

EVALUATING THE EFFECTS OF ANTHROPOGENIC LAND USE AND HABITAT
FRAGMENTATION ON BAT DIVERSITY AND ACTIVITY IN THE OAK OPENINGS
REGION

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ABSTRACT

Karen V. Root, Advisor

Bats are critically important for their control of insects but are experiencing population declines. The biggest reason for these declines is anthropogenic land use. Despite negative impacts, anthropogenic land use has variable impact on bats, with tolerance for more developed areas being species dependent and varying depending on the spatial or temporal scale. Previous studies on land use and bats lack spatial variability and are often single year. My goal was to determine how habitat factors related to human land use impact bat activity and species richness at multiple spatial scales over a period of several years. This research was conducted in the Oak Openings Region, which is a highly developed mixed-use region with high biodiversity that serves as important bat habitat. Specific objectives included determining (1) changes in bat activity and species richness over time, (2) differences in bat activity and species richness between protected and non-protected areas, (3) how factors related to human land use impact bat activity and species richness, and (4) to map current bat habitat suitability and see how it may change in the future. Calls increased each subsequent year during the 2019-2021 period, showing a trend of consistently increasing bat activity. However, during 2011-2019 bat activity significantly decreased. Protected areas had higher species richness and activity than unprotected areas. Higher activity and species richness were found in areas with greater percent upland prairie, sand barrens, and savanna and less floodplain and conifer forest and wet prairie. Activity was higher with less structural clutter at 3-6.5 m, lower understory height, taller canopy height, more canopy cover, and more structural clutter 0-3 m. Number of habitats was positively associated with bat species richness and activity along transects, but negatively associated with activity at stationary points. An opposite trend was observed for cropland. Activity and species

richness along transects was higher when at least one side of the road had natural habitat.

Variables having high impact on suitability included percent savanna and upland forest, distance to agriculture, May NDVI, total annual precipitation, mean diurnal range, and mean annual air temperature. Total percent suitable habitat did not change much between current models and 2050 predicted climate change models, although suitable habitat patches changed in location and level of suitability. These results demonstrate that measuring bat activity and species richness using a variety of spatial and temporal scales allows detection of changes in populations over time and identification of the habitat and environmental variables that are most important to bat populations.

This dissertation is dedicated to my husband Sean Petrick as well as my parents and brother,
whose love and support made this possible

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INTRODUCTION

Bats play important roles for humans and the rest of the ecosystem by controlling insect populations, dispersing seeds, providing fertilizer through guano, and pollinating plants (Kunz et al. 2011). The value of predation services on insect pests by insectivorous bats to the agricultural industry in the United States alone is around \$22.9 billion per year (Boyles et al. 2011). Bats may also serve as bioindicators, since their responses to environmental threats such as agricultural development generally reflect those of other species, they are sensitive to pesticide bioaccumulation, and changes in their abundance may reflect population changes in the species they feed on or pollinate (Jones et al. 2009, Park 2015). Highly mobile animals such as bats are also useful to study because they can provide information on connectivity, movement between multiple habitat types, migration, and tolerance of development in mixed use areas (Runge et al. 2014).

Despite their importance to the ecosystem, the economy, and research, bats have been experiencing major population declines, with 15% of all bat species listed as threatened by the IUCN (Boyles et al. 2011, Voigt and Kingston 2016). There are multiple threats to bats, which include the disease white-nose syndrome (WNS), overhunting, climate change, energy production, and pollution (Frick et al. 2019). Despite these many dangers, the biggest cause of decline for bats worldwide is habitat loss and degradation from anthropogenic land use (Kirkpatrick et al. 2017, Mickleburgh et al. 2002, Frick et al. 2019, Voigt and Kingston 2016). Many species of bats are particularly vulnerable to human development because of their low reproduction rate, long lifespan, and high metabolic rates (Voigt and Kingston 2016).

Due to their vulnerability to human development, potential bioindicator status, and the relative ease in monitoring their populations, bats are good organisms for studying how

variations in landscape heterogeneity and use influence species diversity and what traits promote resilience to human caused disturbance and perturbation (Sutherland et al. 2009). Impacts of urbanization on bats are variable, as some bat species avoid developed areas, while others are attracted to lights by insects clustered there and use the edges created by fragmentation for foraging and movement (Voigt and Kingston 2016, Stone et al. 2009, Ethier and Fahrig 2011, Arroyo-Rodriguez et al. 2016, Kalda et al. 2015, Morris et al. 2015). Rare or threatened bat species and slower-flying species with low wing aspect ratios are more negatively affected by human development, while fast-flying generalist species that forage in open habitats are more often found in urban areas (Stone et al. 2015, Lacoeyuilhe et al. 2014, Longcore and Rich 2004, Fuentes-Montemayor et al. 2013, Barber et al. 2010).

While how human land use impacts bats is well-studied, most studies only include one spatial scale. Habitat variables impact bats differently at various scales, so it is important to include multiple scales in any study of how human development impacts bats (Kalda et al. 2015, Gallo et al. 2017). Regional studies are therefore important because of the high spatial variation in bat activity (Rodhouse et al. 2012). There is also a lack of bat data over long time periods (Tuneu-Corrall et al. 2020). Long-term data are beneficial since they lead to a more accurate view of how populations change over time and avoids bias from the high amount of temporal variety in bat activity (Pelton and van Manen 1996, Hayes 1997).

This study examined how bat activity and species diversity throughout the Oak Openings Region is affected by urbanization and other forms of human development. I used acoustic monitoring and habitat data collected at multiple scales to explore how fragmentation, agriculture, urban areas, roads, and light pollution affect bat activity and species diversity. I also evaluated the influence of general habitat features such as vegetation structure, habitat type, and

landscape heterogeneity. The acoustic data collected was also used to examine spatial and temporal variation in bat activity throughout the Oak Openings Region. Lastly, I created habitat suitability maps to predict the best areas of bat habitat across the region and explore how suitability has changed in the region over time. I predicted that overall bat species diversity and activity would be lower in areas with more fragmentation, agriculture, light pollution, urban areas and roads, but that some species will have higher activity in habitats with more of these characteristics associated with human development, particularly fast flying generalist species that prefer to forage in open areas.

Research Objectives

My research used acoustic bat data combined with field surveys and spatial modeling to examine how bat activity and species diversity/richness was impacted by human land use over multiple years at local and landscape level spatial scales. Work occurred in the Oak Openings Region of the Northwest Ohio, which is an ideal area for this study because of its high bat diversity, importance as bat foraging and roosting habitat, and large amount of human development. It serves as a model for other important bat areas in mixed-use landscapes. This research will provide planning tools for bat conservation, increase knowledge of what habitat features are important for bats, and be used to make land management recommendations. I asked questions related to (1) how bat activity and species diversity have changed over time and space, (2) how bat activity and diversity differ between protected areas (parks) and non-protected areas, (3) how factors related to human land use (light pollution, fragmentation, etc.) impact bat activity and diversity, and (4) how bat habitat suitability has changed over time and how may it change in the future. I answered these questions in the following dissertation sections:

Chapter I

- Prepared for submission to *Acta Chiropterologica*: How bat activity and diversity has changed over time in the Oak Openings Region.

Chapter II

- Examined the effects of human land use (light pollution, residential/urban habitat cover, agricultural cover, roads/impervious surfaces, and habitat fragmentation) on bat activity and species diversity.
- Identified the impacts of natural habitat variables (clutter, canopy cover, and open vs. forested habitat types) on bat activity and species diversity.
- Compared bat activity, species richness, and individual species activity between protected and non-protected areas

Chapter III

- Created bat habitat suitability models (for combined activity and individual species) to determine the best current habitat areas for bats
- Predicted how suitability in the region may change in the future, especially in light of climate change predictions

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CHAPTER 1: TEMPORAL CHANGES IN BAT ACTIVITY AND SPECIES DIVERSITY

Abstract

Bat populations are declining worldwide due to threats such as white-nose syndrome and habitat loss. Multiple year studies are advantageous for looking at population trends over time, to determine the extent of declines, but few have been conducted for bats. I collected multiple years of bat call data from volunteer walking surveys, stationary surveys, and road transects to examine temporal trends in overall bat activity, species richness, individual species, open and forest foraging guilds, and species affected and not affected by white-nose syndrome. Bat activity in volunteer surveys decreased from 2011-2018 but increased from 2019-2021. In volunteer surveys since 2011, activity for big brown bats, northern long-eared bats, and little brown bats decreased and activity of hoary bats and silver-haired bats fluctuated. Two of the three species that declined significantly in activity were those affected the most by white-nose syndrome. For stationary and transect surveys, average activity, species richness, and activity for some individual species increased during the 2019-2021 period. These data show the advantages of monitoring bat activity over longer time periods to get a better picture of likely population trends. There also appear to have been community shifts since 2011 because of declines and increases in individual species activity. My results also indicated declines in bat activity over the last decade, but that local bat populations may be starting to recover.

Introduction

Bat populations have declined worldwide. In the United States, certain bat species have declined up to 99% in some areas (Turner et al. 2011). Extreme declines in the Eastern and Midwest United States are largely a result of the fungal disease white-nose syndrome (WNS), which is caused by the fungus *Pseudogymnoascus destructans* (Turner et al. 2011). This

pathogen harms bats by causing them to wake up during hibernation, causing depletion of their fat reserves and it damages their wings (Frick et al. 2010). The species most harmed by WNS in the eastern United States are the little brown bat (*Myotis lucifugus*), the federally threatened northern long-eared bat (*Myotis septentrionalis*), the federally endangered Indiana bat (*Myotis sodalis*), and the tri-colored bat (*Perimyotis subflavus*) (Nocera et al. 2019). Some cases of big brown bats (*Eptesicus fuscus*) with the disease have been reported, but they seem to be more resistant than other species that can contract it (Ohio Department of Natural Resources 2020, Frank et al. 2014). Other species, especially silver-haired bats (*Lasionycteris noctivagans*) and eastern red bats (*Lasiurus borealis*), are known to be carriers of the disease but not affected by it (Ohio Department of Natural Resources 2020).

Other major threats to bats also exist. The largest threat worldwide is habitat destruction from deforestation, conversion of habitat to agriculture, and destruction of cave roosts (Frick et al. 2019). Additional threats include energy development, climate change, and pollution (Frick et al. 2019). The combination of multiple threats can exacerbate the danger to bats. For example, higher percentage of areas with <15% vegetation cover, which is more likely in more developed areas, are associated with higher probability of white-nose syndrome (Flory et al. 2012). Climate change and habitat fragmentation may also speed up the spread of white-nose syndrome, as well as posing a danger to bats by themselves (Maher et al. 2012, Lilley et al. 2018).

These dangers to bats do not impact all species equally. White-nose syndrome only impacts select species, all of which overwinter in caves or mines, and increasing human land use disproportionately harms rarer specialist species that forage in forested areas (Jachowski et al. 2014, Loeb et al. 2008, Longcore and Rich 2004). Where multiple bat species exist in an area, they typically compete for resources such as food and roosts (Salinas-Ramos et al. 2019). It can

be difficult to measure if exploitative competition, which is defined as indirect negative impacts of individuals on each other through use of a shared resource, is occurring, but it has been recorded in some insectivorous bat species (Morningstar et al. 2019). The presence of competitors can prevent a species from occupying its whole fundamental niche, which is the whole set of conditions under which an animal can survive (Salinas-Ramos et al. 2019). Increases in one or more species may occur when one or more other species rapidly declines due to a natural or anthropogenic disturbance, this indicates that competitive release may be occurring. This change happens when remaining species can better utilize resources and expand their realized niche by foraging in a wider variety of habitats (Jachowski et al. 2014, Mayberry et al. 2020). Competitive release may have lasting destabilizing impacts on the community, reducing overall decreased biodiversity (Tompkins et al. 2003). Prior studies have shown increases in activity for species not affected by white-nose syndrome after the disease was introduced as species with similar niches that were impacted by the disease declined, potentially indicating competitive release (Morningstar et al. 2019, Jachowski et al. 2014, Nocera et al. 2019, Faure-Lacroix et al. 2020, Simonis et al. 2021, Mayberry et al. 2020).

Monitoring over longer time periods is effective in examining shifts in bat communities, because it allows researchers to see temporal trends and it leads to a more accurate view of populations because of the wider timespan covered (Pelton and van Manen 1996, Havstad and Herrick 2003). However, there is a lack of long-term studies for wildlife in general and even less bat-specific studies (Pelton and van Manen 1996, Tuneu-Corral et al. 2020). Long-term studies are hard to conduct because of variation between monitoring efforts, although surveying in the same locations every year can mitigate some of this variety (Ingersoll et al. 2013). Long-term surveys for bats can be especially difficult as a result of their cryptic nature, movement between

populations leading to low recapture rates, and their wide range of roosting behaviors (Ingersoll et al. 2013). However, long-term monitoring is also especially useful for bats because they are longer-lived than most mammal species of the same size. While previously long-term monitoring studies were mainly mark-recapture studies, acoustic surveys have become more commonly used in recent years (Salinas-Ramos et al. 2019). Although acoustic monitoring cannot reliably identify individuals, it has many benefits since it is non-invasive, allows for collection of large amounts of data across a wide spatial and temporal range, is omnidirectional, and captures a wider range of species than mist nets (Adams et al. 2012, O’Farrell et al. 1999, Gibb et al. 2019, Francé et al. 2012).

The main aim of this chapter is to compile multiple-year acoustic bat data to look at how bat populations have changed in the region over time in response to disease, habitat destruction, and other threats. The focus is on changes in activity levels of individual species, species richness, and overall bat activity over a period of multiple years, annually, and within a season. Historic data collected since 2011 was compared to data collected during the 2019-2021 research period. I predicted that the species affected by white-nose syndrome (tri-colored, little brown, and northern long-eared bats) would show continuous reduction in activity and decreased distributions throughout their whole range during the survey period and compared to past data. I also predicted that overall bat activity would drop during the 2019-2021 period, although less so when compared to changes from prior levels (2009-2019). I hypothesized that declines in some species, mainly those affected by white-nose syndrome, would lead to an overall decline in species richness, but that richness would remain steadier than activity. I predicted that bat activity would be highest in July and August, but species richness would not change significantly during the season, which was the case in previous studies in the region (Hollen 2017, Turner

2018). Overall, the goal of this chapter was to get a better idea of how bat populations were changing over time.

Methods

Study Area

The Oak Openings Region is an area of key bat summer habitat that has been impacted by habitat alteration and loss. Local bat populations have also been decimated by white-nose syndrome, which was first detected in the area in 2012 (Ohio Department of Natural Resources 2020). The Oak Openings Region is a 47,600 ha area in Northwest Ohio that consists of a wide variety of natural ecosystems, such as oak savannas, wet prairies, and oak woodlands (Buckman-Sewald et al. 2014). It has undergone large amounts of fragmentation due to an increase in urbanization and agriculture on the Toledo/Detroit corridor and includes a major airport (Becker et al. 2013, Higgins 2003). Despite this development, the area is a biodiversity hot spot and contains over a quarter of all the oak savanna habitat in the world (Becker et al. 2013, Higgins 2003). About 12% of the region is protected, but the rest is open to development (Martin and Root 2020, Abella et al. 2001). The region has experienced major habitat changes since 2009, with a decrease in forests, wet prairie and cropland, and an increase in built-up areas, upland prairie and savanna (Martin and Root 2020). These protected lands include multiple Metroparks. The largest of these parks is Oak Openings Preserve (1200 ha), which consists of a wide variety of habitats including forest, upland prairie, and upland savanna, and is surrounded by a mix of residential areas, cropland, Eurasian meadow, and prairie (Turner 2018). The other protected parks surveyed during this study were Secor (253 ha), which consists mainly of swamp and floodplain forest and upland prairie and is surrounded by a mix of forests, prairies, residential areas and cropland, and Wildwood (199 ha), which is composed primarily of upland deciduous

and floodplain forest and upland prairie and is surrounded by residential and dense urban areas (Turner 2018).

Eight bat species can be found in the region, all of which are insectivorous. These species are the big brown bat, little brown bat, northern long-eared bat, tri-colored bat, evening bat (*Nycticeius humeralis*), hoary bat (*Lasiurus cinereus*), eastern red bat and silver-haired bat (Turner 2018). Most of these bats are southern migrants, except for the big brown bat which hibernates in the area and is present year-round. Northern long-eared bats are listed as threatened on the Endangered Species List and the status of the little brown bat is currently under review (FWS 2020). The IUCN has the little brown bat listed as endangered, the northern long-eared bat listed as near threatened, and the tri-colored bat as vulnerable (Solari 2018, 2018, 2018).

Previous research found that little brown, tri-colored, and northern long-eared bats are decreasing in population, eastern red evening, and silver-haired bat populations are stable, population trends of hoary bats are unknown, and big brown bats populations are increasing (Miller et al. 2016, Gonzalez et al. 2016, Arroyo-Cabrales et al. 2016, Solari 2018a, Solari 2018b, Solari 2018c, Solari 2019a, Solari 2019b). The Oak Openings Region is an excellent place to look at changes in bat populations over time since it functions as key bat summer foraging and roosting habitat. Long-term citizen science data has been collected in the region since 2011 (Buckman-Sewald et al. 2014), but the data has not been compiled to look at temporal changes in activity until now.

Acoustic Data Collection

Following the protocol established previously (Buckman-Sewald 2014), acoustic monitoring surveys were conducted by volunteers from 2019-2021 in Oak Openings, Wildwood, and Secor Metroparks (Figure 1.1). Surveys were conducted at each park once a month from June-August just after sunset. Volunteer groups of 2 or more walked 1 of 3 designated trails in the park with an Anabat SD2 unit and attached Garmin GPS to collect continuous bat call data

and geolocations for approximately one hour. Calls were compared to weather data for 2019-2021 and the same was done for historic data collected 2011-2018 (except for 2014 when there were no data collected). Additional data measured included maximum, minimum, and average temperature and precipitation data for the whole summer collected from the National Weather Services' monthly climate summaries (NOAA); this method was used due to inaccessibility of nightly data for older years.

I collected additional acoustic monitoring data from stationary and moving surveys conducted throughout the Oak Openings Region during the May-September period from 2019-2021. Surveys occurred once a month at each stationary site and twice a month per transect when possible. Stationary surveys took place in 3 local Metroparks (Oak Openings, Wildwood, and Secor). Anabat SD2 (Titley Electronics, Ballina, New South Wales, Australia) monitors were placed at a pair of stationary survey sites each night (Figure 1.2 a). Sites were selected using prior survey locations (Turner 2018, Sewald 2012) and an updated land cover map (Martin and Root 2020) with one site per pair in an open area and another in a forested area for the first field season and a pair consisting of one interior habitat (interior sites were more than 100 m from the edge of the habitat type they were in) and one edge site for the following season. In the 2021 field season both open/forested and edge/interior pairs were placed. Monitors were only set on nights with favorable conditions (i.e. no rain, wind less than 24 km/hr, and temperature over 10°C) (Voigt et al. 2011). Insects were also sampled at points around sunset (directly after each monitor was placed) using 50 sweeps each of a 0.25 m deep and 0.3 m wide sweep net in the air and through the brush, identified to order, and released.

