Habitat in Illinois	Omission Rate (number of occurrences omitted)
Eastern Red bat					
dem + dist_water + evh + qmd + ta_ag_100 + ta_bottomland_1km + ta_forest_100 + ta_water_1km + te_forest_100 + te_water_1k	Active	176	0.864	32.6%	54.6% (48)
	Passive	88	0.812	43.3%	53.4% (94)
	Combined	264	0.791	50.9%	-
Hoary bat					
aspect + dist_roads + dist_water + evh + np_for_100 + sdi + solar_rad + ta_ag_100 + ta_bot_100 + ta_ocd_1km + ta_urb_100 + ta_water_1km	Active	30	0.839	25.4%	72.1% (62)
	Passive	86	0.817	47%	46.7% (14)
	Combined	116	0.803	46.9%	-
Tri-colored bat					
dem + dist_roads + evh + np_for_100 + np_wat_500 + qmd + sdi + ta_ag_500 + ta_bottomland_1km + ta_water_500	Active	77	0.921	19.8%	78.6% (22)
	Passive	27	0.755	33%	61.5% (48)
	Combined	104	0.852	28.3%	-

Table 7. Niche overlap matrix for the three focal species with Schoener's D calculating niche similarity from 0-1 between each model.

Species	Data Types		
	Active vs. Passive	Active vs. Combined	Passive vs. Combined
Eastern red bat	0.4507	0.6245	0.7141
Hoary bat	0.3400	0.4385	0.8355
Tri-colored bat	0.2233	0.6327	0.4898
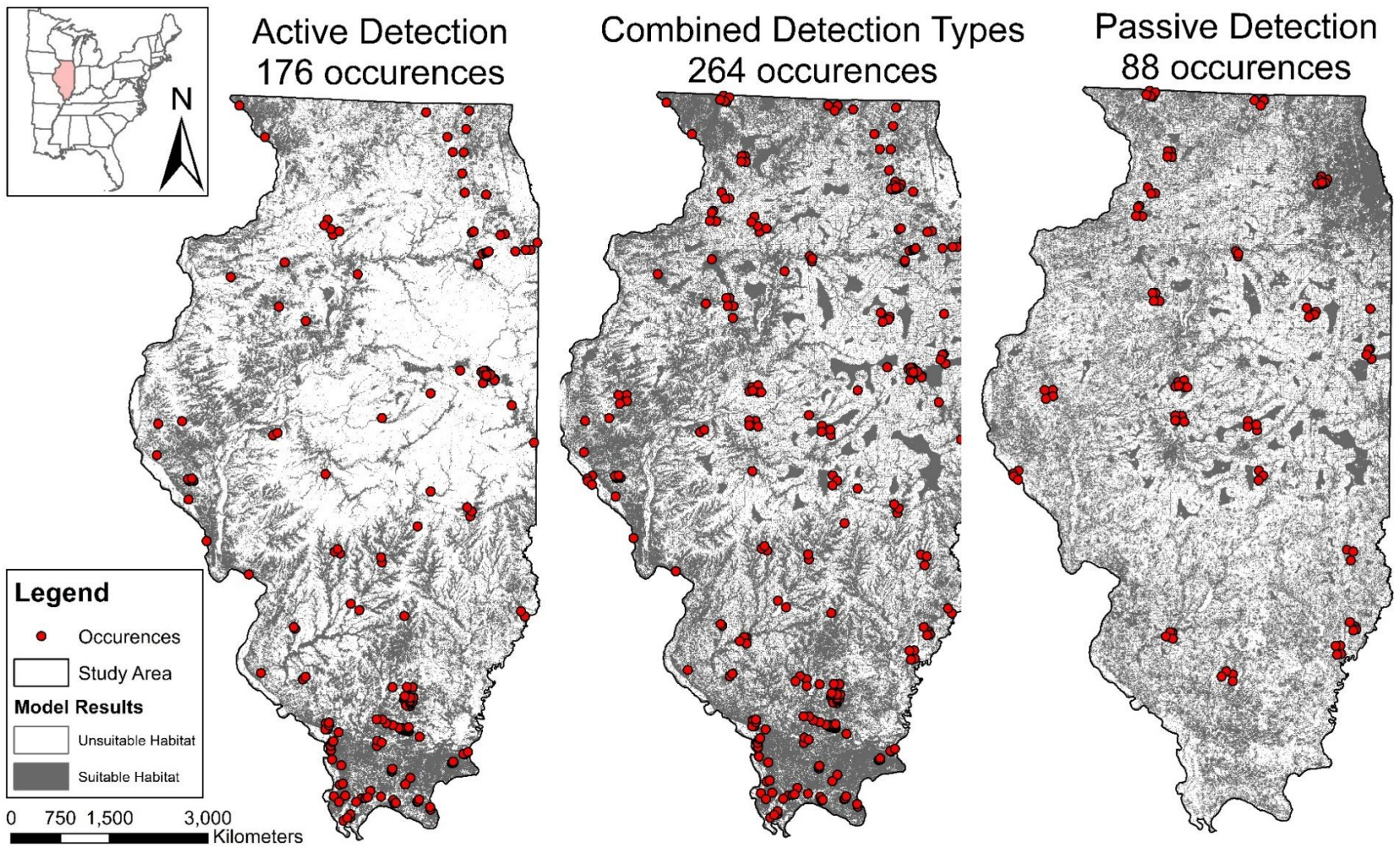
Figure 6. Habitat suitability models for the eastern red bat with detection types; active, combined, and passive.
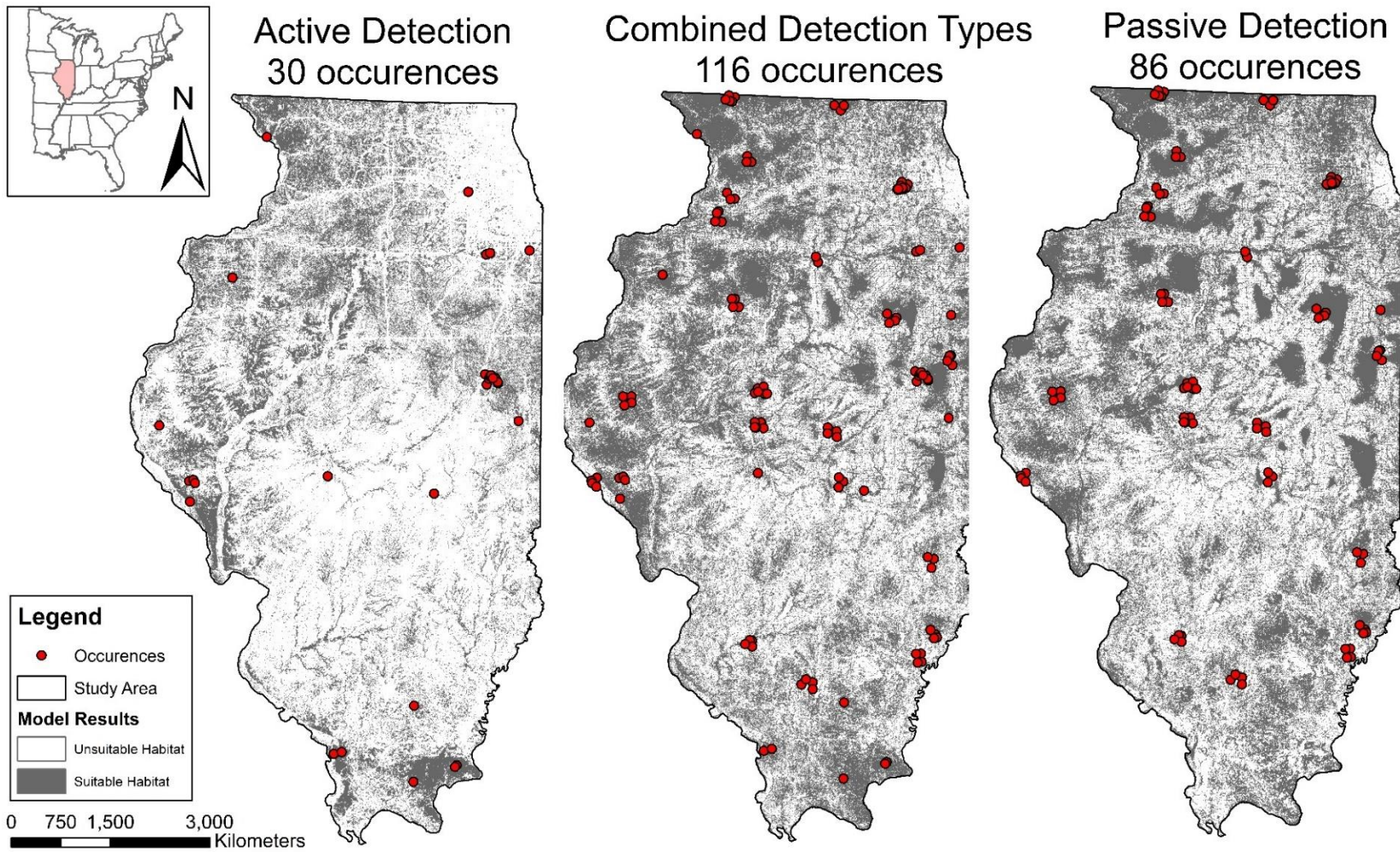
Figure 7. Habitat suitability models for the hoary bat with detection types; active, combined, and passive.
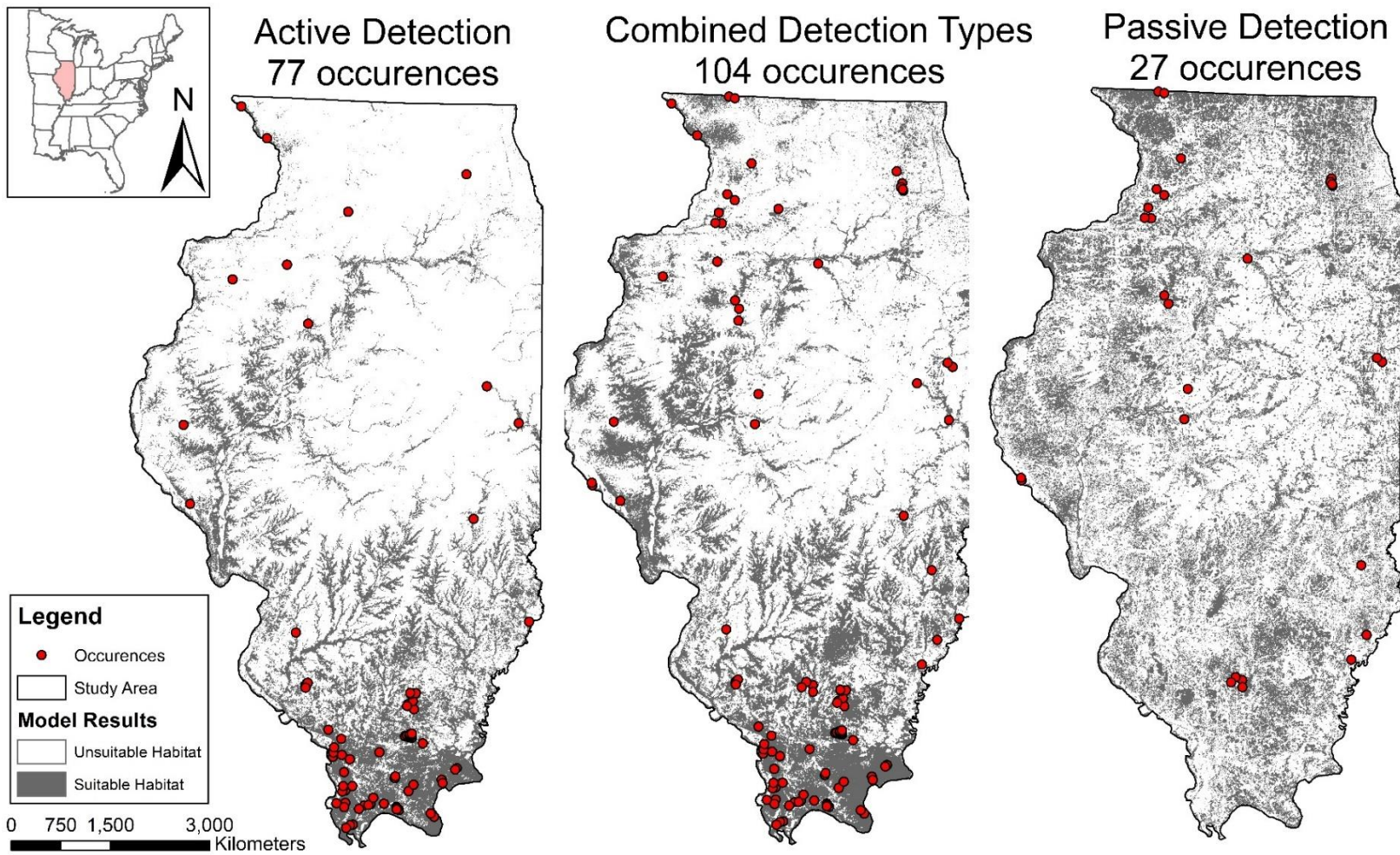
Figure 8. Habitat suitability models for the tri-colored bat with detection types; active, combined, and passive.