Road surveys started around 30 minutes after sunset and ended 3 hours after sunset, which is the timeframe during which bat activity peaks (Hayes 1997, Sewald 2012). Road

transects were surveyed by driving along them at 32 km/hr twice a month and continuously recording using an Anabat SD2 and an attached GPS unit, so that bat calls and their geolocations were continuously recorded (Figure 1.2 b). Sites surveyed within the same night were more than 1 km apart, so that they were not within the same Anabat reception area (Livengood Consulting 2010). Transects were chosen that covered as many different habitat types as possible (e.g. a mix of forested, residential, and savanna areas identified using Martin and Root 2020) and that had annual average traffic volume of less than 4000 (Ohio Department of Transportation). Transects in 2019 were 1-2 km long and 5 km transects were used 2020-2021.

Data Analysis

Identifications of calls were made from sonograms in Analook by comparing to existing call libraries (Sewald 2012) and confirmed with BCID software when possible (BCID, BCID version 9 2.7c) Species identifications were made based on call frequencies and characteristics such as call shape (Table 1.1). Number of calls was used as a measure of relative bat activity.

I collected total and average calls per survey (i.e., relative activity) for each sample night, each month, and each year. Alpha values were set at 0.05. A linear mixed effects model with year as the fixed factor and park as a random factor was used to model specific trends in overall bat activity, species richness, activity of individual species, open and forested guilds, and species affected by white-nose syndrome over time for volunteer surveys since 2011. Differences between years for all types of surveys from 2019-2021 were tested using Wilcoxon signed-rank tests in JMP (Version 11, SAS Institute Inc., Cary, NC). This was done for the shorter-term results because the 3-year period was too short to effectively examine trends. Wilcoxon each-pair tests were then used to determine which years significantly differed from which significantly for average activity per survey, species richness, and per survey averages for individual species, the

three species impacted most by white-nosed syndrome (little brown bat, northern long-eared bat, and tri-colored bat) and open/forested guilds. Open and forested guilds were determined based on prior research, with big brown, hoary, and silver-haired bats in the open habitat foraging guild and little brown, northern long-eared, tri-colored, evening, and eastern red bats in the forested foraging guild (Turner 2018, Sewald 2012, Ford et al. 2005, Henderson et al. 2008, Agosta 2002, Farrow and Broders 2011). The final open guild tests were run without big brown bats, so their high abundance relative to the other species did not skew results. A Bonferroni Correction was performed to adjust for multiple comparisons. A Bray-Curtis dissimilarity index was also used to compare shifts in bat communities in study areas to give another view of how they have changed over time. All tests were run in JMP, except the Bray-Curtis dissimilarity index, which was run in Excel.

Results

Citizen Science Surveys

The linear mixed effects model showed significant changes over time for average bat activity per survey according to p-values for fixed effects ($p = <0.0001$, $R^2 = 0.8558$), which overall declined over time (Figure 1.3 a.). Species richness did not change significantly over time ($p = 0.2233$, $R^2 = 0.5547$). Big brown bats ($p = 0.0002$, $R^2 = 0.8454$), northern long-eared bats ($p = 0.035$, $R^2 = 0.554$), and little brown bats ($p = 0.0258$, $R^2 = 0.6288$) significantly declined in activity over time as well (Figure 1.3 b-d). Hoary bats ($p = <0.0001$, $R^2 = 0.81726$) and silver-haired bat ($p = 0.006$, $R^2 = 0.6903$) significantly changed in activity over time as well and both peaked in activity in 2015 and 2016 (Figure 1.3 e-f). Activity did not change over time for evening bats ($p = 0.1167$, $R^2 = 0.433$), eastern red bats ($p = 0.1381$, $R^2 = 0.8173$), and tri-colored bats ($p = 0.1992$, $R^2 = 0.4995$). There were also patterns in activity over time for the open habitat

guild ($p=0.0002$, $R^2=0.7808$) as well as for the species affected by white-nose syndrome ($p=0.0081$, $R^2=0.6602$) (Figure 1.3 g-h). There were not significant changes over time for forested guild species ($p=0.2474$, $R^2=0.5562$). The open guild species peaked in activity in 2015 and 2016, while the species impacted by white-nose syndrome decreased in activity over time. The generalized linear mixed effect models indicated that overall bat activity, activity of some individual species, and activity of certain groups of species were changing over time. Average bat activity per survey was not significantly correlated with any of the weather metrics across the whole summer.

Stationary Points

There was a 57% decrease in average bat activity per survey between 2011 and 2021. Community dissimilarity, which was measured with the Bray-Curtis dissimilarity index, changed over time for both totals combined from all parks and for individual parks (Table 1.2 a-b). Across all parks, the bat community was most dissimilar between 2011 and 2018, although this was probably attributable to the lack of data from Wildwood in 2018 and the high dissimilarity in Secor data between these years. Only hoary bat average activity changes were significant during the 2019-2021 period ($p=0.0379$), although not when accounting for multiple comparisons. Species richness ($p=0.1787$) and average activity ($p=0.5611$, Figure 1.4 a) did not significantly change between 2019-2021. No individual years were significantly different for any tests for volunteer surveys.

Secor site number 6 in September 2021 was removed from the stationary point surveys since it had unusually high bat activity (3,273 calls) that month compared to the past 10 years of sampling data, so it was considered unreliable and would have skewed analysis. It is unclear why the count was so unusually high in that one site that month, as similarly high numbers were not recorded at that site other months or in other sites the same night. In 2019 a total of 2,881 total

calls were recorded with an average of 103 calls per site, in 2020 a total of 9,042 calls were recorded with an average of 251 calls per site across all months, and in 2021 a total of 18,181 calls were recorded with an average of 505 calls per site. Average bat activity per stationary survey increased from 2019 to 2021 (Figure 1.4 b). Stationary activity differed significantly across years (Table 1.3 a). All years significantly differed from each other using Wilcoxon each-pair comparisons with 2019 being more different than 2020 and 2021 than they were to each other. Big brown bats and silver haired bats were the most common species, with silver-haired bats becoming more common in 2021 (Figure 1.5 a-c). There were significant differences between years for all species except tri-colored bats. All species increased in activity over time. Species richness also significantly increased over time.

Transects

Along transects, there were a total of 624 calls with an average of 4 calls per point in 2019, a total of 1,337 calls with an average of 8 calls per point in 2020, and a total of 1,245 calls with an average of 9 calls per point in 2021. Big brown bats, hoary bats, and silver-haired bats were the most prevalent species along transects and northern long-eared bats were never detected on transects (Figure 1.6 a-c). Average bat activity per survey differed significantly between years and increased over the 3-year period (Table 1.3 b). Wilcoxon each-pair tests revealed that average bat activity per survey differed significantly between 2019 and 2021 and between 2020 and 2021, but not between 2019 and 2020 (Figure 1.4 c). Average eastern red bat and hoary bat activity significantly increased over the 3-year period; the other species did not change significantly in activity after accounting for multiple comparisons (Table 1.4). Species richness significantly increased over the 3-year period.

Discussion

This study evaluated if the bat community in the Oak Openings Region had changed over time and results indicated that significant changes occurred. Contrary to my hypothesis, bat activity increased from 2019-2021 across all surveys, although activity overall decreased across the 2011 to 2021 period as hypothesized. The differences in trends between the whole decade and 3-year period emphasizes the importance of longer-term surveying. As hypothesized, there were significant declines for species impacted by white-nose syndrome. Additionally, there were changes in individual species activity over time. This indicated that community composition has changed since 2011. It is unclear if the recent increase in average activity was attributable to normal year-to-year variation or an actual increase in bat abundance, but it could imply potential recovery after the decline of the past few years. It could also be a response to lower human activity during 2020 due to the pandemic, but subsequent years of monitoring would be needed to determine if this is the case. While migratory bat abundance could be affected by factors in other parts of their range, this is unlikely to be the main factor impacting summer foraging activity, especially since permanent resident big brown bats also had major changes in activity.

It is unclear why the decline followed by increase in activity occurred. Temperature and precipitation differences between summers do not appear to be the main cause for the decline since they were not correlated with activity. However, even if temperature and precipitation were not directly correlated with bat activity, they could be related to insect activity, so they could be indirectly impacting bats. While consistent count data for WNS does not exist in the region, it is likely the primary cause for the observed declines in northern long-eared bats and little brown bats, based on previous research (Reynolds et al. 2016, Thalken et al. 2018). The other species in the region affected by white-nose syndrome, tri-colored bats, experienced declines in activity but

not enough to be significant over time. However, WNS does not affect the other species in the region, so other factors must also play a role in the declining bat activity from 2011-2018. There have been substantial habitat changes to the Oak Openings Region in the past few years that could have impacted bat populations both positively and negatively. For instance, forest, wet prairie, and cropland cover has decreased since 2009 and developed areas, upland prairie, and savanna have increased (Martin and Root 2020). The increases in wet prairie and savanna were a result of restoration efforts by Toledo Metroparks and the Nature Conservancy. There was also an increase in built-up areas along with a decrease in forested areas (Martin and Root 2020). This is likely disproportionately harmful to forest-dwelling bats that are less development tolerant, such as the northern long-eared bat. At the same time, development tolerant species that forage in open areas, such as the hoary bat, are likely to benefit from these habitat changes. However, this hypothesis is complicated by the surprising decline in activity for development tolerant big brown bats. Since other individual factors such as insect population changes and WNS were not directly measured, it is unclear how much these impacted bat populations. More research is needed to determine the exact causes for decline, but it is most likely a combination of causes such as white-nose syndrome and habitat changes. Although unlikely, it cannot be ruled out that these fluctuations are typical for native bat populations over time, but multiple decades of data before the introduction of WNS would be needed to confirm this and no bat data exists in the region before 2011. Previous longer-term studies in other regions show some regular fluctuations in activity, but then settled into patterns of decline or increase (Toffoli and Calvini 2021, Ingersoll et al. 2013). In previous 3-year periods, 5 showed decreases in bat activity, while 2 showed increases (29% chance of increase). Increases in activity in 2020 could also be because of decreased human activity during the Covid-19 quarantine period, but research from

subsequent years would be necessary to determine if this is the case. More research is necessary to determine what is causing the yearly changes in bat activity.

Northern long-eared bats and little brown bats have suffered large declines throughout their range, with declines up to 95% in some areas (Reynolds et al. 2016, Ford et al. 2011, Franci et al. 2012). These declines are mainly due to WNS (Ingersol et al. 2013, Jachowski et al. 2014). It is unclear why these species declined more than tri-colored bats since they are also impacted by WNS. It could also be related to habitat loss combined with disease, since northern long-eared bats are more reliant on dense forest habitat than the other two species and tri-colored bats are the most likely to be found in open areas of the three species (Starbuck et al. 2014, Sewald 2012, Broders and Forbes 2004). Tri-colored bats may be impacted by the loss of forest habitat in the region less than other imperiled species.

Big brown bats were the most common species of the eight but showed significant decline in average activity over time. Because big brown bats made up the majority of recorded calls, this may account for much of the decline in overall bat activity over time. Other studies have mostly recorded increases (Franci et al. 2012, Faure-Lacroix 2020) or no change (Ford et al. 2011) in big brown bat activity after the introduction of WNS. The only other study to see a decrease in big brown bat activity was also in Ohio (Simonis et al. 2021). Since that study also saw a decline in other cave-roosting bats, this may indicate that big brown bat is less resistant to WNS in this region or could be susceptible to physiological impacts when recovering from the disorder (Davy et al. 2016, Simonis et al. 2021). There have been reports of big brown bats that have contacted WNS in Ohio (Simonis et al. 2021). If this species is experiencing declines caused by WNS, the trend may be less steep and therefore only noticeable over longer timeframes, highlighting the need for consistent long-term monitoring. Other factors could also

be negatively impacting caves, such as mining or other intrusions by humans (Frick et al. 2019). Protecting known roost caves would be beneficial for cave-dwelling species. Declines in big-brown bat activity could also be due to habitat changes, insect declines, or natural local fluctuations in population. Continued monitoring is needed to determine if declines in big brown bat activity are because of natural fluctuations in populations or if there is a larger cause specifically harming that species.

The other open-foraging species, hoary bats and silver-haired bats, increased in average activity over time overall but peaked in activity in 2015-2016. These species do not overlap in niche much with the species that were negatively impacted by WNS, but do with big brown bats, since all species are development-tolerant and tend to forage more in open areas (Ford et al. 2005). It is possible that these species may have become more abundant because of competitive release from declining big brown bat populations. Increases in silver-haired and hoary bat activity in parks may also be related to increases in prairie and savanna habitat resulting from restoration efforts, since both species forage more in open areas (Martin and Root 2020, Sewald 2012). It also would be useful to see if any habitat changes, spikes in insect activity, or other changes in the region occurred around 2015-2016 to cause the spikes in activity of these species.

It is unclear why species richness and activity from 2019-2021 increased more over time in the stationary and transect surveys than the volunteer surveys, but it may be related to the stationary surveys covering a wider temporal window, while the driving transects cover a larger spatial one. This illustrates the value of doing a wider range of types of surveys and expanding surveys beyond protected areas.

Since the only data collected was through acoustic monitoring, actual population estimates cannot be made. Despite this limitation of acoustic monitoring, it is often more

accurate than hibernacula or mist-netting surveys and can cover a larger spatial area (O'Farrell et al. 1999, Gibb et al. 2019). Acoustic data has been shown to accurately reflect bat activity levels in previous studies and is a useful method for long-term bat studies (Ford et al. 2011, Morningstar et al. 2019, Nocera et al. 2019, Faure-Lacroix 2020, Tuneu-Corral et al., 2020 Simonis et al. 2021).

Bat communities have changed in the Oak Openings Region of Northwest Ohio, likely due to a combination of WNS and habitat changes. While overall bat activity is starting to increase again, there has not been a notable rebound in the species impacted by WNS. This indicates that the relaxed interspecific competition will probably continue unless active efforts are made to restore the most threatened local species.

Conclusions

There is a critical need for long-term monitoring of bat populations, because of the multiple threats causing their populations to decline. Acoustic calls were collected at stationary points in protected areas (Metroparks) and along road transects from 2019-2021, in addition to volunteer data collected on Metroparks trails. Bat activity has declined over the last decade but increases in activity over the past 3 years give hope for the future. Decreases in activity for several individual species also indicate changes in the local bat community. There should be continued effort for decreasing rates of infection by white-nose syndrome and protecting forested habitat in the area to help declining northern long-eared and little brown bat populations. Increases in open-foraging species indicate that recent restoration of savanna habitat has been successful, although it is unclear why big brown bats declined in activity when other open foragers increased in activity. Further research can help determine the specific habitat factors that contribute the most to the decline and survival of bat populations.

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Tables

Table 1.1. Guide for identifying bat species in Oak Openings Region based on time and frequency, LF= low frequency (only group with tails below 30 kHz, lowest frequency tail <20-30 kHz), MF= medium frequency (lowest frequency tail 30-45 kHz with peak from 50-70 kHz), HF= high frequency (lowest frequency tail 35-50 kHz with peak usually above 70 kHz) (Livengood Consulting 2010).

Bat Species	Key Call Characteristics
Big brown bat (<i>Eptesicus fuscus</i>)- EPFU	LF, lowest frequency tail 20-25 kHz, highest frequency peaks can go above 50 kHz, only low frequency bat with calls that can go above 50 kHz
Eastern red bat (<i>Lasiurus borealis</i>)- LABO	MF, lowest frequency tail bounces around between 30-45 kHz, calls oscillating wildly in frequency, can be very few calls
Silver haired bat (<i>Lasionycteris noctivagans</i>)- LANO	LF, lowest frequency 25-30 kHz, does not go above 50 kHz, calls initially steeper and more hooked at bottom compared to EPFU
Little brown bat (<i>Myotis lucifugus</i>)- MYLU	HF, call tails around 35-50 kHz and not all same frequency, slightly hooked tail
Northern long-eared bat (<i>Myotis septentrionalis</i>)-MYSE	HF, very tall and high frequency calls with straight tails starting around 45-50 kHz, no hook on tail
Tri-colored bat (<i>Perimyotis subflavus</i>)- PESU	HF, all lowest frequency tails in a grouping of calls around same frequency, tails 45-50 kHz (sometimes flat calls as low as 35 kHz)
Hoary bat (<i>Lasiurus cinereus</i>)- LACI	LF, lowest frequency <25 kHz, never above 50 kHz
Evening bat (<i>Nycticeius humeralis</i>)- NYHU	MF, lowest frequency tail of calls constant around 35 kHz

Table 1.2. Bray-Curtis dissimilarity index over time across all 3 protected areas and for each individual Metropark. Comparison between 2011 and other years. Lack of Wildwood comparison for 2011 vs. 2018 is due to lack of Wildwood surveys in 2018. Comparisons were made to 2011 to show long-term trends.

	2011 vs. 2012	2011 vs. 2013	2011 vs. 2015	2011 vs. 2016	2011 vs. 2017	2011 vs. 2018	2011 vs. 2019	2011 vs. 2020	2011 vs. 2021
Oak Openings	67%	11%	29%	12%	27%	58%	60%	51%	60%
Secor	75%	69%	77%	68%	56%	85%	86%	72%	61%
Wildwood	48%	48%	50%	45%	61%	n/a	71%	61%	54%
Total	62%	70%	40%	52%	47%	74%	68%	60%	55%

Table 1.3. Bray-Curtis dissimilarity index between all years 2019-2021 over time across all 3 protected areas and for each individual Metropark using volunteer collected data.

	2019 vs. 2020	2019 vs. 2021	2020 vs. 2021
Oak Openings	23.48%	27.04%	27.52%
Secor	48.05%	67.48%	41.25%
Wildwood	42.68%	45.92%	37.56%
Total	35.37%	25.77%	15.30%

Table 1.4. Test statistics for individual Wilcoxon each-pair comparisons between years and whether tests were significant for total activity, individual species, and species richness for a. stationary surveys and b. transects. Only species found in that specific survey type every year were included. *= significant before Bonferroni's correction ($0.017 < p\text{-value} < 0.05$), **= p-value < 0.005). All variables without an asterisk are not significant.

a.

	Big brown bat	Eastern red bat	Hoary bat	Silver-haired bat	Little brown bat	Tri-colored bat	Evening bat	Total	Species richness
2019 vs. 2020	1.8615	5.3919**	4.7338**	2.9718**	3.6908**	0.2925	-4.2983**	3.5865**	5.2404* *
2020 vs. 2021	1.2165	3.1901**	1.5319	2.4392**	-0.4593	0.6769	-1.3379	2.2916*	-0.2852
2019 vs. 2021	2.9715**	6.0706**	5.5065**	4.3552**	3.4041**	0.8943	-4.8262	4.7788**	5.5102* *
Overall	**	**	**	**	**		**	**	**

b.

	Big brown bat	Eastern red bat	Hoary bat	Silver-haired bat	Evening bat	Total	Species richness
2019 vs. 2020	1.1616	7.8861**	9.5374**	1.9864*	-3.0116**	-0.0565	6.0688**
2020 vs. 2021	0.1054	-0.8847	1.4232	-1.5421	1.6644	5.8028**	1.8504
2019 vs. 2021	1.0078	7.9351**	9.0389**	0.4734	-1.5176	5.2740**	6.9872**
Overall		**	**		**	**	**

Figures

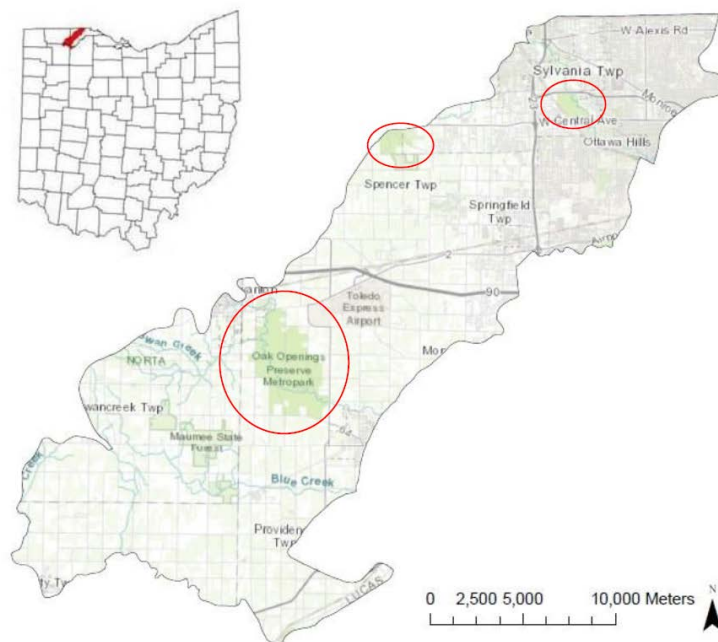


Figure 1.1. Metroparks (shown in circled areas) in the Oak Openings Region where citizen science surveys conducted and stationary monitors placed.

a.



b.



Figure 1.2. Acoustic monitoring set up for (a.) stationary monitor stations with monitor inside lockbox) and (b.) transects

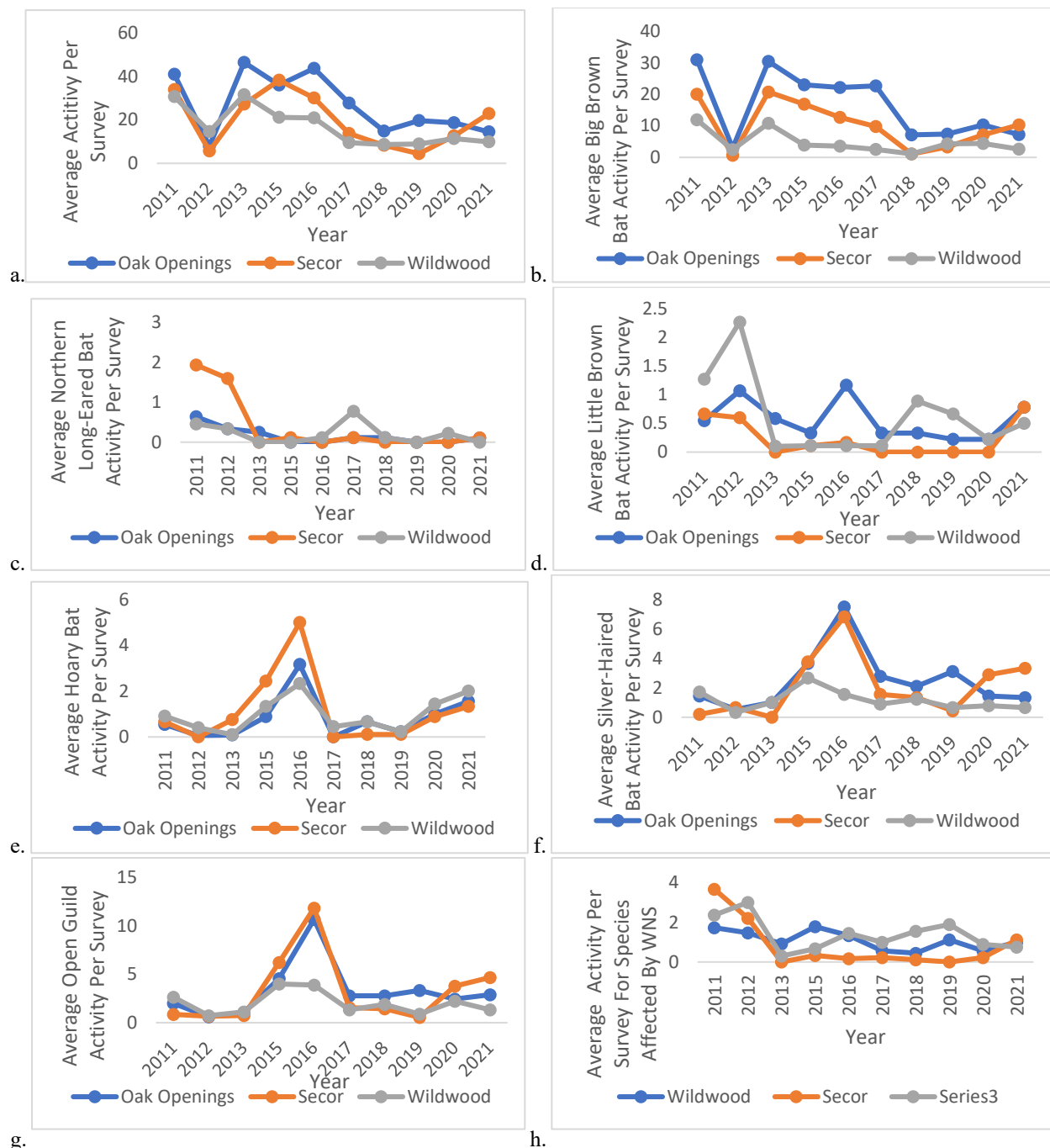


Figure 1.3 Long term trends for different bat activity groups: a. average overall bat activity per volunteer survey, b. average big brown bat activity per volunteer survey, c. average northern long-eared bat activity per volunteer survey, d. average little brown bat activity per volunteer survey, e. average hoary bat activity per volunteer survey, f. average silver-haired bat activity per volunteer survey, g. average open guild species minus big brown bats per volunteer survey, and h. average species impacted most by white-nose syndrome per volunteer survey from 2011-2021 by park. All the results graphed were significant.

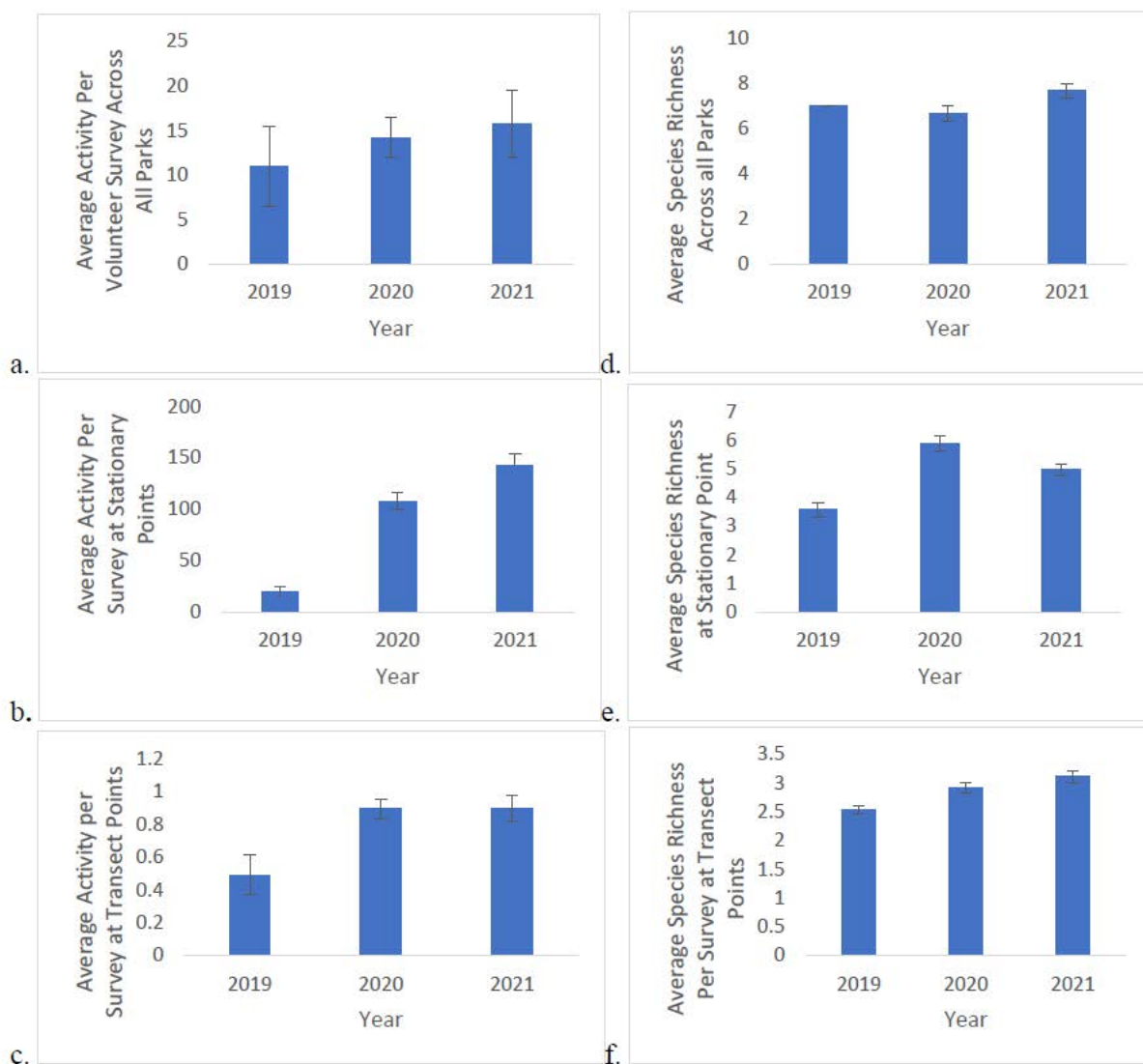


Figure 1.4. Average activity per survey and species richness from 2019-2021. Average activity listed for a. volunteer surveys, b. stationary surveys, and c. transects. Next to it is species richness for d. volunteer surveys, e. stationary surveys, and f. transects. Error bars represent standard error. Results were not significant for volunteer surveys but were for stationary and transect surveys.

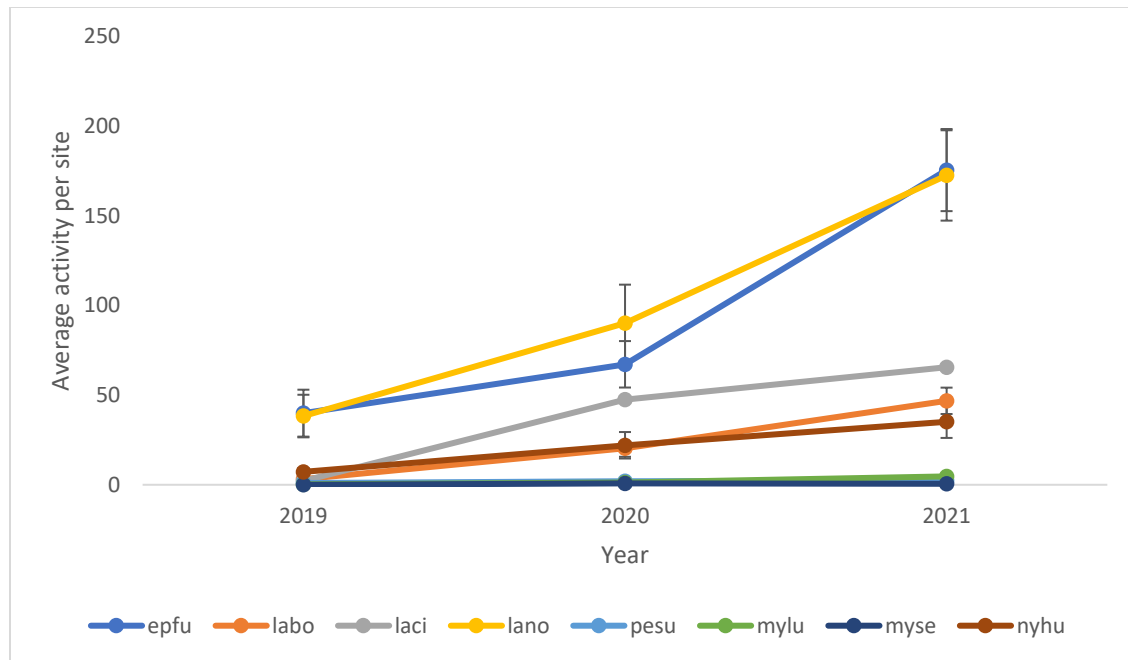


Figure 1.5. Average activity per stationary point for each species per year 2019-2021. Any extreme outliers were not shown to avoid distortion. Error bars represent standard error. epfu= big brown bat (*Eptesicus fuscus*), labo= eastern red bat (*Lasiurus borealis*), laci= hoary bat (*Lasiurus cinereus*), lano= silver-haired bat (*Lasionycteris noctivagans*), pesu= tri-colored bat (*Perimyotis subflavus*), mylu= little brown bat (*Myotis lucifugus*), myse= northern long-eared bat (*Myotis septentrionalis*), nyhu= evening bat (*Nycticeius humeralis*).

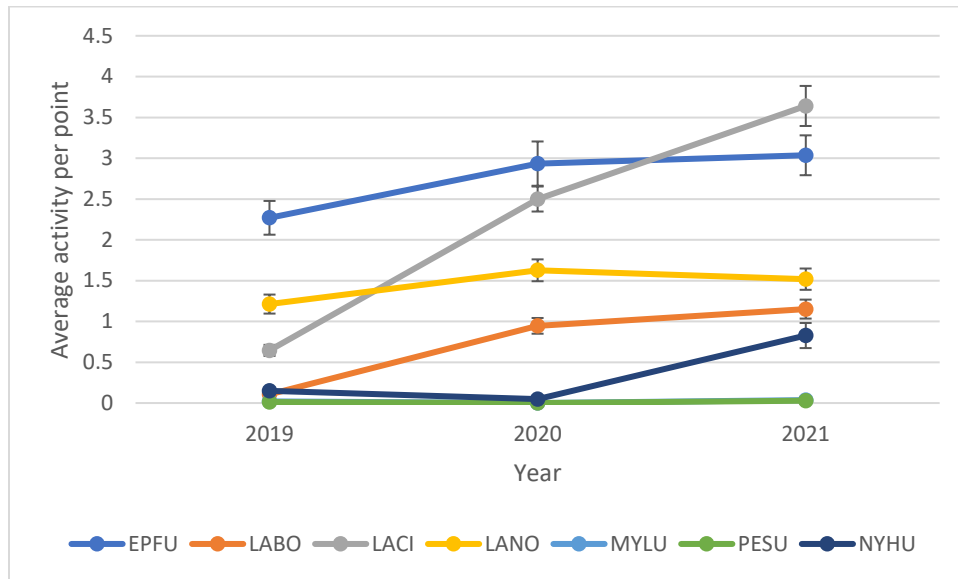


Figure 1.3. Average activity per transect point each species by year 2019-2021. Error bars represent standard error. EPFU= big brown bat (*Eptesicus fuscus*), LABO= eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), LANO= silver-haired bat (*Lasionycteris noctivagans*), PESU= tri-colored bat (*Perimyotis subflavus*), MYLU= little brown bat (*Myotis lucifugus*), NYHU= evening bat (*Nycticeius humeralis*).

CHAPTER 2: THE EFFECTS OF ANTHROPOGENIC LAND USE AND HABITAT VARIATION ON BAT ACTIVITY AND DIVERSITY ACROSS MULTIPLE SPATIAL SCALES

Abstract

Human land use threatens bats because of habitat loss from deforestation, agriculture, and urbanization, with light pollution and fragmentation having variable impacts depending on the species. The high amount of spatial variation in bat data and lack of multi-variable studies on how human land use impacts bats creates a need for more information on how these factors impact bats. The main objectives of this study were to determine how factors related to human land use such as light pollution, fragmentation, and percent of urban/residential and agricultural land cover, as well as general habitat factors such as clutter and canopy cover, relate to bat activity and species richness and to compare bat activity between protected and unprotected areas. Bat activity and species richness were compared to microhabitat characteristics collected in the field and macrohabitat characteristics collected in ArcGIS and FRAGSTATS. AICc was used to evaluate models of the habitat factors most associated with bat activity and species richness. Wilcoxon tests were used to compare species richness and activity between protected and non-protected areas and paired stationary sites. Bat activity and species richness were significantly higher at stationary points than along road transects. Bat activity and species richness were generally higher with higher percentages of dry, open habitats such as sand barrens, savanna and upland prairie; bat activity and richness was lower when percentages of floodplain forest, conifer forest, and wet prairie were higher. Cropland was positively associated with bat activity at stationary points, but negatively associated with richness and activity along transects. Understory height and clutter from 3-6.5 m tended to be negatively associated with bat activity, but clutter at 0-3 m was positively associated with overall activity along transects and

open guild species at stationary points. Canopy height was positively associated with bat species richness and activity along transects and forest dwelling species at stationary points. Months water present and percent ponds in 100 m showed up in the best model for species richness along transects. Patch richness was negatively associated with bat activity at stationary points but positively associated with activity and richness along transects. What habitat factors impacted bats was dependent on scale, area studied, and guild of species surveyed. When managing bat habitat, it would be advantageous to decrease clutter at medium height levels, have an intermediate number of habitat types, and maintain open natural habitats such as sand barrens. Along roads, planting tall trees and providing water sources would be beneficial.

Introduction

As with many other types of wildlife, human land use is the biggest threat to bats worldwide (McKinney 2002, Frick et al. 2019). Land use change is by far the most common threat to bats listed under the IUCN Red List, with deforestation the most common threat followed by non-timber crops (Voigt and Kingston 2016). Deforestation is one of the biggest threats to bats because many bat species require forest habitat for foraging and roosting and around 7-11 million square km of forest have been lost in the past 300 years (Foley et al. 2005, Frick et al. 2019). Agriculture is a main threat for over 50% of threatened bat species and harms bats through direct habitat loss and pollution from insecticides (Frick et al. 2019, Park 2015). Bats generally have lower activity in agricultural regions than natural or residential areas, although the negative impacts of agriculture are less on organic farms (Turner 2018, Wickramasinghe et al. 2003).