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CHAPTER 4: ASSESSING THE EFFICACY OF THE NORTH AMERICAN BAT MONITORING PROGRAM FOR HABITAT SUITABILITY MODELING

ABSTRACT

Landscape-level research and thus landscape-level monitoring programs are essential to identify critical habitat and prioritize conservation measures. The North American Bat Monitoring Program is a long-term continental-wide monitoring protocol that was established in 2015 to monitor the effect of a disease, white-nose syndrome, on bat populations. This protocol standardizes acoustic sampling across the continent, creating terabytes of data available for agencies to understand species populations, distributions, and trends through multiple modeling analysis. Many states are creating habitat suitability models (HSM) to identify critical habitats and prioritize conservation measures. Here we sought to understand how this standardized acoustic protocol influences models for three species. We created HSM from the NABat acoustic protocol to see if it yielded a robust HSM for three focal species (eastern red bat, hoary bat, and tri-colored bat). We found that each species had different distributions and habitat useage across Illinois. Creating a model with solely NABat acoustic data varied among species with eastern red bat having 83% overlap compared to a combined model while the tri-colored bat had only 47% overlap. Across all species, NABat predicted more suitable habitat in agricultural zones while the combined models predicted more habitat in forested zones. The NABat protocol encourages sampling in areas that may be otherwise overlooked, however 20 sampling cells may be insufficient to properly monitor all species in Illinois.

INTRODUCTION

As habitat loss continues unabated (Brooks et al. 2002, Powers and Jetz 2019,
Eichenwald et al. 2020, Williams et al. 2022) and the sixth biodiversity crisis proceeds apace
(Pimm et al. 1995, Singh 2002), landscape-level research is essential to identify critical habitat
and prioritize global conservation measures (Jones 2011, Noon et al. 2012, Bellamy et al. 2013).
As such, landscape-level monitoring programs are being instituted to provide long-term
occurrence data that transcends geopolitical boundaries (Sauer et al. 2003, Jones 2011, Loeb et
al. 2015). Standardizing a protocol that both spatially and temporally maximizes statistical power
and the data's potential to make comparisons and identify change (Noon et al. 2012, Banner et
al. 2019). In addition, collaborative monitoring promotes international species conservation
across jurisdictions and can provide best available knowledge for policy making (Donald et al.
2007, Plummer and Hashimoto 2011, Reichert et al. 2021). Examples of range-wide international
programs include the Audubon Society's Breeding Bird Surveys (Sauer et al. 2003, Ziolkowski
et al. 2010) and the Integrated Tiger Habitat Conservation Programme (International Union of
Conservation for Nature 2022).

Collecting long-term occurrence data is important for monitoring spatio-temporal change
via modeling (e.g. occupancy models, habitat suitability, etc.) (Magurran et al. 2010, Law et al.
2015, Rodhouse et al. 2019). Occupancy models estimate species' presence/absence based on
detection probabilities and environmental covariates (MacKenzie et al. 2002). Habitat suitability
models (HSMs) leverage presence-only occurrences and environmental variables to identify
habitat preferences and predict suitable habitat at the landscape-scale (Elith et al. 2006, 2011,
Phillips and Dudík 2008). Both models give researchers and managers the means to target future

sampling, prioritize restoration, and identify core habitat (Crall et al. 2013, Stevens and Conway 2020, Cable et al. 2021).

One collaborative monitoring program collecting long-term occurrence data is the North American Bat Monitoring Program, (NABat), which was established in 2015 to create a long-term continental monitoring program for bat species (Loeb et al. 2015, Reichert et al. 2021, U.S. Geological Survey 2021). The need for NABat became apparent in the wake of disease called white-nose syndrome (WNS), that was first discovered in 2007 and began decimating bat populations and driving extirpations in North America (Frick et al. 2010, Cheng et al. 2021). In addition to WNS, compounding factors (including increasing wind energy development, pesticide use, and habitat loss) threaten bat populations (Barré et al. 2018, Rodhouse et al. 2019, Sandoval-Herrera et al. 2020), rendering bats among the most threatened taxonomic groups (Frick et al. 2020). NABat combines both top-down and bottom-up strategies to implement an international and multiagency standardized protocol, while also allowing flexibility and ease for agencies to concurrently collect necessary data (Reichert et al. 2021). NABat has three primary goals: (1) create a consensus on monitoring for the effect of WNS on bats, (2) monitor different species vulnerability to WNS, and (3) establish best practices for range-wide population monitoring of species of concern (Loeb et al. 2015). Currently NABat is in the process of releasing range-wide occupancy models and population trends for seven species to inform management decisions and species listings under the Endangered Species Act (Udell et al. 2022).

Advancements in acoustic technology decreases the cost and skill level necessary for bat surveys. NABat's basic monitoring protocol allows for community scientists to collect the data at a local level for biologists to later analyze (Neece et al. 2019, Seguin 2019). NABat uses a generalized random-tessellation stratified (GRTS) system to create a 10km x 10km grid across

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North America and identify priority cells composed of four quadrants (Stevens and Olsen 2004, Larsen et al. 2008, Loeb et al. 2015). While NABat has created a list of priority cells for each state, states can substitute cells based on feasibility and ownership, allowing states sampling flexibility. Ideally, each state surveys 30 GRTS cells with 2-4 stationary points per quadrat and one mobile transect through the entire cell (Loeb et al. 2015). The collection of stationary quadrant points should reflect the diversity of habitat in the GRTS cells, while the mobile transect can estimate bat abundance, as the car will be moving faster than bats can fly (Fisher-Phelps et al. 2017, Neece et al. 2019). After sampling, acoustic files are analyzed with an acoustic identification software and uploaded to the NABat website (Loeb et al. 2015, Reichert et al. 2018, U.S. Geological Survey 2022). The website facilitates data submission and download, allowing researchers, scientists, and land managers to request data that other entities collect, creating unparalleled data accessibility (U.S. Geological Survey 2022).

The Illinois Bat Conservation Program (IBCP) has been following the NABat sampling protocol in 20 GRTS cells across Illinois since 2016. With these data, we seek to answer the following question: does NABat's acoustic protocol create comparable HSMs when compared to a HSM with increased data types and sampling occurrences? HSMs have been a common method for modeling suitable bat habitat as bats are highly mobile and have habitat requirements at multiple scales; roosting, foraging, and migrating (Bellamy et al. 2013, Cruz and Ward 2016, Cable et al. 2021). We predict that NABat will provide a broad and large resolution HSM but will not provide the precise and fine scale accuracy of a HSM with additional data.

METHODS

Study Species

There are diverse life history traits across Midwestern bat species. The eastern red bat, *Lasiurus borealis* (Müller 1776) is a common generalist forager that primarily roosts solitarily in foliage and tree bark (Limpert et al. 2007, Perry et al. 2007). Their longer, narrow wings are adapted for fast flying over long distances and foraging in forest gaps, edges, and openings (Walters et al. 2007, Amelon et al. 2014, Starbuck et al. 2015). The hoary bat, *Lasiurus cinereus* (Palisot de Beauvois 1796), migrates long-distances and primarily forages in open spaces, both behaviors linked with high wind-turbine mortality (Hayes et al. 2015, Weller et al. 2016, Friedenberg et al. 2021). The tri-colored bat, *Perimyotis subflavus* (Cuvier 1832) has the longest hibernation time in Illinois, contributing to devastating losses from WNS and prompting its candidacy for listing under the U.S. Endangered Species Act (ESA) (Turner et al. 2011, Center for Biological Diversity and Defenders of Wildlife 2016, Cheng et al. 2021). They are foliage roosters choosing mature stands and forage above the trees and in partially open habitat (Veilleux et al. 2003, O'Keefe 2009, Farrow and Broders 2011).

Capture Data

Historic capture data was acquired via a data sharing agreement with the Illinois Department of Natural Resources (IDNR) and the U.S. Fish and Wildlife Service for both mist-netting and summer wind farm mortalities from 1999-2021. Since IDNR primarily maintains records for threatened and endangered species, the historic capture data was incomplete for non-listed species. Thus, we contacted IDNR's list of Illinois mist-netting permitees requesting mist-netting records for the three focal species between 1999-2021. Eight additional sources

responded augmenting 46 mist net sites from 2015-2019 generated by the Illinois Bat

Conservation Program (IBCP). We combined windfarm mortality and mist-net records, reducing

the number of individual records to one per site. For all data, we removed sites with low

positional or temporal accuracy, or no data associated with captures.