In addition to deforestation and agriculture, bats can also be negatively impacted by urbanization. Urban areas negatively impact bats through increased exposure to predators such as

feral cats, more conflict with humans, decreased mobility, increased competition, and increased road mortality (Russo and Ancillotto 2014). However, anthropogenic land use may also provide some benefits for bats because certain bat species take advantage of it by sheltering in structures or drinking from water sources made by humans (Russo and Ancillotto 2014). The presence of roads and light pollution in urban areas also impacts bats. Rare and threatened bat species and slower-flying species that prefer forested environments, such as species in the genus *Myotis*, tend to avoid areas with more light pollution (Lacoeuilhe et al. 2014, Longcore and Rich 2004, Stone et al. 2009). However, fast-flying bat species that forage in open areas, such as bats in the genera *Eptesicus* or *Nyctalus* can be attracted to streetlights because of the increased insects there, although this can increase collisions with vehicles (Stone et al. 2015). So, bats that prefer to forage around lights may have a competitive advantage in urban environments over other species (Longcore and Rich 2004). Roads also have a variable impact on bat activity, as some bat species forage on the edges they create. Roads, however, pose a danger to bats because they lead to increased deaths from collisions with vehicles and can be mistaken for water sources from above (Russo and Ancillotto 2014). Both light pollution and roads can lead to the fragmentation of habitats (Stone et al. 2015, Claireau et al. 2018).

Habitat fragmentation divides wildlife populations into isolated groups. This negatively affects wildlife by creating longer distances between resources, which limits the ability to access resources such as food mates, and shelter. It can also affect the distribution of the insect prey bats feed on, with some insect species avoiding overly fragmented areas (Tscharntke et al. 2002). As described by the Theory of Island Biogeography, smaller and more fragmented habitat patches can support fewer species and have a higher chance of extinction (MacArthur and Wilson 1967). This inability of smaller patches to support more species means that fragmentation affects

species richness as well as abundance. While habitat fragmentation has a negative impact on most wildlife species, its impact on bats is more variable, possibly because bats are more mobile than many other groups of wildlife. Fragmentation can also have a positive effect on bat abundance when it allows for increased access to both foraging and roosting sites (Ethier and Faring 2011, Arroyo-Rodriguez et al. 2016). This is likely related to bats' use of edge habitat for foraging and movement (Ethier and Faring 2011, Kalda et al. 2015, Morris et al. 2010). One study in the Oak Openings Region of Northwest Ohio found higher overall bat activity in the center of forest sites rather than on the edge, although the same was not true for savanna sites or for silver-haired bats (*Lasionycteris noctivagans*), so whether bats prefer edge appears species or habitat dependent (Turner 2018). For instance, *Myotis* species generally avoid habitat edges (Morris et al. 2010).

Impacts of increased human land use on bats are variable, as some bat species avoid developed areas, while others are attracted to lights by insect clusters and use the edges created by fragmentation for foraging and movement (Voigt and Kingston 2016, Stone et al. 2009, Turner 2018, Ethier and Fahrig 2011, Arroyo-Rodriguez et al. 2016, Kalda et al. 2015, Morris et al. 2010). One study found higher species diversity and bat activity in urban sites in the Chicago Metropolitan area than in rural sites (Gehrt and Chelsvig 2004), but a different one found lower species diversity with more urban development (Duchamp and Swihart 2008). Another research project also found higher bat species richness in urban-rural transition zones than in either urban or rural areas, suggesting that some bat species prefer intermediate levels of development (Treby and Castley 2016). Rare or threatened bat species and slower-flying species with low wing aspect ratios are more negatively affected by anthropogenic land use, while fast-flying generalist species that forage in open habitats are more often found in urban areas (Stone et al. 2015,

Lacoeuilhe et al. 2014, Longcore and Rich 2004, Fuentes-Montemayor et al. 2013, Barber et al. 2010). Because of these variable effects, increased development can lower species evenness, with more common generalist species such as the big brown bat (*Eptesicus fuscus*) becoming more dominant in urban areas and rarer specialist species such as northern long-eared bat (*Myotis septentrionalis*) declining (Loeb et al. 2008, Longcore and Rich 2004).

This study's main objective was to examine what variables related to human land use were most associated with variation in bat activity and species richness. The variables I focused on were fragmentation, light pollution, roads and land cover. These habitat variables have been important to bat activity and diversity in past habitat studies, so it is important to account for them (Turner 2018, Hollen 2017, Ford et al. 2005). Human land use also affects vegetation structure in an area, which makes these variables even more important to measure in a study looking at human habitat alteration. Previous studies have just looked at one factor, such as fragmentation or land cover type, instead of combining multiple factors or focused on single scale levels (Lacoeuilhe et al. 2014, Gehrt and Chelvig 2004, Stone et al. 2009, Treby and Castley 2016). This study includes point (measured 15 m away from sampling point), local (100 m buffers), and landscape scales (250 or 500 m buffers). This multifactorial and multiscale approach is beneficial, as previous studies have shown that the impact of habitat factors on bats may differ depending on the spatial scale studied (Gallo et al. 2018). This research also highlighted differences in habitat features and bat activity between protected and non-protected areas, which should demonstrate the importance of protected areas for conservation as well as the use of non-protected and more developed areas for some bat species. I also looked at the general spatial patterns of bat activity throughout the region and how it aligned with human land use.

This research is ecologically important, as habitat change due to anthropogenic land use is the largest threat to wildlife, including bats, and knowing what factors are most beneficial or harmful to bat populations will inform on how best to manage landscapes for them. I predicted that overall bat activity and species richness would be lower in areas with more roads, higher fragmentation, more light pollution, and higher percentages of dense urban and agricultural habitat. Furthermore, I predicted that whether areas with more fragmentation, agriculture, light pollution, and roads have higher or lower bat activity would also be species specific, with slower flying, forest foraging, and rarer species having lower activity levels in more developed areas. I also predicted that bat activity and species richness would be lower in areas with more structural clutter and higher understory vegetation.

Another objective of this chapter was to look at differences in bat activity and species diversity between protected and non-protected areas throughout the Oak Openings Region. I predicted that protected areas would have higher species diversity and bat activity per unit of time than non-protected areas. Previous studies found higher bat species richness in protected areas than non-protected ones (William-Dee et al. 2019, Kerbiriou 2018). I predicted that species that prefer open areas would have higher activity in unprotected areas and species that prefer forested habitats and rarer species would be more common in protected areas. This is likely, in part, because of the habitat differences between protected and non-protected areas in the Oak Openings Region, as protected areas had more mature forests and unprotected areas had more agricultural cover and wider roads (Nordal 2016). My overall goal was to examine how habitat factors, especially those related to urbanization and other forms of anthropogenic land use impact bat activity and species richness at multiple spatial scales and for individual species.

Methods

Acoustic survey data from stationary sites and road transects were collected as described in Chapter 1. Bat data were also recorded at four sites in Woodlawn Cemetery in 2021, but these data were not included in final models for the sake of consistency, although they were used as an example of bat data from a more urban site.

Study Area and Species

An area undergoing heavy amounts of anthropogenic land use that also serves as important bat habitat and needs further research is the Oak Openings Region in Northwest Ohio. This 476 km² area has high habitat heterogeneity, has undergone large amounts of fragmentation from an increase in urbanization and agriculture on the Toledo/Detroit corridor, and includes a major airport (Buckman-Sewald et al. 2014, Becker et al. 2013, Higgins 2003). Since 2009, the amount of forested area in the region has decreased, while developed areas have increased (Schetter et al. 2013, Martin and Root 2020). Ten percent of the region is permanently protected (Martin and Root 2020). Despite the heavy development, the area is a biodiversity hot spot that contains 1/3 of Ohio's rare plant and animal species and over 1/4 of all the oak savanna habitat in the world (Becker et al. 2013, Higgins 2003). Oak savanna has been reduced to less than 1% of its original level in the region and is considered a globally endangered habitat (Brewer and Vankat 2004). This area has other rare habitat types in addition to oak savanna, such as wet prairie (Brewer and Vankat 2004).

About 10% of the Oak Openings Region is protected in preserves, but the rest is open to development (Abella et al. 2017). The largest of these preserves is Oak Openings Preserve (1200 ha), which consists of a wide variety of habitats including forest, upland prairie, and upland savanna, and is surrounded by a mix of residential areas, cropland, Eurasian meadow, and prairie (Schetter and Root 2011, Martin and Root 2020). Other parks in the area surveyed include Secor

(253 ha), which consists mainly of swamp and floodplain forest and upland prairie and is surrounded by a mix of forests, prairies, residential areas and cropland, and Wildwood (199 ha), which is composed primarily of upland deciduous and floodplain forest and upland prairie and is surrounded by residential and dense urban areas (Schetter and Root 2011, Martin and Root 2020).

Eight bat species are found in the region, all of which are insectivorous. These species are the big brown bat, little brown bat (*Myotis lucifugus*), northern long-eared bat, tri-colored bat (*Perimyotis subflavus*), evening bat (*Nycticeius humeralis*), hoary bat (*Lasiurus cinereus*), eastern red bat (*Lasiurus borealis*) and silver-haired bat (*Lasionycteris noctivagans*) (Buckman-Sewald et al. 2014). The Oak Openings Region is an ideal area to study how human land use impacts bats due to its high amount of development and status as important bat foraging and breeding habitat.

Microhabitat Data Collection

Canopy cover, vegetation density, canopy height, and understory vegetation height were measured 15 m away from each stationary point in all 4-cardinal directions (N, S, E, and W) once a month. Percent canopy cover was measured once a month using the HabitApp (version 1.1) cell phone app, which measures canopy cover by converting images to black and white and calculating the percentage of black pixels to total pixels. Photos were taken 1.5 m above the ground facing up at the canopy. Canopy height (m) was measured once a season using a Nikon Prostaff 3 laser rangefinder pointed upwards and understory vegetation height was measured once a month with a tape measure. Amount of clutter was measured once a month by counting the number of uncovered squares on a 6.5 m cloth scatter board and subtracting that from the total number of squares at the 0-3 m level, 3-6.5 m level, and total board (Turner 2018) (Figure 2.1). The number of saplings, defined as trees with DBH between 1-4.9 inches (Northern

Research Station Forest Service 2017), was counted starting in 2020 within 15 m from stationary points in each cardinal direction. Also starting in 2020, insects were sampled using sweep nets for each stationary point once a month in a 15 m radius of the stationary point using 50 sweeps in the air and in the vegetation. Insects and other arthropods captured were then identified to order and released.

The previously stated variables (Table 2.1) except insect activity, were also measured every 500 m on both sides of the road (changed to every 1 km after 2019) along road transects. If microhabitat characteristics could not be surveyed at transect points because they were on private land, they were estimated visually. Also recorded at each transect measuring point were: illumination (measured during nighttime transect surveys using a light meter in lux), distance to light (measured using rangefinder in m), and presence/absence of streetlights or ditches were also recorded at transect measuring points. Habitat type was also recorded along transects, with each point given a category from 1-6. Category 1 included points where both sides of the roads were residential; category 2 was when one side was residential and the other was agricultural; category 3 was when both sides were agricultural; category 4 was when one side was residential and the other was natural; category 5 was when one side was agricultural and the other was natural; and category 6 was when habitat on both sides of the road was natural.

NOAA historic weather data for temperature (°C), humidity (%), wind speed (km/hr) and barometric pressure (inHg) were obtained from the Toledo Express Airport Station using Weather Underground (www.wunderground.com) for the survey night during the peak activity period (30 minutes to 3 hours after sunset) at stationary points all years and for the survey time on transects in 2019. Brunton ADC Pro Handheld Weather Stations were used on transects before each survey in subsequent years to get more precise measurements. Moon phase and

percent illumination by the moon were determined through MoonGiant

(<http://www.moongiant.com/phase/today/>). The average, maximum, and minimum for each variable measured at least once a month were calculated for each field season.

Macrohabitat Data Collection

All macrohabitat characteristics (Table 2.1) were analyzed in ArcMap 10 (ESRI, Redlands, California, USA). Percent of each land cover type (cropland, dense urban, residential, floodplain forest, swamp forest, upland deciduous forest, upland coniferous forest, upland savanna, upland prairie, perennial ponds, and wet prairie) was measured in a 100 m and 500 m buffer (250 m around transects in 2019) around each stationary point and data collection point along road transects using a land cover map for the Oak Openings Region (Martin and Root 2020) (Figure 2.2). Large scale light pollution was measured in buffers using Defense Meteorological Satellite Program (DMSP) Operational Linescan System (OLS) imagery (Baugh et al. 2010). This satellite collected data measures visible and near-infrared light sources at night and consists of cloud-free composites made of all the available satellite photos (Baugh et al. 2010). Distance to nearest road and km of roads for each size buffer was determined using previously obtained local road data, Google Earth (US Census Bureau 2018), and ArcGIS distance tools. Habitat on each side of the road was visually characterized as natural, agricultural, or residential every 500 m along road transects. The presence of ditches was also noted along transects. Population density along transects and distance to forest/water/roads at stationary points were measured in 2020 and 2019, respectively, but these data were eliminated in subsequent years due to lack of significance.

FRAGSTATS (McGarigal and Marks 1995) with no sampling was used to measure fragmentation by determining the percentage of each land cover type around each 30 m pixel, as

well as cohesion index, patch area, SIDI, and contagion index for each land cover type. The number of habitat types in each size buffer was also counted.

Data Analysis

Calls were identified to species as described in Chapter 1. A correlation matrix was used to determine if variables were highly correlated with each other (> 0.7). All but one of each set that are highly correlated with each other was removed from further analysis. I used automated forward stepwise regression models and AICc in JMP to examine relationships between activity and species richness and the local and landscape habitat variables. This automatically selected the most significant variables by adding them one at a time to see which contributed most to the model and used them to create the best fitting possible model. Models were created for each set of variables for stationary points and transects with all weather, insect (stationary 2020/2021 only), vegetation structure, land cover in 500 or 250 m buffer, 100 and FRAGSTATS/light pollution variables tested as separate groups. Final models were created using any variables that made the final models for each of these sets (except insects) to see which impacted bat activity and species richness the most. If residuals were non-normal or had unequal variance, the dependent variable (activity or species richness) was transformed using a log-normal distribution. Performing this transformation successfully caused dependent variables to meet assumptions. Models were created each year for average total bat activity, species richness, and averages for open and forested guilds of bats. Models for guilds were only run for stationary points because of the very low activity level of forest-dwelling species on transects. Wilcoxon tests and Bray-Curtis dissimilarity indices were used to compare paired sites (open vs. forested, edge vs. interior, and parking lot vs. 100 m outside parking lot). Hotspot analysis using the Getis-Ord GI* statistic was used to find the major areas of bat activity (overall, for open and forested

guilds and for each species) along transects for each year to examine bat spatial distribution in study areas and how it changed over time (Ord and Getis 1992).

Another objective of this chapter was to look at differences in bat activity and species diversity between protected and non-protected areas throughout the Oak Openings Region. Data for species richness, average activity, and averages for individual species (only the species commonly found along transects: big brown bat, eastern red bat, hoary bat, silver haired bat, and evening bat) were also compared between transect points in unprotected areas and those with protected habitat on at least one side of the road using Wilcoxon tests. Data for species richness, average activity, and averages for individual species commonly found along transects were also compared between that from the peak activity period at stationary points and data from the same time period in unprotected areas along transects from 2021 using Wilcoxon tests. Only 2021 was used for this comparison because that was the only year for which calls from the peak activity period (30 minutes to 3 hours after sunset) were separated out. Activity data from stationary points during the peak activity period were normalized by sampling time.

Results

Stationary Points

The variables of savanna and swamp forest in 100 m (highly correlated with each of their same habitat types at 500 m), contagion index (highly correlated with all light variables and mean area), m of roads in 500 m (highly correlated with all light variables, lepidoptera average, and mean area), maximum light (highly correlated with minimum and average light), and averages of temperature, humidity, and wind speed (highly correlated with maximum and minimum for same variables) were cut from final models since they were highly correlated with other variables. The best overall model for species richness at stationary points included percent sand barrens, savanna and upland prairie in 500 m, maximum temperature, and wet prairie and

upland conifer forest in 100 m (Table 2.2). Higher maximum temperature and percent sand barrens, savanna, and upland prairie in 500 m were positively associated with bat species richness. The percentage of wet prairie and upland conifer forest in 100 m were negatively associated with richness. The best total activity model (Table 2.2) included understory height, patch richness, minimum clutter in 3-6.5 m, maximum temperature, minimum humidity, and percent wet prairie, deciduous forest, floodplain forest, and cropland in 500 m. Understory height, percent wet prairie, floodplain forest and deciduous forest in 500 m, minimum humidity, patch richness, and minimum clutter in 3-6.5 m were negatively associated with bat activity. Maximum temperature and percent cropland in 500 m were positively associated with activity.

The best model for the open guild (Table 2.2) included minimum clutter at the 0-3 m and 3-6.5 m level, percent floodplain forest, deciduous forest, and wet prairie in 500 m, percent sand barrens in 100 m, minimum humidity, patch richness, and understory height in m. Minimum percent clutter in 0-3 m, maximum wind speed, minimum humidity, and sand barrens in 100 m. were positively associated with open guild activity. Percent deciduous forest, floodplain forest, and wet prairie in 500 m, understory height in m, and percent clutter at 3-6.5 m were negatively associated with it. Associations with weather variables were weaker than others except for minimum humidity. The best model for forested guild activity (Table 2.2) included canopy height, percent upland prairie and floodplain forest, mean area, maximum humidity, maximum barometric pressure, and maximum wind speed. Forested guild activity was negatively associated with percent floodplain forest in 500 m and positively associated with mean patch area, maximum wind speed, canopy height, maximum barometric pressure, maximum humidity, and upland prairie in 500 m.

No insect models fit better than the default intercept only model (AICc= 236.1406) for species richness and the best model for activity (AICc= 206.9989, R^2 = 0.0889) included both average Isopoda and Diptera activity, both of which were positively associated with bat activity. The open guild was associated with average Diptera activity (AICc= 218.308, R^2 = 0.0626) and the forest guild (AICc= 189.414, R^2 = 0.1925) was associated with average Diptera, Hemiptera, and Isopoda activity. Diptera and Isopoda activity were positively associated with bat activity and Hemiptera was negatively associated.

There was no difference in species richness or activity between parking lot and non-parking lot sites, although parking lot sites had more hoary bats. Due to the lack of difference, no monitors were placed in parking lots the following year. There were no significant differences in average activity (p = 0.2962) or species richness (p =0.2518) between open and forested sites. There was also no difference in average activity (p = 0.5494) or species richness (p = 0.3406) between edge and interior sites. No individual species differed significantly in average activity between open and forested sites or edge and interior sites after correction for multiple comparisons. Edge and interior sites had bat communities that were 14% dissimilar and open and forested sites were 36% dissimilar.

Transects

Hotspot analysis (Figure 2.3 a-c) revealed consistently high bat activity in the northern part of the survey area near Secor Metropark. There were fewer consistent spots of no activity, although they were usually in the southern part of the region if present.

The variables of wet prairie, residential, cropland, and total forest in 100 m buffers (highly correlated with 250/500 m for same habitat types), maximum and minimum of both clutter levels and canopy cover (highly correlated with average for respective variables), contagion index (highly correlated with cohesion index), maximum light (highly correlated with

average light), minimum moon illumination and average of temperature, humidity, and barometric pressure (highly correlated with maximum of respective variables) were eliminated from final models, as they were highly correlated with other variables. The best model for all variables combined for species richness along transects (Table 2.3) included canopy height, savanna, conifer forest, and cropland in larger buffers, ponds and upland prairie in smaller buffers, average clutter at both height levels, number of habitat types in 500 m, months water present, minimum and maximum barometric pressure, and minimum temperature. For habitat type, points with one side residential and other natural had significantly higher species richness (tested using Wilcoxon each-pair tests) than any habitat types with no natural types of habitat on either side of the road. Points with one side natural had significantly higher species richness than points with one side agricultural and the other residential or both sides agricultural, and points with one side natural and the other agricultural had significantly higher activity than those with both sides agricultural. Canopy height, m of roads in larger buffers, months of water present, clutter at the 0-3 m height level, average light, average percent savanna in larger buffers, number of habitat types in both size buffers, minimum temperature, and maximum barometric pressure were positively associated with species richness. Minimum light, percent upland conifer forest and cropland in larger size buffers, percent clutter at 3-6.5 m, and minimum barometric pressure were negatively associated with bat species richness.

The best final model for bat activity (Table 2.3) included clutter at both height levels, percent upland conifer forest, total forest, floodplain forest and cropland in larger size buffers, maximum temperature, humidity, and barometric pressure, m of road in larger size buffers, number of habitat types in larger size buffers, habitat type, and average canopy cover. Wilcoxon each-pair tests revealed that activity was significantly higher at points with one side of the road

residential and the other natural or both sides of the road natural compared to any of the habitat combinations without natural habitat on either side of the road. Points with agriculture on both sides of the road had significantly lower activity with those with agriculture on one side and natural on the other or residential on both sides of the road. Cropland, upland conifer forest, and floodplain forest in larger size buffers, and average percent clutter at 3-6.5 m were negatively associated with average bat activity. Meters of road inside larger size buffers, maximum temperature, humidity, and barometric pressure, number of habitat types in larger buffers, percent canopy cover, average percent clutter at 0-3 m, and total forest and savanna in larger size buffers were positively associated with it.

Comparing protected and non-protected areas

Transect points in protected areas had significantly higher overall, ($p = 0.0056$), big brown bat (<0.0001), and silver-haired ($p = 0.0022$) activity than those in unprotected areas. There were no significant differences in species richness, hoary bat, evening bat, or eastern red bat activity between protected and non-protected area transect points. Big brown bats were highly correlated with average overall activity in the comparison between stationary points and transects, so they were removed from that final analysis. Stationary points had significantly higher overall activity ($p = < 0.0001$), richness ($p = < 0.0001$) and silver-haired ($p = < 0.0001$) and evening bat activity ($p = 0.0175$). Only evening bat activity was no longer significant when corrected for multiple comparisons. There was no significant difference in hoary bat or eastern red bat activity between protected and non-protected areas.

Discussion

Results were complex and illustrate that bat activity and species diversity are impacted by a wide variety of factors, with structural and contextual characteristics having the greatest

impact. Best fitting models also mainly consisted of many variables with each one making a small contribution instead of one variable contributing the most. The results successfully highlight the habitat variables at multiple scales that are most associated with bat species richness, average activity, or activity of open or forest habitat dwelling species.

Percent sand barrens, savanna, and upland prairie were positively associated with activity and/or species richness at stationary points and/or transects. Positive associations with sand barrens and savanna were supported by previous studies in the Oak Openings Region, especially for open foraging species such as the hoary bat (Stoneberg 2020, Sewald 2012). These habitats have increased in cover in recent years due to restoration efforts (Martin and Root 2020), although additional restoration may be beneficial to at least some species of bats. Higher temperatures were especially positively associated with higher bat activity and species richness both along transects and by stationary points; this was consistent with previous findings (Hollen 2017, Johnson et al. 2010, Brooks and Ford 2005). The reason temperature was significant here but not for the prior chapter may have to do with nightly temperatures being used instead of those for the whole summer.

Upland conifer forest, floodplain forest, and deciduous forest were negatively associated with bat activity and/or species richness. Turner (2018) found especially low bat activity in floodplain forest compared to habitat types in the same region but, Hollen (2017) and Blakey et al. (2017) found opposite results. This may mean the impact of floodplain forests may be somewhat variable depending on spatial or temporal context. It could be related to changes in water availability or habitat quality since 2016 and comparisons would need to be done to see if that is the case. The finding that higher percent conifers was associated with lower activity and species richness is consistent with previous studies (Sewald 2012, Hollen 2017, Yoshikura et al

2011). Many of the conifer forests in the Oak Openings Region are non-native commercial pine stands that generally less diverse than surrounding forests and in declining quality from lack of management (Abella 2010, Abella et al. 2017). Previous studies have found increased plant and wildlife diversity when removing or thinning these pine stands in the region, with additional efforts to remove and convert this land to early successional cover underway (Abella 2010 Abella et al. 2017, Martin and Root 2020). My results suggest that removing or thinning these pine stands could be beneficial for bats. That bat activity was negatively associated with percent deciduous forest cover is the opposite of previous studies although many of these were single species studies focused on forest-dwelling species (Johnson and Lacki 2011, Amelon et al. 2014). The prevalence of open foraging species may be behind the negative impact of this forest type and others, especially as it did not have negative impacts on the forest-dwelling guild. Higher bat activity was also negatively associated with higher understory height, which could also be related to the negative association with forest cover.

For clutter, whether the impact was positive or negative depended on the height level. There were negative associations between clutter at 3-6.5 m and bat activity overall and for the open guild at stationary points and richness and activity along transects. This supports previous findings that bats avoid areas of higher vegetation clutter and taller understory cover (Lintott et al. 2015, Adams et al. 2009, Campbell et al. 1996, Rainho et al. 2010). However, there were positive associations with clutter 0-3 m for the open guild at stationary points and for species richness and activity along transects. This is likely because most open habitats had higher clutter at the lower height level and less clutter at the higher height level, which is ideal for open foraging species, the most common group along transects. These results suggest that it would be

advantageous for open foraging bats for land managers to reduce clutter at the 3-6.5 m level, while increasing low level vegetation along roads.

Some variables that were expected to be important were not, such as light pollution, overall insect activity or species richness, and type of paired site. Light pollution results may be related to the typically variable impacts of lights on bats or because of the relatively low amount of light pollution in the region, especially around stationary points. The lack of difference between open and forested and edge and interior sites is likely a result of bats utilizing both open and forested and edge and interior sites and that overall site preference is complex and based on numerous factors. Similar results have been found in past studies (Turner 2018, Dodd et al. 2012).

While many variables were consistent in their importance across tests, others differed depending on scale, whether focusing on the open or forested guild, and whether measured along transects or at stationary points. Variables that were important at one scale were often not important at another. For instance, variables that were strongly associated with bat activity or species richness at 500 m were often not associated with it at 100 m, and vice versa. This supports previous findings that it is important to use multiple spatial scales (Gallo et al. 2017).

Both the forested and open guild models were fairly similar to the overall activity model and the open guild especially overlapped with the overall activity model, since the open foraging species were some of the most common. However, some variables were more important for certain guilds. There was a positive association with canopy height for forested guild activity at stationary points and species richness at transects. This especially makes sense for the forested guild because canopy height tended to be higher in forested areas. Previous studies have also found positive associations between canopy height and bat activity, especially along roads

(Russell et al. 2009, Jung et al. 2012, Bader et al. 2015). Forested guild species also had higher activity when mean patch area was higher, indicating that this group is especially negatively impacted by habitat fragmentation and loss. This is consistent with past findings (Henderson et al. 2008) and makes sense since this group is more dependent on large continuous blocks of forest.

Which insect orders were associated with bat activity varied depending on guild. Diptera was positively associated with the open foraging guild, but Hemiptera and Isopoda were only associated with the forest guild. These orders may choose similar habitats as bats rather than being preferred food, which is most likely in the case of the order Isopoda, since bats have been known to feed on Hemiptera and Diptera, while Isopoda are not commonly fed on by bats (Pereira et al. 2002, Reimer et al. 2010, Weier et al. 2019, O'Rourke et al. 2021). However, these results should be viewed as preliminary, as dietary analysis would be necessary to see how much of their diet these orders compose in the Oak Openings.

The impact of weather variables could also vary depending on guild. Maximum humidity had a positive association for the forested guild and a negative one for the open guild and at stationary points. The impacts of humidity on bats can be variable since high humidity reduces the intensity of their calls but may also lead to increased prey (Appel et al. 2019), which could explain the contradictory results. The impact of habitat variables also sometimes differed between stationary points and transects.

Total percent forest and ponds and m of road were strongly positively associated with bats along transects but not at stationary points. The total forest results indicate that high overall forest cover may be more important along transects, where it tends to be sparser. Forest cover also has a greater positive impact on bat activity in an agriculture heavy matrix, which could

explain why it had a greater impact along transects (Rodríguez-San Pedro and Simonetti 2015). Higher percent of ponds in 100 m buffers was significantly correlated with higher species richness along transects. Combined with the positive association between months water observed at transect and species richness, this indicates that water is especially important to a diverse bat community along roads. It is worth noting that number of months where water was recorded was only recorded in 2021, while previous years whether ditches were present was only noted once a season (if ditches were present once, they were noted as present all month for those years), so that may have impacted results. Meters of roads were positively associated with bat activity along transects, indicating that roads and fragmentation can have a positive impact on bat activity rather than negative, albeit only for open-foraging species that forage along habitat edges. The importance of forest, water, and roads along roads was consistent with past findings (Hollen 2017, Medinas et al. 2019, Evelyn et al. 2004, Evelyn et al. 2004, Gaisler et al. 1998, Myczko et al. 2017).

There were also variables that were only important at stationary points. Wet prairie was negatively associated with bat activity stationary points (i.e. in protected areas). The percent total habitat for that type was very low, which may have affected the results. Wet prairie sites in the Oak Openings are also more disconnected from each other than those from other types of open habitat, so increased fragmentation in areas of higher wet prairie cover may also be responsible for the lower bat activity (Martin and Root 2020). Wet prairie was also extremely uncommon along transects, which may be why it didn't affect bat activity much there.

Some variables had opposite associations between transects and stationary points. For instance, cropland was negatively associated with bat activity and species richness along transects and cold spots with no activity along transects were found in the southern region where

there was heavy cropland cover. However, cropland in 500 m was positively associated with activity around stationary points. Hollen's (2017) single year study found somewhat opposite results, with no association between cropland and activity along transects, but a negative association at stationary points. This may be a result of the importance of open habitats next to stationary points. Cropland may be utilized by bats up to a point, but the more extensive cropland cover along roads is likely detrimental. While there was not a clear relationship with cropland, average cover was much higher in larger size buffers along road transects (24.62%) than around stationary points (0.97%). Other studies also found that bats generally avoided areas with high agricultural cover (Blakey et al. 2017, Turner 2018, Put et al. 2019). Previous research shows that increasing farmland heterogeneity or using organic farming methods is beneficial to bat activity and diversity, so if possible, encouraging local farms to diversify their crops, plant tree rows, or use organic methods would help bats (Wickramasinghe et al. 2003, Monck-Whipp 2018).

The number of habitat types was negatively associated with bat activity in protected areas, but positively associated with species richness and activity along roads, which fits with Hollen's (2017) results. This may be because bat species foraging along roads tend to be more fragmentation tolerant and prefer to forage along habitat edges. The positive association with the forest guild and mean patch area also suggests fragmentation may especially negatively affect the forest dwelling species that are more common around stationary points. It is also likely that an intermediate amount of patch richness is best for bats. There was a clear non-linear relationship between patch richness and activity, with activity being highest with around 9-12 habitat types in the larger size buffer and dropping off steeply below or above that (Figure 2.5).

Sites at stationary points had higher total activity, species richness, and individual species activity for evening and silver-haired bats than non-protected areas along transects. While stationary surveys recorded all night and transects only covered a 10-minute interval this was corrected for by only using stationary results for the peak activity period and normalizing for sampling time so this should not have impacted results. The same trend being apparent when comparing transect points in protected and unprotected areas, although results were not significant for species richness and evening bats when only using transect points. These results demonstrate the importance of protected areas for bat conservation and these areas should continue to be managed for bats. Similar results showing the importance of protected areas were found in previous studies (Nordal 2016, Tena and Tellería 2021). A few of the transect points (9 of 139) did pass through protected areas but transect points were still primarily in unprotected sites. It is also worth noting that only 10% of the region is protected, so the protected areas cover a relatively small part of the study area.

Northern long-eared bats were never found along transects and little-brown bats and tri-colored bats very rarely were. Hollen (2017) also did not detect northern long-eared bats along transects, although other studies in the region did in very low numbers, which suggests they forage along roads very infrequently (Nordal 2016, Turner 2018). All three of these species are of conservation concern, so this further supports the importance of protected areas for bat conservation, especially for particularly vulnerable species. Silver-haired bats and evening bats were also more common at stationary points than along transects, while big-brown and silver-haired bats were more common at protected transect points than unprotected ones. Evening bats are found mainly in forests, roost in large trees, and avoid high traffic areas, so it makes sense they would be common in interior protected areas like those surveyed for stationary points (Hein

et al. 2010, Nordal 2016). Silver-haired and big brown bats are development tolerant generalists that forage in open areas, so it is unclear why they were more common in protected areas. It may be that the protected areas have more of the types of open habitat (such as savanna) this species prefers to forage in, that they provide more roost trees, or that they have less disturbance by humans (Hollen 2017, Mattson et al. 1996). It is also worth noting that silver-haired bats were more likely to be found at forested than open transect points by previous studies, although this was also the case for eastern red bats, which were not more common in protected areas (Hollen 2017). Hoary bats were also not significantly more common in protected areas. This may be because eastern red and hoary bats often forage in open areas and are more development tolerant (Loeb and O’Keefe 2010, Menzel et al. 2005, Hollen 2017). While some variables were consistently important, the variety in results and that no one variable had an especially large contribution to models shows how complicated the question of what habitat factors impact bats is and how much results can vary.

Conclusions

Habitat variables affect bats in widely varying ways, with results changing based on scale, whether the results were from stationary points or transects, and the guild of species studied. These results also show the importance of protected areas to bats, as protected park areas had higher activity and species richness than road transects that were mainly in unprotected areas. The results from transects and stationary points also differed somewhat in habitat associations, although there was some overlap. Based on our findings, land managers should minimize habitat fragmentation, conifer and floodplain forest cover, and tall mid-level understory cover and promote diverse open habitats such as sand barrens and upland prairie. Canopy height and percent cover and presence of water seemed to positively impact bat activity

along transects, so planting tall shade trees and providing water sources along roads would also be beneficial to bats. Following these suggestions will promote maximum bat activity and species richness.

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Tables

Table 2.1. Habitat factors measured along transects and at stationary points.

Variable name	Transects or stationary points?	Local or landscape scale?	How often measured?	Unit of measurement	How measured
Canopy cover	Both	Local	Monthly	Percent	HabitApp photos
Clutter (0-3 m, 3-6.5 m, total)	Both	Local	Monthly	Percent	Clutterboard (Figure 2.1)
Understory height	Both	Local	Monthly	Meters	Measuring tape
Canopy height	Both	Local	Yearly	Meters	Range finder
Insect abundance and richness (identified to order)	Stationaries	Local	Monthly	Number	Sweep net
Light pollution (using light meter)	Transects	Local	Twice a month after 2020 (monthly in 2019)	Lux	Light meter
Distance to light	Transects	Local	Yearly	Meters	Range finder

Historic weather data during peak activity period (temperature, barometric pressure, wind speed, and humidity)	Stationaries (and transects in 2019)	Landscape-available for Toledo area only	Monthly	Degrees F, inches, miles per hour, and percent	Weather Underground
Weather variables measured in field (temperature, barometric pressure, wind speed, and humidity)	Transects	Local	Twice a month (when transects run)	Degrees F, inches, miles per hour, and percent	Brunton weather station
Moon phase	Both	N/A	Monthly for stationaries, twice a month for transects	Percent	MoonGiant
Presence of ditches	Transects	Local	Yearly	Yes/no	Observation
Presence of streetlights	Transects	Local	Yearly	Yes/no	Observation

Fragmentation and heterogeneity variables (total edge, minimum area, patch cohesion index, patch richness, contagion index, and Simpson's diversity index)	Both	Landscape	One time	Meters, hectares, none, number, percent, and none	FRAGSTATS
Number of habitat types in 100 m and 500 m buffer (250 m for 2019 transects)	Both	Landscape	One time	Number	GIS and land cover map (Figure 2.2)
Percent of each habitat type in buffer	Both	Landscape	One time	Percent	GIS and land cover map (Figure 2.2)
Light pollution (avg in both buffers, min/max in larger one)	Both	Landscape	One time	Digital number-derived from cloud-free light detections multiplied by percent frequency of light detection	DMSP OLS imagery (Baugh et al. 2010)

Road density within buffers	Both	Landscape	One time	Kilometers	GIS and local road data
Habitat type at survey point	Transects	Local	Yearly	Marked as natural, agricultural, or developed	Observation
Distance to road, water, forest, residential/urban and agriculture	Stationaries	Landscape	One time	Meters	GIS distance tools, land cover map, local road data and aerial imagery
Number of saplings within 15 m (N, S, E, W)	Both	Local	Yearly	Number	Counting saplings along measuring tape

Table 2.2. Final stepwise regression models for bat species richness, total bat activity, open guild activity, and forest guild activity at stationary points (32 in 2021, 36 in 2020, 28 in 2019). The best fitting variables from 500 m radius land cover, 100 m radius land cover, fragmentation and light pollution, weather, and vegetation structure models were used to create these. The effect of one unit of change in the predictor on the response (parameter estimate) is written next to it in parentheses.