Acoustic Data

Acoustic data was collected by IBCP, which has been following the NABat protocol

since 2016 for 20 NABat GRTS cells annually (Illinois Bat Conservation Program 2021, U.S.

Geological Survey 2021). A Song Meter SM4+ detector was deployed in 2-4 of the quadrants in

each GRTS cell with a SMM-U1 or U2 microphone (Wildlife Acoustics). Sites in each quadrant

were chosen to represent habitat diversity in each cell. Monitors were deployed for a minimum

of four good weather nights (i.e. no rain, temperatures > 60 degrees, and sustained wind < 8

mph). The same protocol was used for all years, and sites remained largely unchanged, with

some exceptions due to landowner permissions or personnel changes. Data was recorded from

19:00 to 7:30 each night. IBCP also generated acoustic monitoring sites across Illinois that were

surveyed with a similar acoustic protocol as the GRTS cells. These data are considered presence-

only; the survey effort at each site (i.e. four nights) is not enough to determine absence (Moreno

and Halffter 2000, Skalak et al. 2012).

We used the NABat protocol to process the acoustic data (Reichert et al., 2018).

Specifically, we processed all files recorded in the field through Sonobat 4 (Arcata, CA) using

the medium filter to reduce noise files (Szewczak 2010).. Due to time and data storage

constraints, we ran Kaleidoscope Pro 5.4.0 as the auto-identifier (Kaleidoscope Pro n.d.).

Kaleidoscope is a powerful auto-classifier that, in addition to identification, provides maximum

likelihood estimates of species occupancy. We considered below $\alpha = 0.05$ to be present and

above $\alpha = 0.05$ to be absent following standard conservative protocols (Nocera et al. 2019, U.S. Fish & Wildlife Service and U.S. Geological Survey 2019). These acoustic data were not manually vetted since NABat does not require manual vetting for their data upload. All data was re-processed in 2021 to ensure that the classifier's conditions were the same through all analyses.

Data Cleaning

Active and passive data were combined and processed in R 4.1.2 (R Core Team 2021). To reduce spatial autocorrelation, we removed records within 1 km of each other. Records were also temporally restricted from May 15- Aug 15 to ensure that no records were from migration time periods following the U.S. Fish and Wildlife Guidelines (U.S. Fish & Wildlife Service 2020). After data cleaning and quality control, there were 264 occurrences for eastern red bats, 116 occurrences for hoary bats, and 106 occurrences for tri-colored bats spread across Illinois.

Environmental Layers

We used sixteen landcover variables (Table 8) (per Cable, 2020) created from the Illinois Geospatial Clearing house land cover layer (Illinois Department of Natural Resources et al. 2003). Cable then used Fragstats (McGarigal and Marks 1995) to find the number of patches of four landcover types, total area of eight landcover types, and total edge of two landcover types. Each metric was calculated at three different scales (0.1km, 0.5km, and 1km) representing roosting, foraging, and landscape distances.

An additional nine variables were also considered based on the top models of published chiropteran habitat suitability or occupancy models (Table 8). Many of these variables were forest stand structure metrics or topographical landscape metrics, gathered from publicly available GIS layers and resampled in ArcGIS for 100m resolution to match layers (Esri Inc.

2021). Both temperature and precipitation layers were taken from a 30-year normal and averaged across May-Aug to represent the summer average (PRISM Climate Group 2021).

Modeling

For all variables, we created univariate models in MaxEnt to optimize spatial scale for variables and chose the top 15 variables for each species by AUC_{test} scores. 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 landcover variable. We ranked the top scaled landcover variables among the non-scaled variables, selecting the top 15 variables for each species with AUC_{test} >0.5. The top 15 variables for each species were carried on throughout the analysis. A correlation matrix was created in ArcGIS for the fifteen variables for each species and highly correlated variables (>0.7) were removed based on their univariate rank. With the remaining non-correlated variables, a global model was created for each species.

Using the global model, we tested differing regularization multipliers ranging from 1-12 using the same default parameters of 20 replicates and 10% as a random test percentage. The regularization multiplier with the top AUC_{test} scores was carried out through the rest of the analysis. Each species had two models run with the same global model for each data set: all combined occurrences and NABat-only acoustic model. This yielded six models across all species. All models were identically run MaxEnt using presence-only data, using the top regularization multiplier, 20 replicates, 10% of datapoints withheld from the dataset, and 5000 maximum iterations. For pseudo-absence points, MaxEnt randomly sampled background points across the state using bootstrapping.

Model Analysis

Model goodness-of-fit was assessed via AUC_{test} scores and omission rates. 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). The dataset from the opposite data types was used to test the omission rate. 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).

$$logistic = (raw * e^{entropy})/(1 + raw * e^{entropy})$$

To create binary models, we created a threshold of omission for each species based on the bottom 10% of suitability scores for true presences in the test datasets (Hovick et al. 2015). For a comparison of the binary models, we ran a niche overlap function in ENMTools and used the Schoener's D value for comparison which calculates the proportion of shared pixels between the two models (Schoener 1968, Warren et al. 2010, Suárez-Mota and Villaseñor 2020).

RESULTS

Based on life history traits affecting detection probabilities, there was a range in the number of occurrences among species (Table 10) (Gorresen et al. 2008, Coleman et al. 2014, Hohoff 2016). Most hoary bat occurrences (n = 116 occurrences) came from NABat detections (n = 81), whereas NABat detections (n=27) for the tri-colored bat were far less, despite combined occurrences (n = 104) being approximately the same. The eastern red bat had the highest number of occurrences (n=264) with a third of them being from NABat (n=82).

The top 15 variables for each species were similar for the tri-colored and eastern red bat, while more open habitat variables defined the hoary bat (Table 9). After removing correlated variables, the eastern red bat's global model included elevation, distance to water, existing vegetation height, quadratic mean diameter, total area of agriculture in 100m, total area of bottomland forest in 1km, total area of forest in 100m, total area of water in 1km, total edge of forest in 100m, and total edge of water in 1km (Table 10). Similarly, the tri-colored bat's global model included elevation, distance to roads, existing vegetation height, number of patches of forest in 100m, number of patches of water in 500m, quadratic mean diameter, stand density index, total area of agriculture in 500m, total area of bottomland forest in 1km, and total area of water in 500m. Contrary to the other two, the hoary bat's global model included aspect, distance to roads, distance to water, existing vegetation height, number of patches of forest in 100m, stand density index, solar radiation, total area of agriculture in 100m, total area of bottomland forest in 100m, total area of open canopy deciduous forest in 1km, total area of urban in 100m, and total area of water in 1km.

For the eastern red bat, the NABat model and the combined model reveal diverging suitable habitat between forested and urban areas. However, highest degree of overlap (83%) and the lowest omission rate of 37% between all three focal species was recovered (Fig. 10, Table 10). The NABat model revealed dense, contiguous suitable habitat in the urban and suburban areas of Chicago, while the combined model finds dense suitable habitat in and around the Shawnee National Forest of southern Illinois. Both models similarly project suitable habitat in the central regions where row crop agriculture is the predominant land cover. Between the two models, the NABat model overall projects suitable habitat in urban areas across the state while the combined sampling method projects suitable habitat in forested regions of the state. Despite

the discrepancy, both models predicted an equal percentage of suitable habitat in the state (51%). In addition, both models had lower AUC values (AUC < 0.8) indicating poor model fit for eastern red bats.

For the hoary bat, model projections recover less overlap (72%) with a significantly higher omission rate of 60% (Fig. 11, Table 10). Model comparison reveals a divergence among landcover types as well, as NABat projects more suitable habitat in row crop agriculture, while combined sampling projects more suitable habitat in forested regions of the state. The combined model overall predicted more suitable habitat (46.9% for combined, 39.9% for the NABat model) across the state, while the NABat model had a higher AUC value (0.819) than the combined (0.803).

Lastly, the tri-colored bat had the least amount of suitable habitat across the state between all species with the combined model projecting 28.3% suitability and the NABat model projecting 31.3%. These models also had the highest AUC values among all species with 0.832 for the NABat model and the 0.852 for the combined model. The two models had an overlap value of 47%, lowest among focal species. Similar to the eastern red bat, the tri-colored NABat model projects a larger amount of suitable habitat in northern Illinois, while the combined model projects a larger amount of suitable habitat in the forested southern part of Illinois. Most of the combined model's suitable habitat is constrained to the riparian corridors along Illinois' big rivers while there is no riparian association seen in the NABat model.

DISCUSSION

The difference between the combined model and the NABat HSM varied among species. The two generalist species, eastern red bats and hoary bats, exhibited greater niche overlap values relative to the forest specialist tri-colored bat (Ford et al. 2005, Menzel et al. 2005, Cox 2019). Across all three species, the difference between the two models is highlighted by different habitat predictions based on land use type. The NABat model projects more suitable habitat in agricultural areas, while the combined model projects more suitable habitat in the forested regions. This discrepancy is an artifact of sampling biases between acoustic and conventional (i.e. mist netting) sampling methods especially as acoustic microphones have a farther range in open habitat vs. forested habitat. NABat GRTS cells are chosen based on a stratified random sampling design, meaning that cells are not prioritized based on quality of habitat (Loeb et al. 2015). Given this, many of the NABat GRTS cells in Illinois are in or very close to row-cop agriculture. Moreover, no NABat GRTS cells were sampled in the heavily forested southern extent of the state. By contrast, mist-netting sites are disproportionately concentrated in forested areas, as stand structure, proximity to water, and other factors improve chances of catching bats (O'Farrell and Gannon 1999, MacCarthy et al. 2006, Geluso and Geluso 2012). Wind turbine mortalities, another form of capture, are often sited in row crop agriculture, and disproportionately affect migratory species like the eastern red and hoary bats (Grodsky et al. 2011, Frick et al. 2017, Rodhouse et al. 2019). Between the two models, the increased number of occurrences in agricultural settings reflects an increased suitability in those habitat types, while underemphasizing the suitability of forested habitat. Further discussion of the difference between acoustic vs. capture is in Chapter 2.

With the dichotomy of suitable habitat between models, the definition of suitable habitat calls for clarification. For forest-dependent species such as tri-colored and eastern red bats, detections in agricultural areas may be a result of commuting between forested patches (Farrow and Broders 2011, Trubitt et al. 2019). If a bat commutes through an agricultural area once or twice per night, should this habitat still be classified as suitable? Removing or degrading those commuting habitats can be as detrimental as altering habitat patches where bats spend more time (Roscioni et al. 2014, Barré et al. 2018). Considering these patches as valuable, which at face value are not highly beneficial for forested species, is important (Elmore et al. 2005, Rainho and Palmeirim 2011). Generalist species, such as the hoary bat and big brown (*Eptesicus fuscus*), also use agricultural patches for foraging, so many species may find these patches as valuable (see stacked HSM in Chapter 1) (Trubitt et al. 2019).