Model	Variables	AICc	R²
Species richness	% Sand barrens in 500 m (7.3246) % Savanna 500 m (2.3325) % Upland prairie in 500 m (2.8380) Max. temperature °F (0.0934) % Wet prairie in 100 m (-16.4107)	327.1215	0.4858
Total activity	Understory height m. (-0.6312) % Wet prairie in 500 m (-29.5092) Patch richness in 500 m (-0.5562) Min. % clutter in 3-6.5 m (-0.0137) Max. temperature °F (0.0324) Min. humidity % (-0.0201) % Deciduous forest in 500 m (-2.4328) % Floodplain forest in 500 m (-3.8566) % Cropland in 500 m (11.5240)	265.3525	0.6315
Open guild activity	Min. % clutter 0-3 m (0.0176) Min. % clutter 3-6.5 m (-0.0164) % Floodplain forest in 500 m (-4.1097) % Deciduous forest in 500 m (-3.3023) % Wet prairie in 500 m (-34.2678) % Sand barrens in 100 m (1.8927) Min. humidity % (-0.0336) Understory height m. (-1.0421) Patch richness in 500 m (-0.2713)	276.3924	0.5985
Forested guild activity	Canopy height m. (0.5671) % Upland prairie in 500 m (26.6148) % Floodplain forest in 500 m (-31.5920) Mean area ha. (8.8056) Maximum humidity % (0.4068) Maximum barometric pressure in. (18.1581) Maximum wind speed mph (1.4559)	774.5724	0.3079

Table 2.3. Final stepwise regression models for bat species richness and total bat activity at transect points (139 points in 2021, 166 points in 2020, and 141 points in 2019). The effect of one unit of change in the predictor on the response (parameter estimate) is written next to it in parentheses. The best fitting variables from 500 m radius land cover, 100 m radius land cover, fragmentation and light pollution, weather, and vegetation structure models were used to create these. Lower AICc values show a stronger fit.

Model	Variables	AICc	R ²
Species richness	Canopy height m (0.0115) % Savanna in 250/500 m (3.5352) % Conifer forest in 250/500 m (-2.1997) % Cropland in 500/250 m (-0.6962) % Ponds in 100 m (9.2928) % Upland prairie in 100 m (0.9315) Avg. % clutter 0-3 m (0.007) Avg. % clutter 3-6.5 (-0.0042) Patch Richness in 500/250 m (0.0654) Months water present (0.0435) Habitat type (0.0500) Min. barometric pressure in (-2.0506) Max. barometric pressure in. (1.7551) Min. temperature °F (0.04225)	1313.22	0.3387
Total activity	Avg. % clutter 0-3 m (0.0020) Avg % clutter 3-6.5 m (-0.0013) % Upland conifer forest in 500/250 m (-0.5987) % Total forest in 500/250 m (0.2034) % Floodplain forest in 500/250 m (-0.8982) % Cropland in 500/250 m (-0.1587) Max. temperature °F (0.0093) Max. humidity % (0.0037) Max. barometric pressure in. (0.2822) M. of road in 500/250 m (<0.0001) Patch richness in 500/250 m (0.0064) Habitat type (0.0147) Avg. % canopy cover (0.0011)	-35.6885	0.2883

Figures



Figure 2.1. Clutter board used for measuring vegetation clutter at multiple height levels

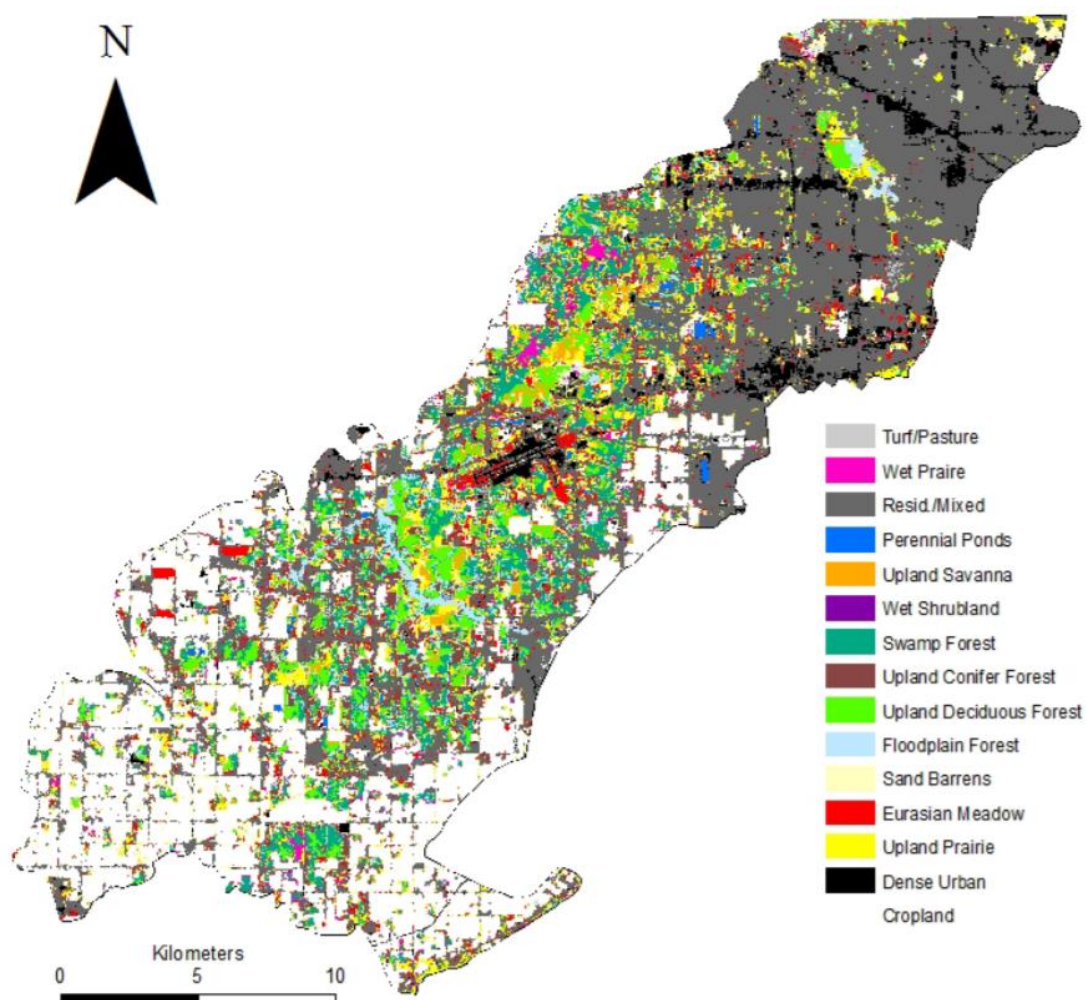


Figure 2.2. The Oak Openings Region land cover map of northwestern Ohio using the Brewer-Vankat boundary (Martin and Root 2020).

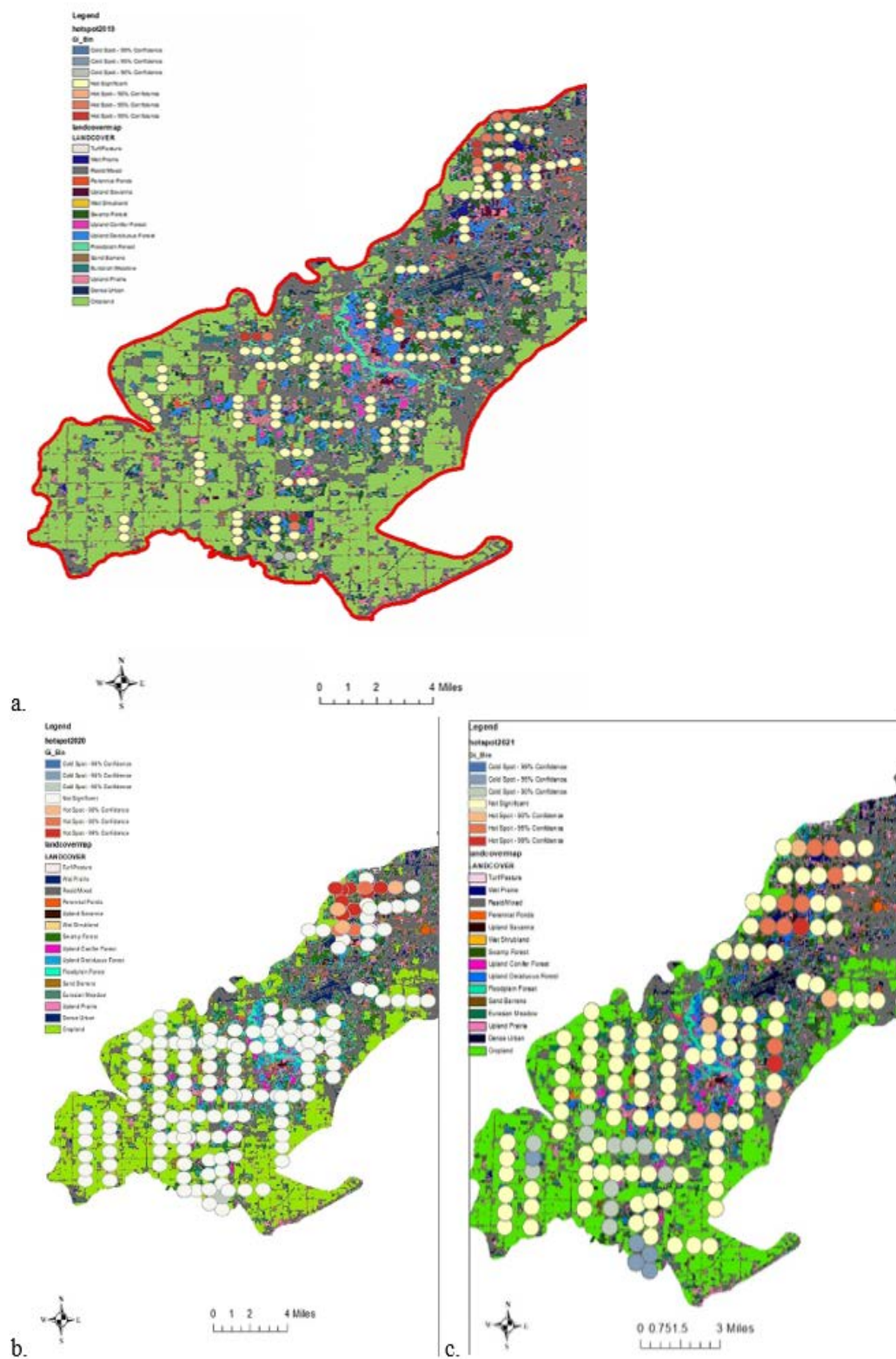


Figure 2.3. Hotspot maps for bat activity from a. 2019, b. 2020, and c. 2021

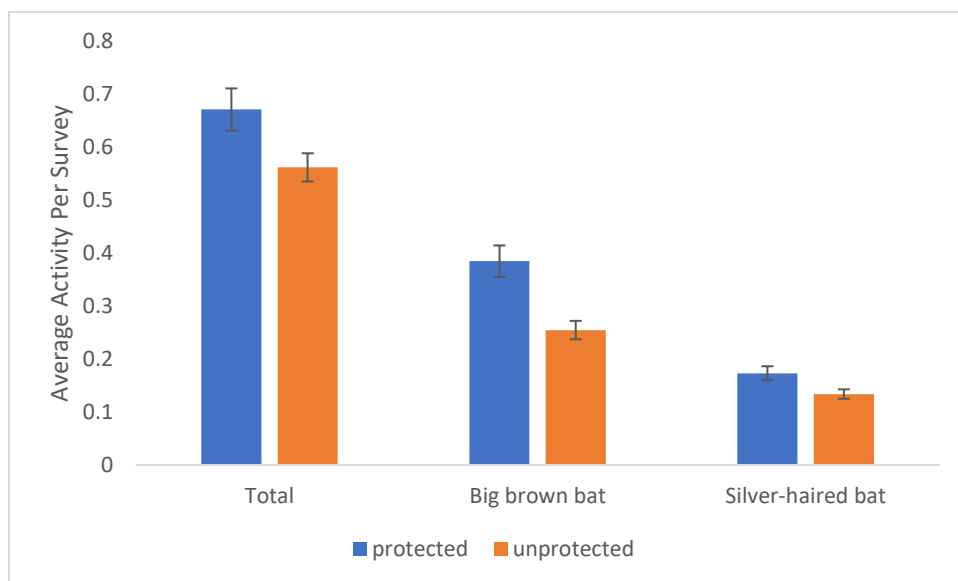


Figure 2.4. Comparison between transect points with at least one part of the road protected (142 points) and those in unprotected areas (305 points) for total, big brown bat, and silver-haired bat activity (all significant). Error bars represent standard error.

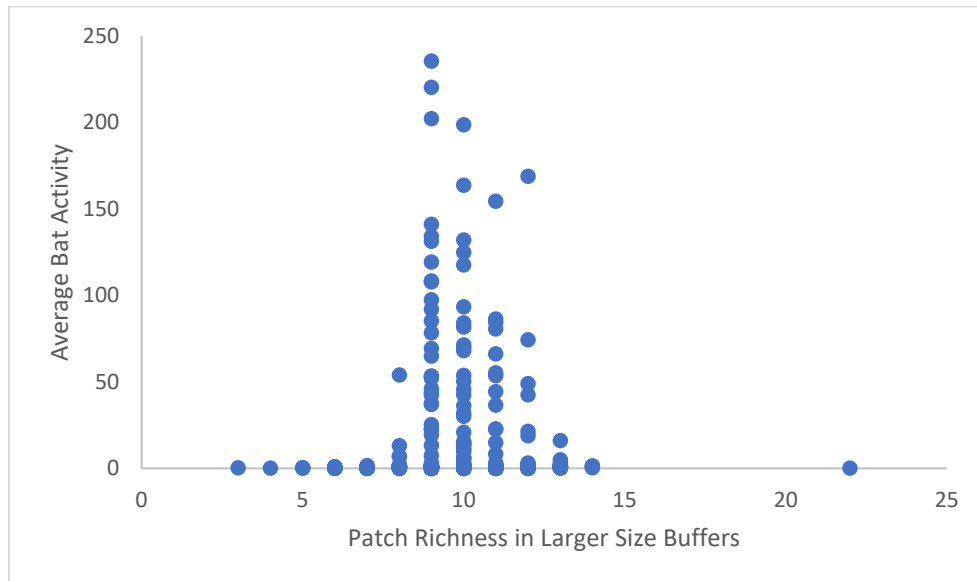


Figure 2.5. Average bat activity for both stationary points and transects compared with patch richness in larger size buffers.

CHAPTER 3: FACTORS INFLUENCING BAT HABITAT SUITABILITY AND PREDICTIONS OF FUTURE HABITAT SUITABILITY

Abstract

Updated habitat suitability models are important for making accurate conservation decisions. The most recent habitat suitability maps for bats in the Oak Openings Region were made in 2015 and based on old land cover data, so there is a need for updated models. Habitat suitability models were created in Maxent for total bat activity, species richness, open/forested guilds, species with and without white-nose syndrome (WNS), and individual species using bioclimatic and habitat data. Presence data was collected using acoustic data at stationary points and transects. Updated models including additional variables performed better than models using the same variables as the 2015 models. Some of the most important factors in models were percent savanna, distance to agriculture, May NDVI, annual precipitation, mean diurnal range, and annual mean temperature. Upland forest was especially important for species affected by WNS. Bats affected by WNS and forest-dwelling species had a smaller amount of suitable habitat compared to species not affected by white-nose syndrome and open foraging species. Protected areas were especially high in bat habitat suitability. In addition to current habitat suitability models, predictive models were created using expected climate changes for 2050. Climate models were not as good predictors of suitability as models using both climate and habitat variables. Suitable habitat for bats was predicted to move north slightly and the most suitable areas decreased under higher emission scenarios, but the amount of total suitable habitat was not expected to change. Areas of high bat habitat suitability outside current protected areas should be prioritized for protection.

Introduction

An understanding of how species respond to environmental changes is required for long term-conservation. This information needs to be up to date, because conservation decisions made from incomplete or out of date information can lead to decisions that harm instead of helping the target species (Spencer et al. 1991, Nordal 2016). One type of information that needs to be regularly updated is models, whether delineating current or predicting future species distribution.

Updating models is especially important when habitat preferences have changed, for instance if disturbances occurred that have altered species niches (Kearney and Porter 2009). Highly mobile species are especially reliant on up-to-date estimates of species distributions (Abrahms et al. 2019). Bats are one highly mobile taxon undergoing major change from disturbances such as white-nose syndrome (WNS), which has altered the niches of several bat species (Jachowski et al. 2014, Loeb et al. 2008, Longcore and Rich 2004). It has been shown that increases in activity for species not affected by WNS after the disease was introduced as species with similar niches declined, which indicates potential competitive release (Morningstar et al. 2019, Jachowski et al. 2014, Nocera et. al 2019, Faure-Lacroix et al. 2020, Simonis et al. 2021, Mayberry et al. 2020). Competitive release occurs when remaining species can better utilize resources and expand their realized niche, by foraging in a wider variety of habitats (Jachowski et al. 2014, Mayberry et al. 2020). These influential dynamics necessitate up-to-date bat distribution models.

Habitat suitability models, which are a type of species distribution model, predict species distribution over a large range using a combination of occurrence records and habitat data (Bellamy et al. 2013). These can be used to evaluate areas of potential habitat, determine areas to prioritize for protection, identify areas where conflicts between wildlife and human interests are

more likely, and predict past, present and future species distributions (Scharf and Fernandez 2018). Advantages of habitat suitability modeling are that models can use presence only data and can produce large-scale fine-resolution maps that can be generated from small data sets, are easy to interpret, can easily be updated, and include many interactions between species and their environment (Bellamy et al. 2013).

Modeling can be used to compare past, present, and future spatial patterns and predict what spatial arrangements of human settlements and other habitat types are most beneficial for bat activity and species diversity (Sutherland et al. 2009). Few studies have developed predictive habitat suitability models for bats, but there have been some looking at the impacts of climate change on bats. These models generally anticipated reductions in bat distributions and species richness due to climate change (Hughes et al. 2012, Aguiar et al. 2016, Loeb and Winters 2013). Climate change may harm bats by changing insect abundance, causing dehydration, changing roost temperatures, altering reproductive behavior, increasing extreme weather events, affecting the locations of habitable ranges, and potentially increasing proliferation of WNS (Sherwin et al. 2012). Simple habitat suitability models predicting how bats will respond to existing habitat conditions are more common than predictive models (Razgour et al 2011, Duff and Morrell 2011). Therefore, habitat suitability models that incorporate potential habitat changes resulting from climate change can help increase our understanding of potential future shifts in distribution and losses or gains in habitat for these vulnerable species.

Habitat suitability models were created for bats in the Oak Openings Region of Northwest Ohio in 2009 and again in 2015 (Buckman-Sewald 2014, Nordal 2016). These models were successful for predicting bat occurrence across the region (Buckman-Sewald 2014, Nordal 2016). However, these models need to be updated for this key region of habitat considering the

significant land cover changes (Schetter and Root 2011, Martin and Root 2020a) and changes in bat activities and distributions in recent years (Nordal 2016). My prior work in chapter one indicates that overall and individual species activity levels have changed over time. Significant land cover changes since the original land cover map used for the older models include increases in savanna and prairie cover and a decrease in forest cover (Martin and Root 2020a). No predictive models looking at future habitat changes have been done for bats in this region and are lacking for bats in general. A climate change model was previously made in the region for Eastern box turtles (*Terrapene carolina carolina*), which demonstrated noticeable variation in bioclimatic variables even across the relatively small region (Martin and Root 2020b). The rapid decline of bat populations and the habitat changes occurring throughout this region highlight the importance of updating habitat suitability models and creating predictive models.

My aim was to develop new habitat suitability maps of bats for the Oak Openings Region in Ohio. I also attempted to model future habitat suitability maps based on projected changes to the climate in the region. I hypothesized that suitability would have decreased in general in the Oak Openings Region since 2015 due to habitat loss, especially for forest dwelling species and those impacted by white-nose syndrome. I predicted that the variables in 2015 would have decent predictive power, but that additional climate and habitat variables would improve the model. I also predicted that bat species ranges would move north slightly because of increased temperatures and decrease in area. These results will be used to predict how bats will respond to future changes in habitat development and determine what spatial arrangements of habitat are best for bat populations. These updated models will also allow land managers to accurately identify the highest priority areas to protect for bats.

Methods

Data Collection for Presence Localities

Acoustic survey data from stationary sites (one call per species per site used for model) and road transects during the peak activity period (30 minutes to 3 hours after sunset) were collected as described in chapter 1. This protocol was also the same as that used by Nordal in 2015 (Nordal 2016). Any records less than 50 m apart for the same species were removed. Only data for 2021 was used, as that was the only year for which the peak activity period was separated out.

Call Analysis

Call analysis was the same as described in chapter 1 except BCID was not used, although all calls were still double-checked and compared to an existing call library.

Macrohabitat Characteristics

Identical procedures and variables were used as Sewald (2012) and Nordal (2016) for initial models so a direct comparison could be made. Percent land of specific habitat types (upland forest, prairie, meadow, and savanna) and number of forest patches was extracted using an updated land cover map (Figure 3.1) (Martin and Root 2020a) and FRAGSTATS (McGarigal and Marks 1995). Distance to roads, agriculture, and water were extracted using the Euclidean distance tool in ArcMap 10 (ESRI, Redlands, California, USA). Additional variables were tested as well, including NDVI for May and September of 2021, other land cover types not previously tested (ponds, upland conifer and deciduous forest individually instead of lumped together), contagion index, fragmentation variables (patch richness and contagion index), and bioclimatic variables downloaded from CHELSA (annual mean temperature, mean diurnal range (max temp – min temp) isothermality, temperature seasonality (standard deviation), max temperature of warmest month, temperature annual range, mean temperature of wettest quarter, mean

temperature of driest quarter, mean temperature of warmest quarter, annual precipitation, precipitation of wettest month, minimum temperature of coldest month, mean temperature of coldest quarter, and precipitation of coldest quarter) (Karger et al. 2017, Karger et al. 2018). CHELSA was used for bioclimatic data because that was used by prior studies in the region and has overall higher predictive power for multiple variables compared to other climate data sets (Martin and Root 2020b, Karger et al. 2017, Bobrowski and Udo 2017). For models including new variables, bioclimatic and habitat variables were tested separately initially and models using the best variables from each test model (importance of more than 5%) were then created. Only variables that were correlated with each other less than 0.7 were used in final models.

Model Development

Maxent (Phillips et al. 2017) was used to build occupancy or habitat suitability models under a variety of scenarios (e.g. current, future). Maxent models extrapolate the probability of occurrence based on presence locations and their associated attribute (Elith et al. 2010). Advantages of Maxent over other predictive modeling methods are that it has higher predictive power than other modeling approaches, uses presence-only data, is useful for modeling a wide variety of taxa in a quick and easy manner, and works with low sample sizes (Elith et al. 2010, Martin and Root 2020b). Models were run with 10 replicates (bootstrap), 10% of points set aside for test data, and using a random seed; the default values were used for all other settings. Models were run for total activity (combined), individual species, open guild (big brown, hoary, and silver-haired bats), forested guild (eastern red, northern long-eared, tri-colored, evening, and little brown bats), species affected by WNS (northern long-eared, tri-colored and little brown bats), and species not affected by WNS (big brown, hoary, silver-haired, evening, and eastern red bats). Species with 10 or fewer sample points were excluded from species specific models (northern long-eared bat, little brown bat, and tri-colored bat). Each pixel of the final map

(model) was assigned a value between 0 (lowest suitability) and 1 (highest suitability) based on whether it was below or above the threshold. To calculate the percent suitable and unsuitable habitat, distribution maps were made using the logistic threshold for the maximum test sensitivity plus specificity (MSS). Anything below the threshold was unsuitable while anything above is suitable. This statistic has reliably been used in the past to denote suitable and unsuitable habitat and is often more reliable than similar statistics and it balances the omission (false negatives: a species is present but identified as absent) and commission (false positives; a species is absent but identified as present) error rates (Martin and Root 2020b, Dias 2019, McGowan et al. 2021, Thapa et al. 2021).

The area under the receiver operator curve (AUC of ROC) was used to evaluate the model. AUC values < 0.8 indicate a good model and values lower than 0.8 indicate a poor performance (Zhu et al. 2010). The model with the highest AUC was used for each species or guild of species. Each best individual species model was then combined to make the species richness model by adding together the average model outputs for each species from a model including just the variables that were in the final model for every species. These new models were made so that each species model would have the same variables. The resulting richness map had pixels ranging from 0-5, where 0 meant no species likely present and 5 meant all species for which models ran likely present.

Predictive Climate Change Model

Maxent was also used to project species distributions for bats based on climate predictions from the most recent IPCC reports for 2050 under 4 scenarios (2.6: low emissions, 4.5: stabilization before 2100, 6.0: stabilization after 2100, 8.5: high emissions) from www.ccafs-climate.org (Hosseini Yousefkhani et al. 2017). The bioclimatic variables found to be most relevant in current models (more than 5% contribution to at least 2 final models) were

used to create future prediction models based. Future climate variables and current (2021) bat data were used to make models. Models predicting future change were compared to a current species distribution model using the same variables. For the best fitting set of models (species or guild with highest AUC values), each average model was converted into a binary suitable and unsuitable distribution map using the logistic threshold for the maximum test sensitivity plus specificity (MSS). Anything below the threshold was considered unsuitable and anything above it was suitable.

Results

Initial models

Initial models using the same variables as the 2015 models had relatively low AUC values (0.72-0.791), except for the models for evening bats (0.867) and species with WNS (0.962). This indicated that the variables used in the previous models may no longer be the best indicators of bat habitat suitability.

Improved models

Contagion and patch richness were highly correlated (>0.8) with each other, so only patch richness was included in models. Many of the bioclimatic variables were highly correlated with each other, so only a select group that were not highly correlated with each other (annual mean temperature, annual precipitation, minimum temperature of coldest month, mean diurnal range, mean temperature of wettest quarter, mean temperature of warmest quarter, precipitation seasonality, and precipitation of driest month) were included in final models.

AUC mostly improved when bioclimatic variables and additional habitat variables were added and all AUC values were over 0.8 for these models. The WNS model was the only one where the initial model had a higher AUC than the one with extra variables (Table 3.1). The percentage contribution for all variables in each best model is shown in Table 3.2.

NDVI was a large contributing factor for most models, especially May 2021 NDVI. May NDVI was the largest contributing factor to the models for total activity, big brown bats, hoary bats, silver-haired bats, species without WNS, and open foraging species. It was only not in the models for species impacted by WNS and evening bats. Bat activity was highest at moderate values of NDVI. Percent savanna cover was important in multiple models and was the largest contributing factor for the species impacted by WNS and eastern red bats. Percent savanna cover was positively associated with bat activity. Some of the older habitat variables were still important in models. Distance to agriculture contributed the most to the evening bat model and higher distance was positively associated with activity. Percent upland forest (conifer and deciduous combined) contributed the most to models for the WNS affected group and was positively associated with bat activity.

Weather variables were also important in many models, especially annual precipitation, mean diurnal range, and annual mean temperature. Annual precipitation and mean diurnal range were the only variables to be in every best fitting model, except for the WNS model, which didn't include any weather variables due to using the same variables as the 2015 model. Annual mean temperature was the largest contributing factor to the forested guild model. Annual mean temperature was negatively associated with suitability in all models it was in.

Maps were generated to show the best areas in the Ohio portion of the Oak Openings Region for overall bat activity (Figure 3.2), individual species (Figure 3.3), species affected by and not affected by WNS (Figure 3.4), and open and forested guilds (Figure 3.5). The species richness map highlights areas that were suitable for the most bat species (Figure 3.6). As might be expected, predicted species richness was highest in protected areas. Binary models were also produced to show the amount of suitable habitat according to the MSS threshold for each model

(Figures 3.7 and 3.8). Percent suitable habitat did not exceed 25% of the Oak Openings Region for any model, but percent suitability did differ between models (Table 3.3). The highest percent of suitable habitat was for hoary bats (24.14%) and the lowest could be utilized by species affected by WNS (1.18%).

Climate Models

The variables used in the climate models were annual precipitation, precipitation in driest month, annual mean temperature, mean temperature in wettest quarter, mean diurnal range, and minimum temperature of coldest month. Annual mean temperature and mean temperature of wettest quarter data were missing from climate scenario 6.0 (stabilization after 2100), so those variables were excluded from that model.

AUC values were lower for climate models than for models including both habitat and bioclimatic variables for the same species or guild. The AUC values for current models were mostly above 0.8, except for the combined and hoary bat models and the test AUC values for silver-haired bats, the open guild, and the no WNS group (Table 3.3 a). AUC values were often not above 0.8 for models using scenarios 8.5 (high emissions) or 6.0.; they were often in the 0.7-0.79 range, although some AUC values were above 0.8 for scenario 6.0 (Table 3.3 b-c). Scenarios 4.5 (stabilization before 2100) and 2.6 (low emissions) had higher AUC values, although some were still under 0.8 (Table 3.3 d-e).

For current suitability models, mean diurnal temperature range made the highest contribution to the model (Table 3.4 a). It was also the variable contributing most to models in scenario 2.6 (Table 3.4 b) and scenario 4.5 (Table 3.4 c). Annual precipitation had the highest contribution to models in scenario 6.0 (Table 3.4d) and scenario 8.5 (Table 3.4e).

Evening bat models had the highest AUC values out of all the models, with all values above 0.8 except for the test AUC for scenario 6.0, so comparison maps were made for that

model (Figure 3.7). It was a forest dwelling species with a limited suitability range in the region, which also made it valuable to model. The scenario 6.0 evening bat model was excluded from this comparison due to having a different set of variables than the other scenario models because of missing data. For evening bats AUC values were highest for scenario 2.6 and lowest for scenario 8.5 out of the ones mapped (Table 3.5). The most important variable was annual precipitation for the current and scenario 8.5 models, mean diurnal range for scenario 2.6, and mean temperature of wettest quarter for scenario 4.5. There were noticeable differences between the models, with suitability levels within the 0.8-1 range disappearing under higher emissions, but the amount of lowest suitability areas (0-0.2) also decreasing under the highest emission scenario (Figure 3.7). While there were overall changes in continuous suitability values between models, the overall amount of suitable habitat defined by the MSS value did not change much between models (Figure 3.8). RCP 4.5 had slightly more suitable habitat than the other models, but it wasn't a large difference (Table 3.6).

Discussion

Combining road surveys and stationary points seemed to give a better picture of the local community overall, especially since northern long-eared bats were not found along road transects. The low AUC values when using the same variables as the 2015 and 2009 models compared to updated ones with additional variables indicated that the previous models may no longer accurately predict current bat habitat suitability. The 2015 and 2009 models both had high AUC values above 0.8 when originally tested, so it is likely that the best conditions for bats in the region have changed (Nordal 2016, Sewald 2012). Species impacted by WNS were the only ones for which the previous models had higher explanatory power.

A relatively small amount of the whole landscape was considered suitable for bat activity, as no group had more than 25% of the region classified as suitable habitat. Percent suitable habitat was especially low for forest foraging species and those impacted by WNS, particularly when compared to open foraging species and those not impacted by WNS. These results show the advantage that species not affected by WNS, especially the ones that are open foragers (big brown, hoary, and silver-haired bats), have compared to other bat species since they can utilize a much larger area. WNS and forested species were especially clustered in protected areas. While this was partially because of the location of stationary points in protected areas, suitability was also higher in protected areas that were not surveyed. This further supports the findings from chapter 2 that protected areas are important for bats. Any areas with high suitability that are not already protected should be prioritized for protection.

Percent of suitable habitat across the landscape differed depending on the species or group. The most habitat could be utilized by the hoary bat, followed by the eastern red bat and silver-haired bat, then followed by the big-brown bat. The evening bat could utilize much less of the landscape than the other individual species, which may be because it was found on road transects less. These results indicate that open-foraging species can use more of the landscape than the forest foraging guild. The eastern red bat is a forest-forager but has been found in both open and forested habitats (O’Keefe et al. 2009, Amelon et al. 2014). It was slightly surprising that big-brown bats could utilize less habitat than three other species, since they are known as a generalist (Agosta 2002), but they could still utilize much more than the evening bat. Big brown bats may be limited by vegetation or bioclimatic variables, since NDVI and bioclimatic factors were the most important variables in that species model. The species suffering from WNS, which are all forest foragers, could utilize the least habitat of all the groups. They could only use about

1% of available habitat, most of which was in protected areas. In contrast, the species that don't get WNS could utilize over 20% more habitat. These findings are not surprising given the loss and degradation of forest, which these species rely on, particularly outside of protected areas within the region (Martin and Root 2020a). Habitat changes may be needed to increase populations of these species in addition to decreasing white-nose syndrome, including protecting not currently protected suitable habitat and increasing savanna and upland forest habitat, which models indicate were important to those species.

Many of the variables not used in previous models made large contributions to final models for 2021. NDVI, especially May NDVI, was important in many models. One explanation for these results is that early spring vegetation may be more important to bats or more limited than later in the season, which is probably linked to prey abundance and distribution. The only available September Landsat 8 file did have some cloud cover, which could have impacted results. Moderate levels of NDVI seemed to be most positively associated with bat activity, with activity being low at very high and low levels. This suggests that low vegetation cover makes habitat less suitable, but too much vegetation creates excessive clutter for bats to fly through. Previous studies have also found positive associations between bat activity and NDVI (Meierhoffer et al. 2021, Medina et al. 2021, Straka et al. 2021). Higher NDVI was also associated with higher abundance of the insects bats commonly feed on (Straka et al. 2021). These previous studies do not indicate that bat activity drops at very high values of NDVI though, so this may be a regional specific impact.

Another habitat variable that was especially relevant was percent savanna cover. This was the largest contributing variable to several models and generally was positively associated with higher bat habitat suitability. Interestingly, savanna had the highest contribution to models

for forest foraging species such as the species with WNS (northern long-eared, little brown, and tri-colored bats) and eastern red bats. Little brown bats, eastern red bats, and tri-colored bats can often be found in open areas, especially natural ones, but northern long-eared tend to be found mainly in forests (Starbuck et al. 2014, Ford et al. 2005). However, too much vegetation density is still detrimental for even the forest-dwelling species (Starbuck et al. 2014). Previous research in the region did find an association between all of these species except northern long-eared bat (which shared a model with 2 other species in the 2021 models) and percent savanna, so there was some precedent for these species to be found in savanna in the Oak Openings Region (Buckman-Sewald et al. 2014) It may be that savanna habitats provide a variety of plants promoting insect diversity while lacking high clutter that may be detrimental for them. Much of the oak savanna in the region is also clustered in protected areas where active restoration has occurred, which may explain the higher prevalence of these species where percentages of savanna are higher (Abella et al. 2004, Abella et al. 2018). Since savanna seems to be especially beneficial for species of conservation concern, increasing savanna may aid in protecting these species. Savanna appeared to be more important than other open habitat types. Percent prairie showed up in most of the individual species models but made a small contribution to all models, although it did have a positive overall relationship with bat suitability. Percent meadow (which is primarily grass), however, was negatively associated with higher bat habitat suitability, although it was in very few final models. All measures of open habitat were important in 2009 models, but not in 2015 models.

Forest cover was also important to bats, especially the WNS group. Percent upland forest was the most important factor for this group, as it had higher habitat suitability with higher percent upland forest. This makes sense, because all three of these species tend to dwell in

forests. It is worth noting that deciduous and conifer forest were only combined for this one model, as this was the only one to use the variables from the 2015 models. The WNS species were run again with upland forest separated into conifer and deciduous, but the AUC values were higher when they were kept together for this model, suggesting that upland forest is important to these species regardless of type. The 2015 models (Nordal 2016) found upland forest to be especially important for northern long-eared bats, which was one of the WNS affected species. Forest cover was found to be important to northern long-eared, little brown, and tri-colored bats in prior studies too (Rodhouse et al. 2012, Ford et al. 2005, Farrow and Broders 2011). Other types of forest were not often important in models. Deciduous forest was in none of the best models and conifer only contributed a small percentage to silver-haired bat models. Floodplain forest was only in the WNS species model and swamp forest was in the models for open foragers, WNS group, and evening bats; these forest types were negatively associated with bat activity. Forest seems to be most important to the WNS group compared to others and upland forest appears to be advantageous for these species, while too much swamp or floodplain forest is detrimental.

Distance to road was especially important in 2015 models (Nordal 2016), but it was less so in 2021 models. It showed up in a few best models but contributed <9% to all models and was the most important variable in none of them, unlike in 2015. The 2015 models only used road transect data in the model though, while mine used transect and stationary data. Combining types of survey data may give a better representation of where bats are found.

Distance to water was important in 2009 models but was less so in 2015 models. In 2021 it was in several best fitting models but had a relatively small effect (<8%) on all of them. Bat habitat suitability was still usually higher closer to water. Since water was measured using

distance to streams, this may indicate that while stream access was important for bats, that they were also using other sources of water and were not completely dependent on streams. The stream data used was also delineated on a national level and may be outdated, so getting updated local stream data may lead to more accurate models. Percent ponds were included in models and found to be relatively unimportant, although distance to ponds was not measured. Other water sources in the region that may be useful to include in future models include lakes, wetlands, and agricultural ditches.