The robustness of NABat models compared to combined models is species-specific. While the eastern red bat has the highest overlap between our focal species, the dichotomy between the northern urban and southern forested areas is striking enough to warrant discretion in model interpretation. The hoary bat exhibited considerable overlap, yielding perhaps the most robust of the models with similar distributions. The tri-colored bat has less than 50% overlap between the two models indicating that the NABat model is insufficient for informing management decisions. Generally, all easily accessible occurrences are used for HSMs, however these models show that acquiring additional occurrence points of different data types can substantially influence model outputs which may be extremely beneficial depending on the model's purpose (Chapter 2). Ultimately, these results indicate that, at present, NABat sampling in Illinois is insufficient to make a robust HSM, although the degree of robustness is species-specific.

A Case Study of the Tri-Colored Bat and NABat Models

In 2022, NABat achieved one of the main programmatic objectives and released their first summer occupancy models for several species, including the tri-colored bat (Fig. 13) (Loeb et al. 2015, Udell et al. 2022). Occupancy models and HSMs utilize two different data sets and model two different distributions; i.e. occupancy models calculate the probability that a species is present/absent at the site while incorporating imperfect detection, while HSMs only model the suitability of a location based on species' relationships with the environment (MacKenzie et al. 2002, Elith et al. 2006). Therefore, these models cannot be directly compared, especially considering NABat's occupancy model is a larger-resolution range-wide model. However, one would expect some overlapping distributions, as sites with a higher probability of occupancy should be expected to occur more often in suitable habitat (Larson et al. 2004, Martin et al. 2010, Iglecia et al. 2012).

In comparing NABat's tri-colored occupancy model to the combined HSM created herein, the difference between the two models is striking. Higher occupancy regions are nearly opposite the suitable habitat regions. The combined HSM largely comports with expected tri-colored bat habitat preferences (see Chapter 1), as they are known to be forest specialists, while the NABat occupancy model recovers higher occupancy in Illinois' agroecosystem and lower occupancy in forested zones, contrary to species biology/ecology (Farrow and Broders 2011, Schaefer 2017, Cox 2019).

Differences between these models further underscores the biases associated with different sampling techniques utilized in models (Chapter 2). Both the NABat HSM and NABat occupancy model project strikingly different results than one would expect for each model type based on tri-colored biology and habitat preferences (Chapter 1). Utilizing only acoustic data

creates biased models (Chapter 2). One of the major objectives of NABat is to create a

continental monitoring protocol that is accessible to states, however this inherently limits the

amount of sampling to acoustic-only data as mist-netting is too time-intensive, expensive, and

skilled for the average non-bat biologist (Loeb et al. 2015, Reichert et al. 2021). Models created

with only NABat data are affected by this sampling bias and, as illustrated here, differ from what

conventional (Chapter 1) and/or combined-data (Chapter 2) models may show. NABat allows for

and highly encourages the input of mist-netting records, however data accumulation is slow and

many states have yet to upload records.

This case study emphasizes the cautionary tale of modeling. Models approximate reality

and utilizing different data types, distributions, and time periods introduces biases with each

approximation (Phillips et al. 2009, Merow et al. 2013, Barnes et al. 2014). Managers need to be

cautious in the way that they utilize and interpret models (Lozier et al. 2009, Barnes et al. 2014,

Anderson et al. 2016). Both the occupancy and HSM may be used in management decisions as

they are provided to forest managers in Illinois, however these diverging models require careful

analyses and consideration, as they could lead to different management decisions and

interventions that could, in fact, be detrimental to target species. As time passes and the

continental NABat implementation continues apace, the accumulation of data will contribute to

creating more robust models with larger data sets and broader geographic sampling.

Nevertheless, continued caution should be exercised in the interpretation of these models.

Conclusion

While the current NABat sampling reflects a broad distribution across Illinois, there are

no GRTS in the southern extent of the state, which may underrepresent the importance of

forested habitat for Illinois bat species. In range-wide modeling, GRTS cells in other states may

be able to provide sufficient forested sampling, yet the management decisions are often made on ecologically irrelevant political boundaries creating a need for state-specific HSMs. In the summer of 2022 and beyond, IBCP and the Midwest Bat Hub will be adding an additional 20 GRTS cells throughout the state, increasing sampling overall, but especially by adding GRTS cells in predominately forested regions of the state (Fig. 9). Illinois will then exceed NABat's recommended 30 GRTS cells per state (Loeb et al. 2015). As Illinois is among the leading states for NABat implementation in the Midwest, these results further emphasize that states with lesser data may have less robust models, that models derived from these scant data should be carefully assessed, and data expansion will be necessary to update and improve modeling efforts.

NABat is an incredible continental-wide initiative that standardizes, organizes, and facilitates an open, extensive, continental chiropteran dataset (Loeb et al. 2015, Neece et al. 2019, Reichert et al. 2021). While the importance and magnitude of this program cannot be understated, the applications and outputs of this dataset must be thoroughly vetted for biases. Given that these initial NABat HSMs have too large of a discrepancy compared to the combined model to make management decisions, doubling the number of GRTS cells on the landscape and/or merging with conventional sampling data may create much more robust models with higher discriminatory power, ultimately providing greater value to forest managers interested in or required to manage for imperiled bat populations.

TABLES AND FIGURES

Table 8. Variables tested in univariate models. The X in variable name representing the scales at which it was tested.

Variables	Spatial Scale (km)	Variable Name	Original Data Source	Creator
Aspect	0.1	aspect	(U.S. Geological Survey 2018)	Gaulke
Canopy Cover	0.1	canopy_cover	(U.S. Geological Survey 2018)	Gaulke
DEM	0.1	dem	(U.S. Geological Survey 2018)	Gaulke
Distance to Roads	0.1	dist_roads	(Illinois Department of Transportation 2018)	(Cable et al. 2021)
Distance to Water	0.1	dist_water	(U.S. Geological Survey n.d.)	(Cable et al. 2021)
Existing Vegetation Height	0.1	evh	(U.S. Department of Interior et al. 2013)	Gaulke
Number of Patches of Agriculture	0.1, 0.5, 1	np_ag_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Forest	0.1, 0.5, 1	np_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Urban	0.1, 0.5, 1	np_urb_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Number of Patches of Water	0.1, 0.5, 1	np_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Null	0.1	null	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Precipitation (30-year average of monthly summer precipitation)	0.1	precip	(PRISM Climate Group 2021)	Gaulke
Quadratic Mean Diameter	0.1	qmd	(U.S. Forest Service 2012)	Gaulke
Stand Density Index	0.1	sdi	(U.S. Forest Service 2012)	Gaulke
Solar Radiation	0.1	solar_rad	(Solargis 2019)	Gaulke

Table 8 (cont.).

Total Area of Agriculture	0.1, 0.5, 1	ta_ag_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Bottomland Forest	0.1, 0.5, 1	ta_bot_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Closed Canopy Deciduous Forest	0.1, 0.5, 1	ta_ccd_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Coniferous Forest	0.1, 0.5, 1	ta_conif_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Forest	0.1, 0.5, 1	ta_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Open Canopy Deciduous Forest	0.1, 0.5, 1	ta_ocd_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Urban	0.1, 0.5, 1	ta_urb_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Area of Water	0.1, 0.5, 1	ta_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Forest	0.1, 0.5, 1	te_for_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Total Edge of Water	0.1, 0.5, 1	te_water_x	(Illinois Department of Natural Resources et al. 2003)	(Cable et al. 2021)
Temperature (30-year average of monthly minimum summer temperature)	0.1	temp	(PRISM Climate Group 2021)	Gaulke

Table 9. Univariate model results ranked by AUC$_{test}$ values. The top 15 variables were used in the multivariate models.

Rank	Eastern red	AUC	Hoary	AUC	Tri-colored	AUC
1	ta_ag_100	0.7231	ta_ag_100	0.6376	dist_roads	0.9056
2	ta_for_100	0.7206	dist_roads	0.6172	sdi	0.8071
3	evh	0.7193	ta_urb_100	0.6038	ta_bot_1km	0.8033
4	sdi	0.7169	dist_water	0.5968	ta_for_500	0.798
5	np_for_100	0.7016	np_for_100	0.5871	evh	0.7959
6	qmd	0.6999	ta_water_1km	0.586	ta_ag_500	0.7858
7	canopy_cover	0.6985	solar_rad	0.5819	dem	0.7721
8	te_for_100	0.6967	evh	0.5812	qmd	0.7719
9	ta_bot_1km	0.6548	ta_for_100	0.579	canopy_cover	0.7678
10	te_water_1k	0.647	te_for_100	0.5741	ta_water_500	0.762
11	dem	0.6434	sdi	0.573	temp	0.7502
12	ta_water_1km	0.6412	aspect	0.57	te_for_500	0.7444
13	np_water_1km	0.6355	np_urb_100	0.5611	np_for_100	0.7362
14	temp	0.6258	ta_ocd_1km	0.5568	np_wat_500	0.7313
15	dist_water	0.6243	ta_bot_100	0.5554	te_water_500	0.7134
16	np_ag_500	0.6186	te_water_1k	0.5509	ta_ccd_1km	0.7124
17	ta_ccd_1km	0.6126	temp	0.5501	ta_ocd_1km	0.6996
18	dist_roads	0.611	ta_ccd_100	0.5447	np_ag_1km	0.6993
19	solar_rad	0.6039	precip	0.5421	solar_rad	0.6782
20	ta_ocd_1km	0.5914	canopy_cover	0.5418	precip	0.6563
21	precip	0.5723	np_ag_1km	0.5271	dist_water	0.637
22	aspect	0.5719	qmd	0.5261	ta_conif_500	0.6255
23	ta_conif_1km	0.5475	np_wat_100	0.5259	aspect	0.5804
24	null_	0.5388	dem	0.5244	np_urb_1km	0.5566
25	ta_urb_100	0.5278	ta_conif_1km	0.5136	ta_urb_100	0.5504
26	np_urb_500	0.52	null_	0.4507	null_	0.5279

Table 10. Global model ran for each species and each data type. AUC$_{test}$ values show model's goodness-of-fit. The percent of suitable habitat is the percent of Illinois that has been found as suitable after the binary threshold. The omission rate is the percent of opposite data type points modeled in unsuitable habitat in the binary model with the number of occurrences omitted in parentheses- i.e. the active data type's omission rate is the percent of passive occurrences that were omitted.

Global Model Variables	Data Type	Total Number of Occurrences	AUC$_{Test}$ Value	% Suitable Habitat in Illinois	Omission Rate (number of occurrences)	Niche Overlap Indices
Eastern Red bat						
dem + dist_water + evh + qmd + ta_ag_100 + ta_bottomland_1km + ta_forest_100 + ta_water_1km + te_forest_100 + te_water_1k	NABat	82	0.7652	51%	36.8% (67)	0.8334
	Combined	264	0.7914	50.9%	-	-
Hoary bat						
aspect + dist_roads + dist_water + evh + np_for_100 + sdi + solar_rad + ta_ag_100 + ta_bot_100 + ta_ocd_1km + ta_urb_100 + ta_water_1km	NABat	81	0.819	39.9%	60% (21)	0.7247
	Combined	116	0.8025	46.9%	-	-
Tri-colored bat						
dem + dist_roads + evh + np_for_100 + np_wat_500 + qmd + sdi + ta_ag_500 + ta_bottomland_1km + ta_water_500	NABat	27	0.8316	31.3%	69.6% (59)	0.4763
	Combined	104	0.8522	28.3%	-	-
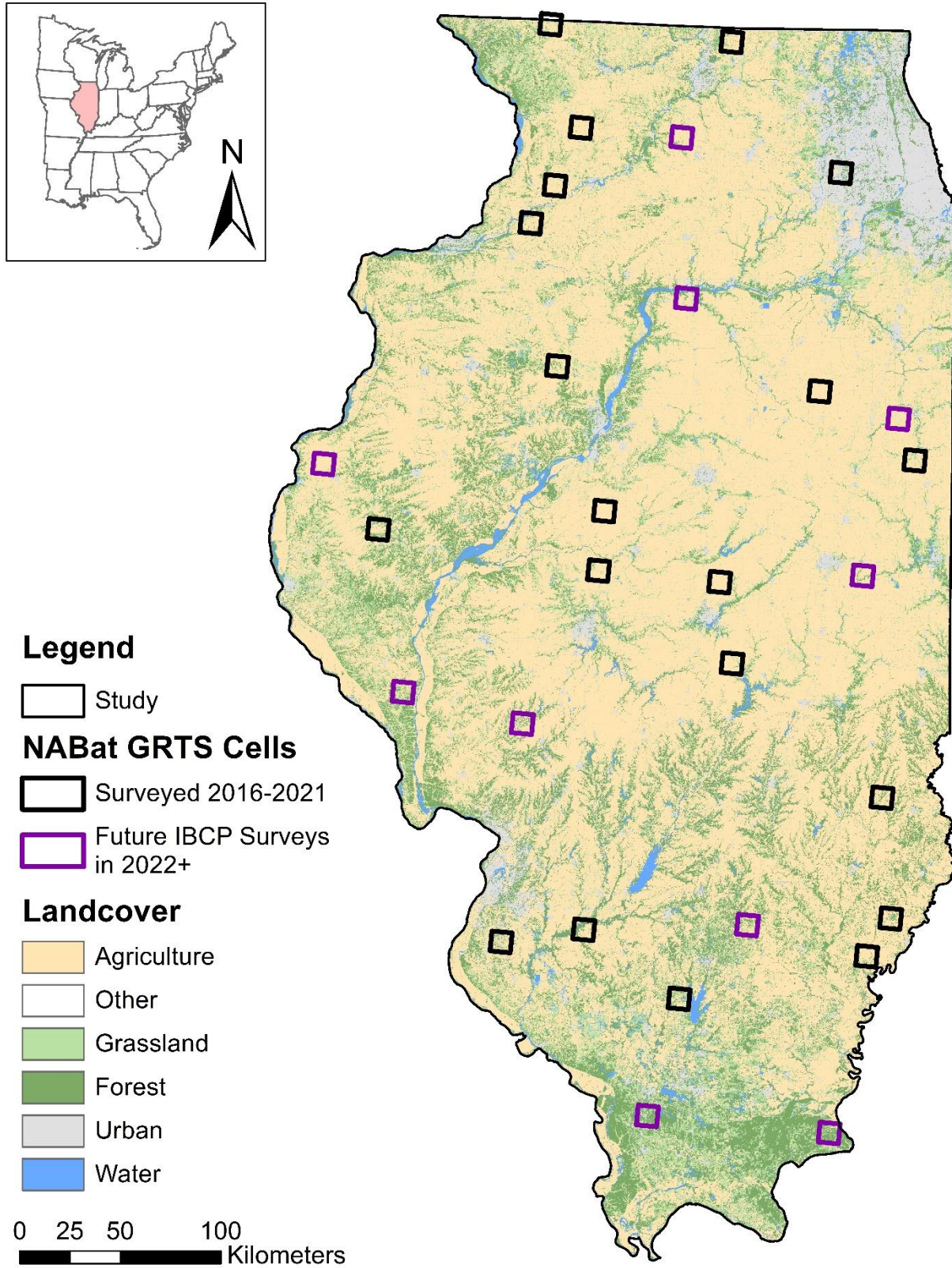
Figure 9. Current (black) and future (purple) NABat GRTS cell locations in Illinois
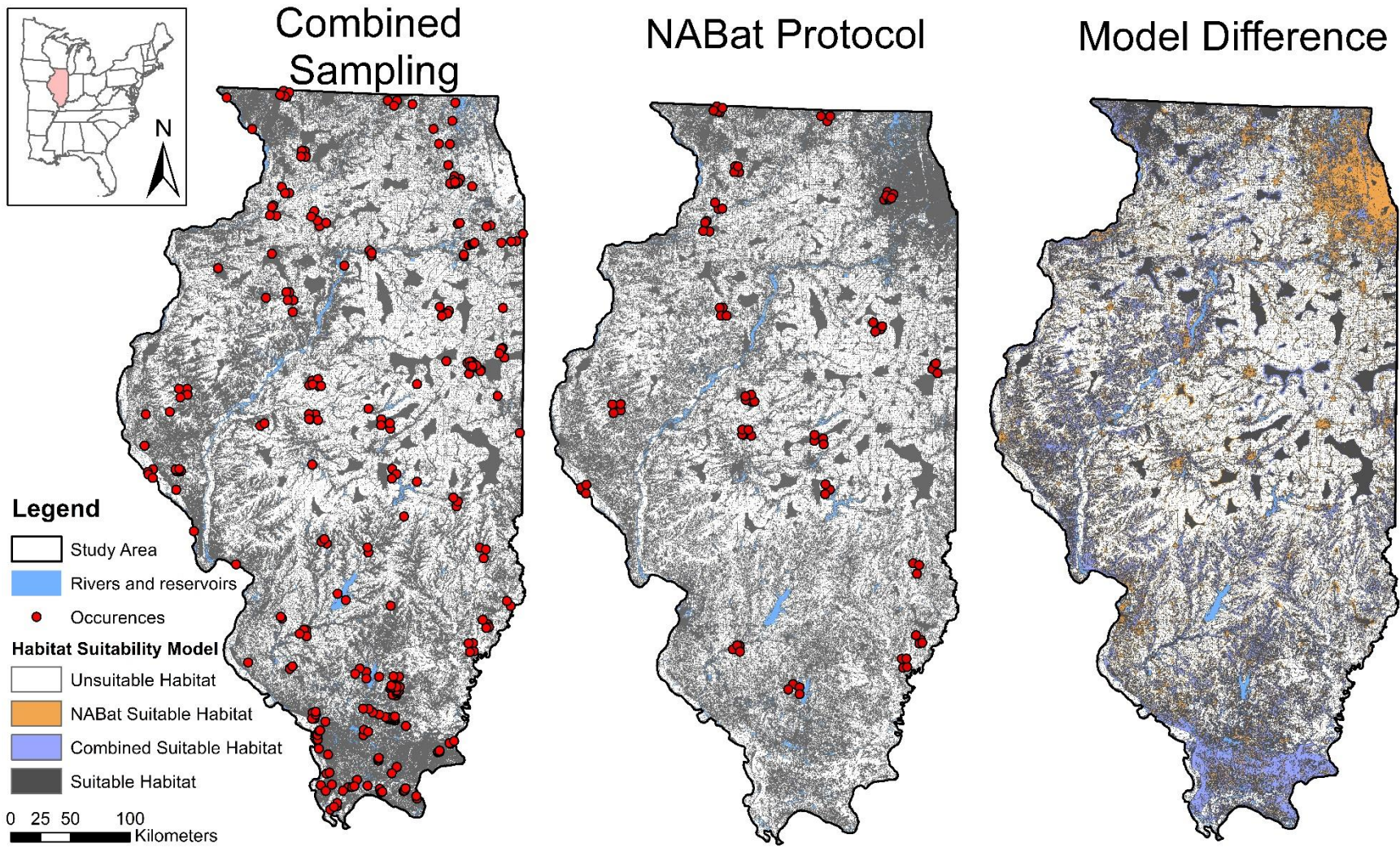
Figure 10. Habitat suitability models for the eastern red bat using a combined sampling method and just NABat cells. The far right map shows the difference between the two models with habitat that was only modeled as suitable by the combined model in purple and habitat that was only modeled as suitable by the NABat model in orange.
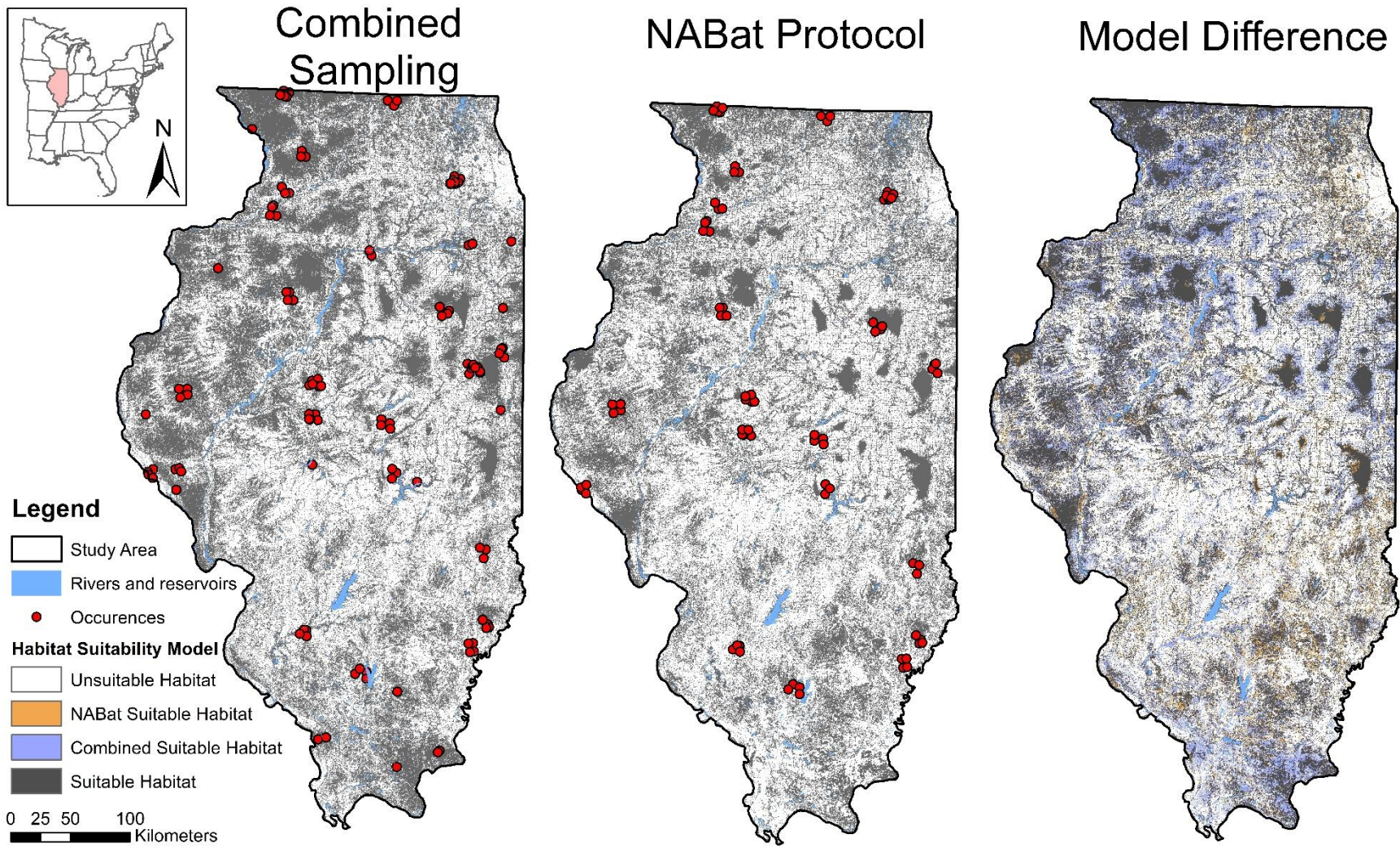
Figure 11. Habitat suitability models for the hoary bat using a combined sampling method and just NABat cells. The far right map shows the difference between the two models with habitat that was only modeled as suitable by the combined model in purple and habitat that was only modeled as suitable by the NABat model in orange.
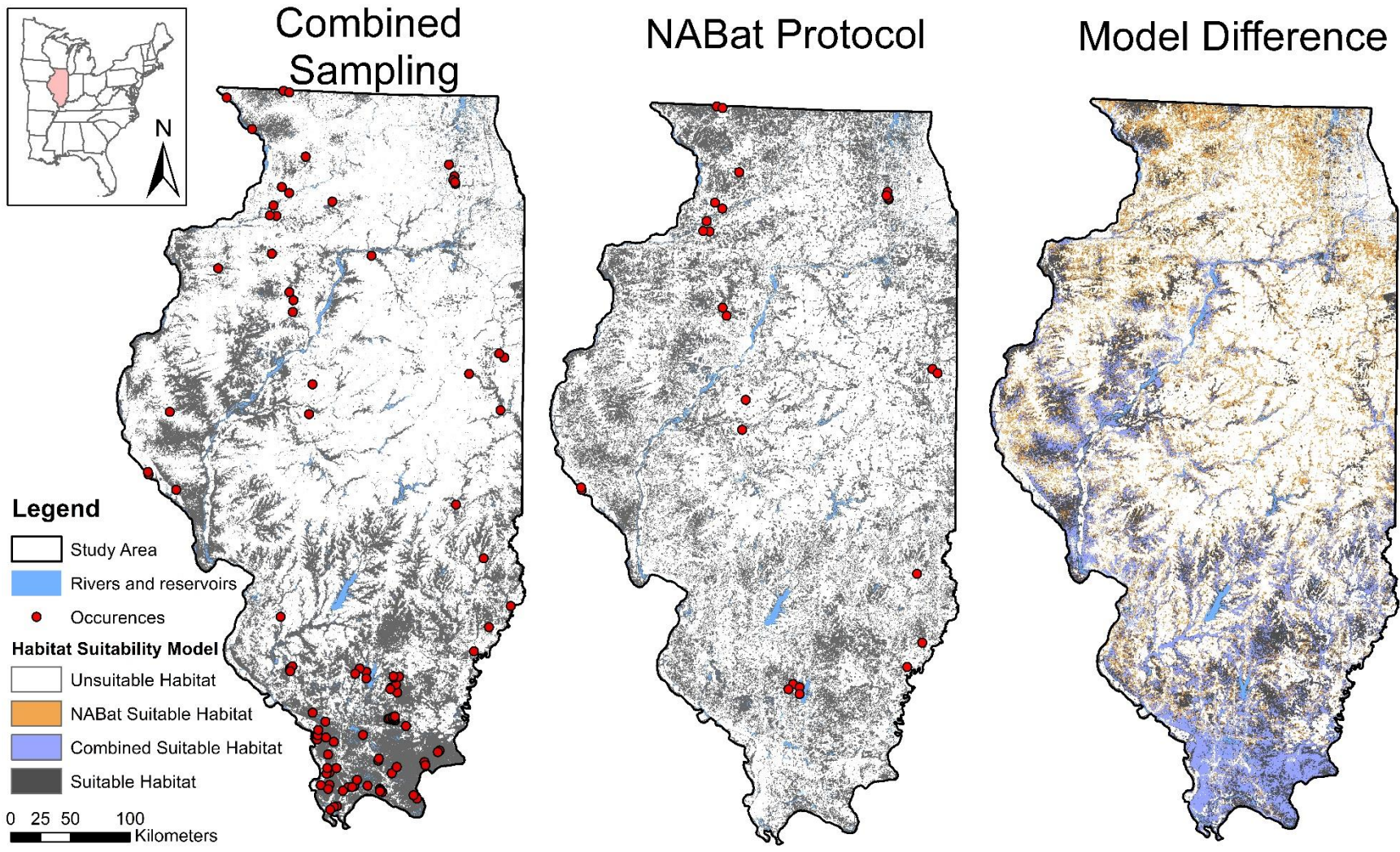
Figure 12. Habitat suitability models for the tri-colored bat using a combined sampling method and just NABat cells. The far right map shows the difference between the two models with habitat that was only modeled as suitable by the combined model in purple and habitat that was only modeled as suitable by the NABat model in orange.
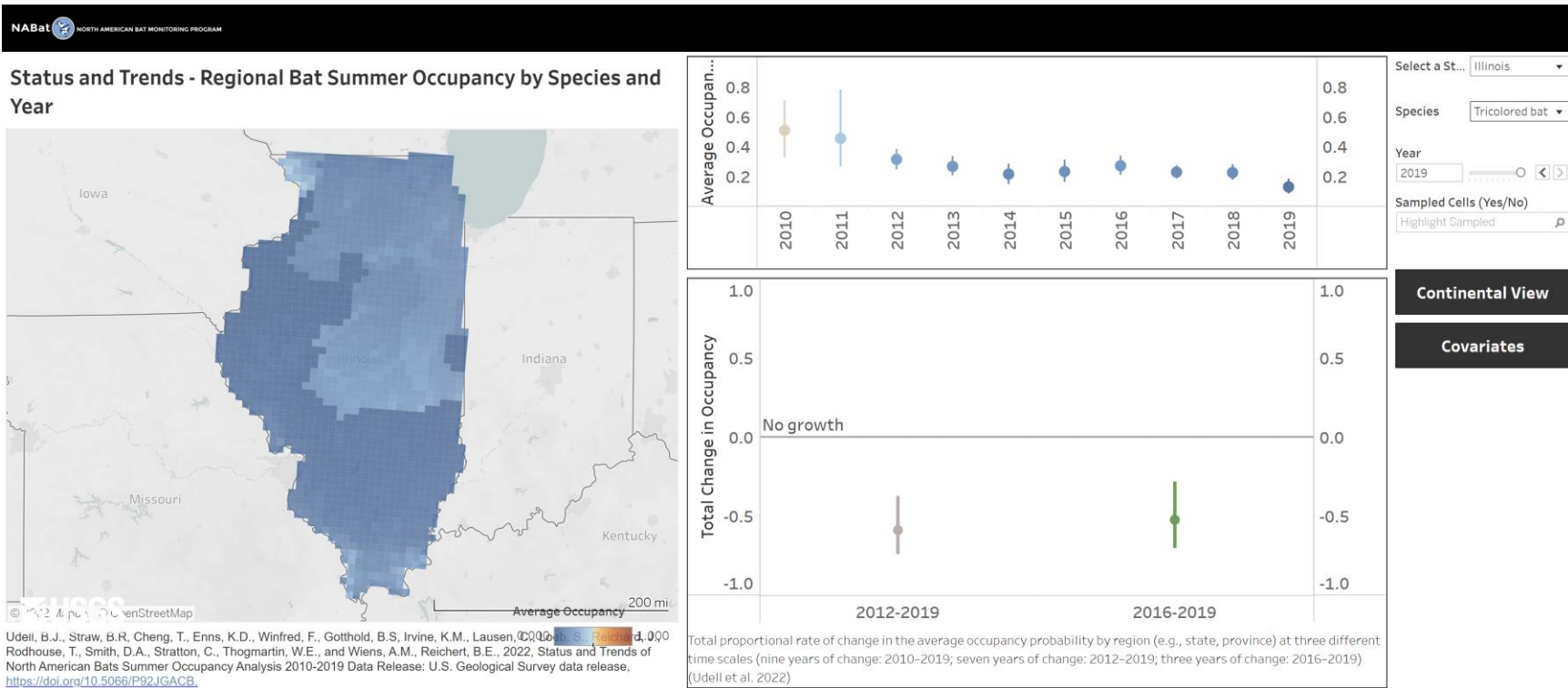
Figure 13. A summer occupancy model by the NABat program for the tri-colored bat in 2019 with darker areas indicating less occupancy. Screenshot taken from their interactive occupancy map web portal (Udell et al. 2022).

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CHAPTER 5: CONCLUSION

In an effort to conserve species across the landscape due to increasing pressures from habitat loss, urbanization, and other factors, researchers and managers looks for ways to identify quality habitat for restoration, conservation, and education (Noon et al. 2012, Zellmer et al. 2019, Stevens and Conway 2020). One method that researchers use to accomplish this is through habitat suitability modeling (HSM) which predicts habitat suitability across various scales based on occurrence data and environmental variables (Elith et al. 2006, Phillips et al. 2006). HSM have gained popularity since they were first introduced and are now a common methodology (Phillips et al. 2009). However, models are inherently impacted by the data provided to them and sampling biases within the data can impact the outcome and validity of the model (Flaquer et al. 2007, Clare et al. 2017, Risch et al. 2021). My research adds to the growing literature about the impact of sampling biases and species-specific ecologies on HSM. Passive and active detection are common methods of detection for many species, beyond just bats (Coxen et al. 2017, Watts et al. 2019, Mehdi et al. 2021). Considering the impacts of detection is important to creating robust HSM for conservation and management (Barnhart and Gillam 2014, Ford et al. 2016, Risch et al. 2021).

In addition, bats populations are under growing concern as numerous factors such as disease, wind energy development, and habitat loss contribute to the decline of many bat species (Bellamy et al. 2013, Rodhouse et al. 2019, Sandoval-Herrera et al. 2020, Cheng et al. 2021). Bats play an essential role in ecosystem services across the nation and especially in Illinois with reducing disease vectors and agricultural pests (Feldhamer et al. 2009, Kunz et al. 2011, Maslo et al. 2022). These habitat suitability models contribute to landscape scale research around predicted habitat and important environmental covariates for three species of bat which can be

used to conduct beneficial conservation and management interventions (Bellamy et al. 2013, Cooper-Bohannon et al. 2016, Cable et al. 2021). While these maps only predict suitable habitat in Illinois, the important environmental covariates and suitable habitat patterns may reflect range-wide for many species, and especially in states across the Midwest with similar landcover types.

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APPENDIX: SUPPLEMENTAL MATERIALS

Table A.1 Scaled variables and the Area Under the Curve (AUC) values from the univariate model for each species sampled across Illinois from 1999-2021. Eastern red bats had 264 total occurrences: 17 from wind turbines, 159 from mist-netting, and 88 from acoustics. The hoary bat had 116 total occurrences for hoary bats; 9 from wind turbines, 21 from mist-netting, and 86 from acoustics, while the tri-colored bat had 106 total occurrences for tri-colored bats with 77 from mist-netting, and 27 from acoustics.

Variable	Resolution (km)	Eastern red AUC	Hoary AUC	Tri-colored AUC
Number of patches of agriculture	0.1	0.6072	0.4995	0.6257
	0.5	0.6186	0.4959	0.6673
	1	0.6173	0.5271	0.6993
Number of patches of forest	0.1	0.7016	0.5871	0.7362
	0.5	0.6148	0.5774	0.6858
	1	0.5874	0.5211	0.5968
Number of patches of urban	0.1	0.5172	0.5611	0.5147
	0.5	0.52	0.5577	0.5275
	1	0.5197	0.5442	0.5566
Number of patches of water	0.1	0.5508	0.5259	0.6026
	0.5	0.6334	0.4946	0.7313
	1	0.6355	0.4872	0.7188
Total area of agriculture	0.1	0.7231	0.6376	0.77
	0.5	0.652	0.5588	0.7858
	1	0.6777	0.559	0.7709
Total area of bottomland forest	0.1	0.63	0.5554	0.7244
	0.5	0.6474	0.5221	0.7329
	1	0.6548	0.5361	0.8033
Total area of closed canopy deciduous forest	0.1	0.5953	0.5447	0.611
	0.5	0.6037	0.4818	0.6802
	1	0.6126	0.5406	0.7124
Total area of coniferous forest	0.1	0.5167	0.5056	0.5375
	0.5	0.5394	0.5002	0.6255
	1	0.5475	0.5136	0.6185
Total area of forest	0.1	0.7206	0.579	0.7408
	0.5	0.7046	0.5141	0.798
	1	0.6587	0.5701	0.7679
Total area of open canopy deciduous forest	0.1	0.5008	0.4932	0.5223
	0.5	0.5428	0.5037	0.55
	1	0.5914	0.5568	0.6996

Table A.1 (cont.).

Total area of urban	0.1	0.5278	0.6038	0.5504
	0.5	0.4994	0.5852	0.5187
	1	0.5233	0.5666	0.5371
Total area of water	0.1	0.5506	0.5315	0.5878
	0.5	0.6176	0.513	0.762
	1	0.6412	0.586	0.701
Total edge of forest	0.1	0.6967	0.5741	0.7418
	0.5	0.6482	0.5565	0.7444
	1	0.6262	0.5392	0.7166
Total edge of water	0.1	0.5741	0.5456	0.6314
	0.5	0.6295	0.5141	0.7134
	1	0.647	0.5509	0.6981

Table A.2 Multivariate models for the eastern red bat ranked by the AICc values from 264 occurrences sampled from 1999-2021 across Illinois. AUC$_{test}$ values show model's goodness-of-fit. AICc values is Akaike's Information Criterion for small sample size which ranks the model selection. The difference between the top AICc value and that model's AICc value is the ΔAIC$_c$. The AIC$_c$ w_i is the models' weight.

Model	Rationale	Variables	AUC$_{Test}$	AIC$_c$	ΔAIC$_c$	AIC$_c$ w_i
(Amelon et al. 2014)	Access to water, high prey availability, and commuting by topographic features	elevation + total area of ag in 0.1km + total area of forest in 0.1km + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km	0.7837	8423.76	0	0.5151
(Limpert et al. 2007)	Preferred roosting habitat and foraging habitat in riparian zones	canopy cover + distance to water + quadratic mean diameter + total area of ag in 0.1km + total area of bottomland forest in 1km + total area of forest in 0.1km + total area of water in 1km + temperature	0.7927	8424.4	0.6417	0.3737
Global Model		elevation + distance to water + existing vegetation height + quadratic mean	0.7922	8426.83	3.0681	0.1111

Table A.2 (cont.).

		diameter + total area of ag in 0.1km + total area of bottomland forest in 1km + total area of forest in 0.1km + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km				
(Starbuck et al. 2015)	Open forest to commute with enough roost opportunities in tree canopies	distance to water + total area of ag in 0.1km + total area of forest in 0.1km + total edge of forest in 0.1km	0.7789	8443.58	19.8184	0
Goldilocks	Where there is more agriculture, more forest edge, closer to water, and less forest density	distance to water + stand density index + total area of ag in 0.1km + total edge of forest in 0.1km	0.7731	8453.26	29.505	0
(Hutchinson and Lacki 2000)	Lower susceptibility to terrestrial predators	canopy cover + elevation + quadratic mean diameter	0.7337	8462.31	38.5546	0
Fragmentation	Where the available forest is more fragmented	number of patches of forest in 0.1km + number of patches of water in 1km +	0.782	8464.9	41.1437	0

Table A.2 (cont.).

		total area of ag in 0.1km + total area of bottomland forest in 1km				
(Limpert et al. 2007)	Preferred roosting and foraging habitat in riparian zones where closed canopies provide protection from elements, while open understory allows less predation and easier flying	canopy cover + distance to water + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km	0.769	8468.92	45.1631	0
(Starbuck et al. 2015)	Open forest to commute with enough roost opportunities in tree canopies	distance to water + number of patches of forest in 0.1km + stand density index + total area of ag in 0.1km	0.7669	8470.97	47.2116	0
(Walters et al. 2007)		total area of ag in 0.1km + total area of forest in 0.1km + total area of water in 1km	0.7695	8472	48.247	0
Riparian	Where there are more riparian areas and closer to water	distance to water + number of patches of water in 1km + total area of	0.7462	8475.93	52.1721	0

Table A.2 (cont.).

		bottomland forest in 1km + total area of forest in 0.1km				
(Limpert et al. 2007)	Preferred roosting and foraging habitat in riparian zones where closed canopies provide protection from elements, while open understory allows less predation and easier flying	distance to water + total area of forest in 0.1km + total area of water in 1km + total edge of forest in 0.1km + total edge of water in 1km	0.7469	8481.15	57.3958	0
Open areas	Where there is more open space	stand density index + total area of ag in 0.1km + total area of water in 1km	0.7357	8496.01	72.2521	0
(Mager and Nelson 2001)	Large trees for protection and thermal cover for roosting that are located close to preferred foraging areas.	existing vegetation height + quadratic mean diameter + total edge of forest in 0.1km	0.7416	8503.37	79.6092	0
Insects	Where there should be more insect abundance	number of patches of water in 1km + total area of ag in 0.1km + total edge of forest in 0.1km + temperature	0.7329	8504.16	80.4074	0

Table A.2 (cont.).

Stand metrics	Where the forest is older, taller, and denser	existing vegetation height + number of patches of forest in 0.1km + quadratic mean diameter + stand density index	0.7489	8509.18	85.4268	0
(Loeb and O'Keefe 2003)	Small gaps and openings within stands and may be related to greater insect availability, proximity to roosts, or decreased structural complexity	existing vegetation height + quadratic mean diameter + stand density index	0.7272	8512.65	88.8964	0
Forest Complexity	Where there is more complex forest landcover	total area of forest in 0.1km + total edge of forest in 0.1km	0.7248	8514.69	90.9284	0
(Limpert et al. 2007)	Preferred roosting and foraging habitat in riparian zones where closed canopies provide protection from elements, while open understory allows less predation and easier flying	canopy cover + quadratic mean diameter	0.7416	8516.52	92.7645	0

Table A.2 (cont.).

(O'Keefe 2009)	Proximity to commuting corridors for decreased commuting costs to forage in open spaces	elevation + distance to water + total edge of forest in 0.1km	0.7332	8517.09	93.3303	0
(Mager and Nelson 2001)	Large trees for protection and thermal cover for roosting that are located close to preferred foraging areas.	existing vegetation height + quadratic mean diameter	0.7254	8517.59	93.8295	0
(Vanausdall et al. 2018)	Forests, particularly forest edges or gaps, may be important for roosting, traveling, and some foraging opportunities within a small spatial scale	total area of forest in 0.1km + total edge of forest in 0.1km	0.7138	8519.96	96.2032	0
(Perry et al. 2008)	Partially harvested areas with mature overstory pines and hardwoods for roosting and reduced vertical clutter	number of patches of forest in 0.1km + stand density index	0.7221	8528.8	105.046	0
Forest Availability	Where more forest is available	total area of forest in 0.1km	0.686	8535.05	111.289	0

Table A.2 (cont.).

(Loeb and O'Keefe 2003)	Small gaps and openings within stands and may be related to greater insect availability, proximity to roosts, or decreased structural complexity	quadratic mean diameter + stand density index	0.6954	8539.11	115.354	0
Agriculture	Where more agriculture is available	total area of ag in 0.1km	0.7214	8545.96	122.204	0
Water	Where there is more water available	distance to water + total area of water in 1km + total edge of water in 1km	0.6678	8618.29	194.536	0
(O'Keefe 2009)	Proximity to commuting corridors for decreased commuting costs to forage in open spaces	elevation + distance to water	0.6651	8627.88	204.122	0
Basic landscape/climate	Elevational gradient	elevation	0.6502	8650.83	227.071	0
Null		null	0.5098	8715.03	291.271	0

Table A.3 Multivariate models for the hoary bat ranked by the AICc values. AUCtest values show model's goodness-of-fit. AICc values is Akaike's Information Criterion for small sample size which ranks the model selection. The difference between the top AICc value and that model's AICc value is the ΔAIC_c. The AIC_c w_i is the models' weight.

Model	Rationale	Variables	AUC$_{\text{Test}}$	AIC$_c$	ΔAIC$_c$	AIC$_c$ w_i
Land Use History Bias	Where most historical human impact has occurred	distance to roads + total area of ag in 0.1km + total area of urban in 0.1km	0.7444	3742.44	0	1
(Veilleux et al. 2009)	Roosts close to open foraging areas	distance to roads + total area of ag in 0.1km + total area of forest in 0.1km	0.744	3768.3	25.8605	0
Insects	Areas with more insect abundance	distance to water + total area of ag in 0.1km + total area of urban in 0.1km + total edge of forest in 0.1km	0.7021	3770.88	28.4397	0
Land Cover Type	Areas of different land cover types	total area of ag in 0.1km + total area of bottomland forest in 0.1km + total area of forest in 0.1km + total area of open canopy deciduous forest in1km + total area of urban in 0.1km + total area of water in 1km	0.7744	3774.2	31.7557	0
Agriculture & Urban	Areas with agriculture and higher human impact	number of patches of urban in 0.1km + total area of ag in 0.1km	0.6817	3784.6	42.1566	0
Goldilocks	Less dense forest, closer to water and roads, more solar	distance to roads + distance to water + number of patches	0.7239	3790.15	47.7043	0

Table A.3 (cont).

	radiation, and more ag and urban areas	of urban in 0.1km + stand density index + solar radiation + total area of ag in 0.1km + total area of open canopy deciduous forest in 1km				
(Morris et al. 2010)	Edges serve as windbreaks for large densities of insects	distance to roads + distance to water + number of patches of forest in 0.1km + total area of water in 1km	0.646	3795.73	53.2834	0
(Hayes et al. 2015)	Avoid areas of heat that might threaten energy, water balance, and reduce reproductive success	solar radiation + total area of forest in 0.1km	0.615	3796.49	54.0443	0
Patches	Most patches of habitat types	number of patches of forest in 0.1km + number of patches of urban in 0.1km	0.6625	3798.1	55.6571	0
(Willis and Brigham 2005)	Thermal benefits to minimize heat loss and easy flights	aspect + number of patches of forest in 0.1km + stand density index	0.6293	3801.95	59.5021	0
(Veum 2017)	Generalist foraging bats prefer opening and edges	distance to roads	0.6287	3804.62	62.1815	0
Basic Landscape		aspect + solar radiation	0.6078	3806.69	64.2465	0
(Willis and Brigham 2005)	Minimize heat loss & flyway concept	aspect + stand density index +	0.6249	3809.25	66.8049	0

Table A.3 (cont.).

		total edge of forest in 0.1km				
Forest Availability	Areas with more forest	total area of bottomland forest in 0.1km + total area of forest in 0.1km + total area of open canopy deciduous forest in 1km	0.5851	3811.45	69.0066	0
(Owen et al. 2004)	Forages in open areas away from forest structure and clutter, where highly maneuverable flight is less critical	number of patches of forest in 0.1km + stand density index + total area of forest in 0.1km	0.5898	3813.73	71.2872	0
(Menzel et al. 2005)	Open-adapted bats forage as high as they can in all other habitat types	distance to water + stand density index + total area of bottomland forest in 0.1km + total area of open canopy deciduous forest in 1km	0.6462	3814.93	72.4892	0
Water	Areas where there is more water	distance to water + total area of water in 1km	0.6023	3815.06	72.6172	0
(Veum 2017)	Generalist foraging bats prefer opening and edges	distance to roads + total area of open canopy deciduous forest in 1km + stand density index	0.6802	3815.76	73.3162	0
(Ford et al. 2005)	Forested areas for foraging are a premium among agriculture and urban land	distance to water + existing vegetation height + total area of forest in 0.1km	0.6515	3818.35	75.9113	0

Table A.3 (cont.).

(Jung et al. 1999)	Open canopy with a high density of large trees for open foragers and foliage roosters	existing vegetation height + stand density index + total area of open canopy deciduous forest in 1km	0.5883	3824.56	82.1208	0
(Menzel et al. 2005)	Open-adapted bats forage as high as they can in all other habitat types	stand density index + total area of bottomland forest in 0.1km + total area of open canopy deciduous forest in 1km	0.5527	3825.72	83.2721	0
(Klug et al. 2012)	Minimizing energy spent on thermoregulation allows for more energy on lactating, increasing reproductive output, and fitness	aspect + stand density index	0.5967	3827.91	85.4647	0
(Veum 2017)	Generalist foraging bats prefer opening and edges	total area of open canopy deciduous forest in 1km	0.5624	3828.45	86.0114	0
(Veum 2017)	Generalist foraging bats prefer opening and edges	stand density index	0.5805	3830.05	87.604	0
(Willis and Brigham 2005)	Thermal benefits & easy flight	aspect + stand density index + total area of open canopy deciduous forest in 1km	0.6143	3837.23	94.7899	0
Global		aspect + distance to roads + distance to water + existing vegetation height + number of patches of forest in 0.1km + stand	0.766	3889.14	146.702	0

Table A.3 (cont.).

		density index + solar radiation + total area of ag in 0.1km + total area of bottomland forest in 0.1km + total area of open canopy deciduous forest in1km + total area of urban in 0.1km + total area of water in 1km				
(Wieringa et al. 2021)	North-south migration movement	solar radiation	0.6231	3890.46	148.019	0
Open Area	More open forest	stand density index + total area of open canopy deciduous forest in 1km + total edge of forest in 0.1km	0.6078	3806.69	64.2465	0

Table A.4 Multivariate models for the tri-colored bat ranked by the AICc values. AUCtest values show model's goodness-of-fit. AICc values is Akaike's Information Criterion for small sample size which ranks the model selection. The difference between the top AICc value and that model's AICc value is the ΔAIC_c. The AIC_c w_i is the models' weight.

Model	Rationale	Variables	AUC_{Test}	AIC_c	ΔAIC_c	AIC_c w_i
(O'Keefe 2009)	Minimize commuting costs as a smaller bat and prefer riparian habitats for roosting and maximizing foraging costs	canopy cover + elevation + distance to roads + number of patches in 0.1km + total edge of forest in 0.5km + total edge of water in 0.5km	0.8832	3261.34	0	0.56
(O'Keefe 2009)	Minimize commuting costs as a smaller bat and prefer riparian habitats for roosting and maximizing foraging costs	canopy cover + elevation + distance to roads + total edge of forest in 0.5km + total edge of water in 0.5km	0.8704	3261.8	0.4658	0.44
Land Use History Bias	Areas that have been more historic human impact	elevation + distance to roads + total area of ag in 0.5km	0.8466	3282.18	20.8446	0
Goldilocks	Areas with more water, more forest edge and patches of forest, more agricultural land, more bottomland forest	number of patches of forest in 0.1km + total area of ag in 0.5km + total area of bottomland forest in 1k + total area of water in 0.5km + total edge of forest in 0.5km	0.8772	3285.38	24.0455	0
Global Model		elevation + distance to roads + existing vegetation	0.8784	3287.55	26.2146	0

Table A.4 (cont.).

		height + number of patches of forest in 0.1km + number of patches of water in 0.5km + quadratic mean diameter + stand density index + total area of ag in 0.5km + total area of bottomland forest in 1km + total area of water in 0.5km				
(Ford et al. 2005)	Favors larger watercourses at lower elevations with open spaces and is probably more related to overall prey abundance and foraging ease	elevation + existing vegetation height + quadratic mean diameter + total area of bottomland forest in 1km	0.8378	3301.19	39.8577	0
(Morris et al. 2010)	Linear forest edges may improve connectivity between foraging areas and increase insect abundance	distance to roads + stand density index + total edge of forest in 0.5km + total edge of water in 0.5km	0.8416	3315.4	54.064	0
Stand Metrics	Areas with denser, older, taller forests	existing vegetation height + number of patches of forest in 0.1km + quadratic mean diameter + stand density index + total area of	0.8434	3327.98	66.6414	0

Table A.4 (cont.).

		bottomland forest in 1km + total edge of forest in 0.5km				
(Starbuck et al. 2015)	Landcover variables represent large areas for different uses from foraging to roosting	total area of ag in 0.5km + total area of bottomland forest in 1k + total area of water in 500	0.8335	3328.581	67.24437	0
(Farrow and Broders 2011)	Abundant roosting opportunities and avoiding energetically expensive cooler areas with less insect abundance	total area of ag in 0.5km + temperature	0.8118	3339.9	78.5663	0
(Morris et al. 2010)	Linear forest edges may improve connectivity between foraging areas and increase insect abundance	distance to roads + total edge of forest in 0.5km + total edge of water in 0.5km	0.8596	3344.68	83.34	0
Riparian	More forested areas closer to riparian zones	number of patches of water in 0.5km + total area of bottomland forest in 1km + total area of water in 0.5km	0.758	3351.54	90.2035	0
(Perry and Thill 2007)	Older taller trees to reduce predation and fires while having	existing vegetation height + quadratic mean diameter + stand density index	0.8062	3360.83	99.4953	0

Table A.4 (cont.).

	improved young rearing				
(Starbuck et al. 2015)	Basic landcover	total area of forest in 0.5km + total area of water in 0.5km	0.8268	3363.58	102.244	0
Basic Landscape	Elevational gradient	elevation	0.7453	3374.42	113.084	0
Agriculture	More agricultural areas	total area of ag in 0.5km	0.7542	3390.97	129.629	0
Forest Complexity	Areas with more forest edge and patches of forest	number of patches of forest in 0.1km + total edge of forest in 0.5km	0.7615	3393.51	132.172	0
Insects	Areas with more insect abundance	number of patches of water in 0.5km + total area of ag in 0.5km + total edge of forest in 0.5km + temperature	0.8704	3393.58	132.242	0
Forest Availability	More forest available	total area of forest in 0.5km	0.7874	3395.76	134.42	0
(Loeb and O'Keefe 2003)	Higher vegetation density means increased prey	stand density index	0.7785	3395.92	134.587	0
Water	More water available	number of patches of water in 0.5km + total area of water in 0.5km	0.7331	3407.65	146.313	0

Table A.4 (cont.).

(Farrow and Broders 2011)	Abundant roosting opportunities and avoiding energetically expensive cooler areas with less insect abundance	total area of ag in 0.5km + total area of water in 0.5km + temperature	0.8182	3410.78	149.445	0
Null		no variables	0.5332	3503.18	241.842	0

Table A.5 Variable importance based on summing the AICc weights of all models in which the variable was used.

Variable	Importance
L. borealis	
Canopy cover	0.3737
Elevation	0.6262
Distance to water	0.4848
Existing vegetation height	0.1111
Quadratic mean diameter	0.4848
Total area of ag in 0.1km	1
Total area of bottomland forest in 1km	0.4848
Total area of forest in 0.1km	1
Total area of water in 1km	1
Total edge of forest in 0.1km	0.1111
Total edge of water in 1km	0.1111
Temperature	0.3737
L. cinereus	
Distance to roads	1
Total area of ag in 0.1km	1
Total area of urban in 0.1km	1
P. subflavus	
Canopy cover	1
Elevation	1
Distance to roads	1
Number of patches of forest in 0.1km	0.56
Total edge of forest in 0.5km	1
Total edge of water in 0.5km	1