Distance to agriculture was important in both 2009 and 2015 models (Nordal 2016, Sewald 2012) and it continued to be important in the 2021 models. It was in every best model except for the silver-haired bat one and was especially important for evening bats, for which it was the most important variable in the best fitting model. Greater distance from agriculture was generally positively associated with bat activity, although for the combined model smaller distances to agriculture were better and the most suitable habitat for eastern red bats and hoary bats was intermediate distances from agriculture. The evening bat findings were the opposite of the 2015 models (Nordal 2016), where evening bats were only found close to and intermediate distances from agriculture. Evening bat niches have changed in recent years in response to the declining activity of other species affected by white-nose syndrome (Thalke et al. 2018). This may cause evening bats to utilize forest habitat away from agriculture more as other forest foraging species have declined. More research is needed to verify if that is the case. Other studies have found distance to water, agriculture, and road to all be important and they should continue to be included in future models, even if their level of importance in the region has changed (Scherrer et al. 2018, Rainho and Palmerian 2011).

Bioclimatic variables, which were also not included in prior models, were also important predictors of bat habitat suitability. The most important were annual precipitation, mean diurnal range, and annual mean temperature. Previous studies have also found mean diurnal range to be important for bat habitat suitability and the impacts were variable depending on the species (Zegarra et al. 2020, Kusch and Schmitz 2013, Ancillotto et al. 2019). Our study found that intermediate values are generally associated with higher bat activity. The importance of annual precipitation and annual mean temperature were also consistent with past research (Ancillotto et al. 2016, Bradie and Leung 2016, Razgour et al. 2011, Hayes and Adams 2017). Bat suitability was generally higher with intermediate annual precipitation. Lower suitability at the highest amounts of annual precipitation could be related to insect abundance since insects are less active when rainfall is higher (Williams 1951). This lack of insect activity in particularly cool and wet periods can lead to decreased bat reproduction (Burles et al. 2009). However, high temperatures can also be harmful to bats. Bat suitability was lower with higher average mean temperature. Average mean temperature was especially important for the forest-dwelling guild. Habitats these species prefer are potentially more susceptible to climate change. Bat suitability was highest at intermediate levels for mean diurnal range and mean temperature of wettest quarter. Associations between bat habitat suitability and bioclimatic variables indicated that rising temperatures could be detrimental to bats, since they seem to have low habitat suitability in areas of highest heat. The negative association with temperature was surprising given that the opposite result was found in chapter 2, but that may be due to chapter 2 temperature being nightly temperature during the peak period as opposed to the average of the whole year. Temperature may have a detrimental impact on bats on a longer scale and a positive one on the shorter temporal scale in

this region. Previous studies generally found positive associations between annual mean temperature and bat activity (Thapa et al. 2021, Liang et al. 2019).

Climate models did not have as high AUCs as the ones containing both bioclimatic and habitat variables, which suggests that climate conditions alone are not as good predictors of bat habitat suitability. Climate conditions may not be the driving force behind bat distributions. However, bioclimatic changes from climate change may have some impact of bat suitability. While overall percent of suitable habitat changed little between models, the total level of suitability did. These models indicated that under the most extreme climate change conditions, total habitat bats live in may not change, but the highest quality habitat areas may become less suitable. Previous studies have predicted mostly detrimental effects of climate change on bat populations, including reduced populations and distributions (Hayes and Adams 2017, Loeb and Winters 2013). Suitable habitat in our models also shifted northward in 2050 models, especially in the highest emission model (8.5). This is consistent with past findings (Thapa et al. 2021). Maps were only created for evening bats since other AUC values were low, so it is unclear if all other species will be affected the same way. Since evening bats are tree roosters that migrate during the winter, they may not be as affected by changes in winter cave hibernacula temperatures as some other species (Lee et al. 2011). Since changes in the fundamental niche of a species can affect accuracy of predictions, all predictions may not hold, so models should be updated periodically (Razgour et al. 2016). Mapping over a larger area, including non-bioclimatic variables in climate models, and including multiple years of data may increase accuracy and generalizability of climate change models for bats.

Conclusion

The added habitat variables increased model accuracy and the use of multiple survey types allowed our model to provide a better picture of bat habitat suitability throughout the region. Models should be updated in the future and additional variables can be added, such as other types of bodies of water, sand barrens, and urban land cover. Sand barrens and water sources would be especially useful, since these were found to be advantageous to bats in the prior chapter. These models can be used to determine what areas to prioritize for protection. Increased bat habitat suitability in protected areas suggests that protecting high suitability areas that aren't currently protected would be advantageous for bat survival. The importance of savanna and upland forest for the highly threatened species impacted by WNS suggests that increasing these habitat types would be beneficial as well. Our models can both serve as a guide for what areas to prioritize for conservation in the Oak Openings Region and to determine what factors may be most important for bats.

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Tables

Table 3.1. Results of Maxent models' "Area Under the Curve" ROC analysis for the best fitting model for each species and guild using 2021 data from stationary points and transects. Test AUC was calculated from the random points removed from analysis (10% of total points). Values closer to 1 indicate a more discriminatory model. EPFU= Big brown bat, LABO= eastern red bat, LACI= hoary bat, LANO= silver-haired bat, NYHU= evening bat

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.888	0.920	0.904	0.921	0.903	0.965	0.950	0.871	0.911	0.871
Test AUC	0.865	0.873	0.895	0.884	0.854	0.900	0.962	0.852	0.839	0.838

Table 3.2. Percentage of contribution of each environmental variable to each best fitting 2021 Maxent species distribution model within the Oak Openings Region. EPFU= Big brown bat, LABO= eastern red bat, LACI= hoary bat, LANO= silver-haired bat, NYHU= evening bat. Any variables saying N/A were not run for that specific model. “+” indicates variable associated with activity increase, “-“ indicates variable associated with activity decrease, “-/+” indicates decrease in activity followed by increase, and “+/-“ indicates variable associated with initial increase in activity followed by decrease. No symbol indicates no position or negative association with activity.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
NDVI May	35.4 +/-	42.7 +/-	5.8 +/-	43.2 +/-	22.9 +/-	N/A	N/A	38.5 +/-	34.9 +/-	13.9 +/-
NDVI September	8.8 -/+	8.3 -/+	2.1 -	N/A	N/A	N/A	N/A	7.6 -	8.1 -	3.6 -/+
Distance to road (m)	8.2 -	N/A	2.8 -	N/A	N/A	N/A	1.1 -	N/A	N/A	1.5 -
Distance to ag. (m)	7.1 -	6.8 +	9.6 -/+	6.5 +/-	N/A	24 +	5.2 +	5.7 +	4 +	9.5 -/+
Prairie (%)	6.9 +	2.4 +/-	11.3 +	10.9 -/+	3.6 +	8 +	2.5 +	N/A	N/A	N/A
Distance to stream (m)	3 -	N/A	N/A	N/A	7 -	3.8 +/-	2.9 +	1.5 -	N/A	1.4 -
Annual precipitation (mm)	19.7 -/+	10.1 +/-	16.6 -/+	8.6 -/+	8.9 +/-	20.2 +/-	N/A	6.6 -/+	2.9 -/+	26.3 -/+
Mean temperature of wettest quarter (°C)	10.8 +/-	4.1 +/-	N/A	8.1 +/-	3 +/-	1.4	N/A	5 +/-	4.7 +/-	N/A
Mean diurnal range (°C)	N/A	23.7 +/-	7.7 +/-	22.8 +/-	14.6 +/-	3.4	N/A	31.7 +/-	29.3 +/-	9.2 +/-
Minimum temperature of coldest month (°C)	N/A	4.2 +/-	N/A	N/A	3.7 +/-	N/A	N/A	N/A	3.1 -	4.3 +/-
Precipitation in driest month (mm)	N/A	N/A	N/A	N/A	6.2 +/-	N/A	N/A	N/A	3.8 -	N/A
Annual mean temperature (°C)	N/A	N/A	15.6 -	N/A	N/A	3.8 -	N/A	N/A	N/A	30.4 -
Savanna (%)	N/A	N/A	25.3 +	N/A	N/A	20.5 +	32.2 +	2.4 -	N/A	N/A
Number of forest patches	N/A	N/A	1.6 -/+	N/A	N/A	N/A	0.1	N/A	N/A	N/A
Floodplain forest (%)	N/A	N/A	N/A	N/A	N/A	N/A	5.7 -	N/A	N/A	N/A
Precipitation seasonality	N/A	N/A	N/A	N/A	6.2 -	N/A	N/A	N/A	N/A	N/A
Patch richness	N/A	N/A	N/A	N/A	2.4 +/-	1.2 +	N/A	N/A	N/A	N/A
Pond (%)	N/A	N/A	1.6 -	N/A	2.5 -	N/A	N/A	N/A	N/A	N/A
Conifer forest (%)	N/A	N/A	N/A	N/A	2 -	N/A	N/A	N/A	N/A	N/A
Upland (%)	N/A	N/A	N/A	N/A	N/A	N/A	37.2 +	N/A	N/A	N/A
Meadow (%)	N/A	N/A	N/A	N/A	N/A	N/A	11.3 -	2.9	N/A	N/A
Swamp forest (%)	N/A	N/A	N/A	N/A	N/A	6.8 -/+	1.8 -	N/A	2.7 -	N/A
Mean Temperature of Warmest Quarter (°C)	N/A	N/A	N/A	N/A	N/A	6.9 -	N/A	N/A	N/A	N/A

Table 3.3. The maximum test sensitivity plus specificity logistic threshold (MSS) and percentage of suitable and unsuitable habitat for all best final models for total activity, individual species, open/forested guilds, and WNS/no WNS groups.

Model	MSS	Suitable Habitat (%)	Unsuitable Habitat (%)
Combined	0.3334	23.03%	76.97%
Big brown bat	0.3585	15.64%	84.36%
Eastern red bat	0.3082	21.21%	78.79%
Hoary bat	0.3747	24.14%	75.86%
Silver-haired bat	0.3564	21.21%	78.79%
Evening bat	0.2514	6.07%	93.93%
WNS	0.6862	1.18%	98.82%
No WNS	0.3540	22.65%	77.35%
Open	0.3558	23.43%	76.57%
Forested	0.2939	17.50%	82.50%

Table 3.4. Results of Maxent models' "Area Under the Curve" ROC analysis for the best fitting model for each species and guild using 2021 bat data from stationary points and transects and current and predictive climate models using 30 arc sec bioclimatic data from CHELSA Test AUC was calculated from random points removed from analysis (10% of total points). Values closer to 1 indicate a more discriminatory model. EPFU= Big brown bat, LABO= eastern red bat, LACI= hoary bat, LANO= silver-haired bat, NYHU= evening bat. Models included were a. current conditions (1979-2013) and models using 4 future scenarios for 2050. The future scenarios were low emissions/2.6 (b.), stabilization before 2100/4.5 (c.), stabilization after 2100/6.0 (d.), and high emissions/8.0 (e.).

a.

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.823	0.841	0.880	0.824	0.827	0.916	0.873	0.816	0.883	0.812
Test AUC	0.792	0.817	0.821	0.775	0.743	0.852	0.845	0.791	0.842	0.779

b.

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.771	0.806	0.848	0.749	0.856	0.952	0.886	0.807	0.914	0.795
Test AUC	0.773	0.784	0.789	0.738	0.851	0.927	0.838	0.790	0.880	0.788

c.

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.791	0.808	0.875	0.788	0.879	0.942	0.836	0.821	0.904	0.757
Test AUC	0.773	0.809	0.850	0.776	0.818	0.903	0.766	0.813	0.893	0.739

d.

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.762	0.765	0.804	0.739	0.816	0.855	0.746	0.769	0.987	0.871
Test AUC	0.753	0.750	0.851	0.739	0.832	0.776	0.768	0.785	0.860	0.838

e.

	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Forested	Open
Training AUC	0.743	0.754	0.794	0.770	0.8002	0.862	0.796	0.779	0.779	0.758
Test AUC	0.750	0.709	0.614	0.726	0.7011	0.815	0.777	0.753	0.753	0.758

Table 3.5. Percentage of contribution of each bioclimatic variable to each best fitting 2021

Maxent species distribution model within the Oak Openings Region using 30 arc sec bioclimatic data from CHELSA. EPFU= Big brown bat, LABO= eastern red bat, LACI= hoary bat, LANO= silver-haired bat, NYHU= evening bat. Any variables saying N/A were not run for that specific model. “+” indicates variable associated with activity increase, “-“ indicates variable associated with activity decrease, “-/+” indicates decrease in activity followed by increase, and “+/-“ indicates variable associated with initial increase in activity followed by decrease. No symbol means no increase or decrease with change in variable. Models included were a. current conditions (1979-2013) and models using 4 future scenarios for 2050. The future scenarios were low emissions/2.6 (b.), stabilization before 2100/4.5 (c.), stabilization after 2100/6.0 (d.), and high emissions/8.0 (e.).

a.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
Annual precipitation (mm)	11.6 +/-	19.6 +/-	37.4 +/-	37.4 /+	18.2 +/-	40.8 +/-	15.9 +	10.3 - /+	11.7 - /+	35.2 +/-
Mean temperature of wettest quarter (°C)	19 +/-	14.8 +/-	2.4 +/-	25.9 +/-	5.5 +/-	4.2 +/-	7.6 -	21.8 +/-	17.4 +/-	2.6 +/-
Mean diurnal range (°C)	49.1 +/-	37.6 +/-	14.3 +/-	22.8 +/-	37.3 +/-	9.8 +/-	0	50.4 +/-	50.3 +/-	14.9 +/-
Minimum temperature of coldest month (°C)	3.5 +/-	10.1 +/-	3.9 +/-	4.5 +/-	15 +/-	1 +/-	0.5 -	5.1 +/-	6.8 +/-	4 +/-
Precipitation in driest month (mm)	15.9 -/+	14.4 - /+	7 +/-	14.3 - /+	7.2 -/+	8.5 +/-	3.3 +	11.6 -	9.9 - /+	9.2 -
Annual mean temperature (°C)	0.9 +/-	3.5 +/-	34.8 -	1.6 +	16.6 +/-	35.7 -	72.6 -	0.8 +/-	3.6 +/-	34.1 -

b.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
Annual precipitation (mm)	13.5 -/+	17.1 -	36.7 - /+	14.2 +	28.5 +/-	21.1 +	0	17.7 +/-	13.6 +/-	35.2 +/-
Mean temperature of wettest quarter (°C)	28 +/-	40.9 -	9.1 -/+	14.7 - /+	27.9 -/+	20.7 -/+	0.5 +	21.8 - /+	25 -/+	14.2 -/+
Mean diurnal range (°C)	41.9 +/-	20.6 +/-	26.5 -	26 +/-	21.4 -/+	34.6 -	50.4 -	28.6 +/-	26.4 +/-	35.3 +
Minimum temperature of coldest month (°C)	12.8 -/+	11.9 - /+	14.4 +/-	11.4 +/-	16.4 +/-	4.9 +/-	1.2 -	7.9 +/-	0.9 +/-	14.2 +/-
Precipitation in driest month (mm)	1.6 +	0.8 +	7.3 +	2.5 -	0.7 +	20.7 +	1.3 -	1 -	0.9 -	2.6 +
Annual mean temperature (°C)	2.1 -	8.6 -	6 -	31.3 +/-	5 +/-	7.8 -	46.7 -	23.1 -	27 -	5.9 -

c.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
Annual precipitation (mm)	14.4 +/-	13.5 -	13.1 +	20.7 -	20.8 -	11.8 +/-	0.7 +	15.8 +/-	20.5 -	21.6 +
Mean temperature of wettest quarter (°C)	28+/-	40 -	20.6 -	15 -	3 +/-	38.2 -	12.9 -	28.9 -	26.2 -	15.4 +/-
Mean diurnal range (°C)	40.5 +/-	27.1 +/-	29.8 +/-	46.7 +/-	8.8 +	21.4 +/-	42.2 -	28 +/-	30 +/-	34 +/-
Minimum temperature of coldest month (°C)	12.5 +/-	12.1 -/+	19 +/-	12.3 -/+	27.3 +/-	5.4 +/-	4.6	19.3 +/-	16.2 -/+	11.6 +/-
Precipitation in driest month (mm)	1.4 +	1.4 +	6.7 +	1.7 +	0.8 +	5.1 +	1.7 -	1.3 -	1.3 +	1.3 +/-
Annual mean temperature (°C)	3.2 -	27.1 -	10.9 -	3.6 -	9 -	18.1 -	37.9 -	6.5 -	5.8 -	6.5 -

d.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
Annual precipitation (mm)	61.1 +/-	70.3 +/-	33.3 +/-	46.2 -/+	47.3 +/-	35.4 +/-	69.4 -	57.3 +/-	61.7 +/-	47.6 +/-
Mean diurnal range (°C)	30 +/-	16.8 +/-	10.9 -	42.7 +/-	32.6 +/-	30.1 -	27.5 -	25.7 +/-	26.6 +/-	10.2 -
Minimum temperature of coldest month (°C)	6.6 -	10 -	47.2 +/-	9.4 +/-	18.4 +/-	20.3 +/-	2.9 -	13.8 +/-	9.3 +/-	32.4 +/-
Precipitation in driest month (mm)	2.3 +	2.9 +	8.7 +	1.7 -	1.7 +	14.1 +	0.3 -	3.2 +	2.4 +	9.7 +

e.

Environmental Variable	Combined	EPFU	LABO	LACI	LANO	NYHU	WNS	No WNS	Open	Forested
Annual precipitation (mm)	52.7 +/-	25.9 +/-	49.5 +/-	63.6 +/-	38.5 +/-	30.9 +/-	0.2 -	58.9 +/-	62 +/-	43.1 +/-
Mean temperature of wettest quarter (°C)	21.7 +/-	31.7 +/-	32.1 -	16.7 +/-	36.3 +/-	7.2 -	49.1 -	19.9 +/-	16.6 +/-	34.3 -
Mean diurnal range (°C)	12.5 +/-	25.5 +/-	3.9 -	10.7 +/-	20.3 +/-	8.6 -	35.5 -	11.5 +/-	14.1 +	6.6 -
Minimum temperature of coldest month (°C)	11.1 +/-	7.8 +/-	4.9 +	6.4 +/-	2.1 +/-	20.1 -	15.2 -	7.7 +/-	5.9 +/-	5.6 +/-
Precipitation in driest month (mm)	0.6 -	3.1 -	2.9 +	0.3 -	2.3 +	20 +	0	0.4 +	0.9 +	4 +
Annual mean temperature (°C)	1.3 -	6 -	6.6 -	2.3 -	0.6 +	13.2 -	0	1.5 +	0.5 +	6.5 -

Table 3.6 The maximum test sensitivity plus specificity logistic threshold (MSS) and percentage of suitable and unsuitable habitat for current conditions and four future Representative Concentration Pathway (RCP) scenarios for evening bats (*Nycticeius humeralis*)

Scenario	MSS	Suitable Habitat (%)	Unsuitable Habitat (%)
Current	0.3495	9.82	90.18
RCP 2.6	0.3568	9.73	90.27
RCP 4.5	0.2658	14.63	85.37
RCP 8.5	0.5112	9.80	90.20

Figures

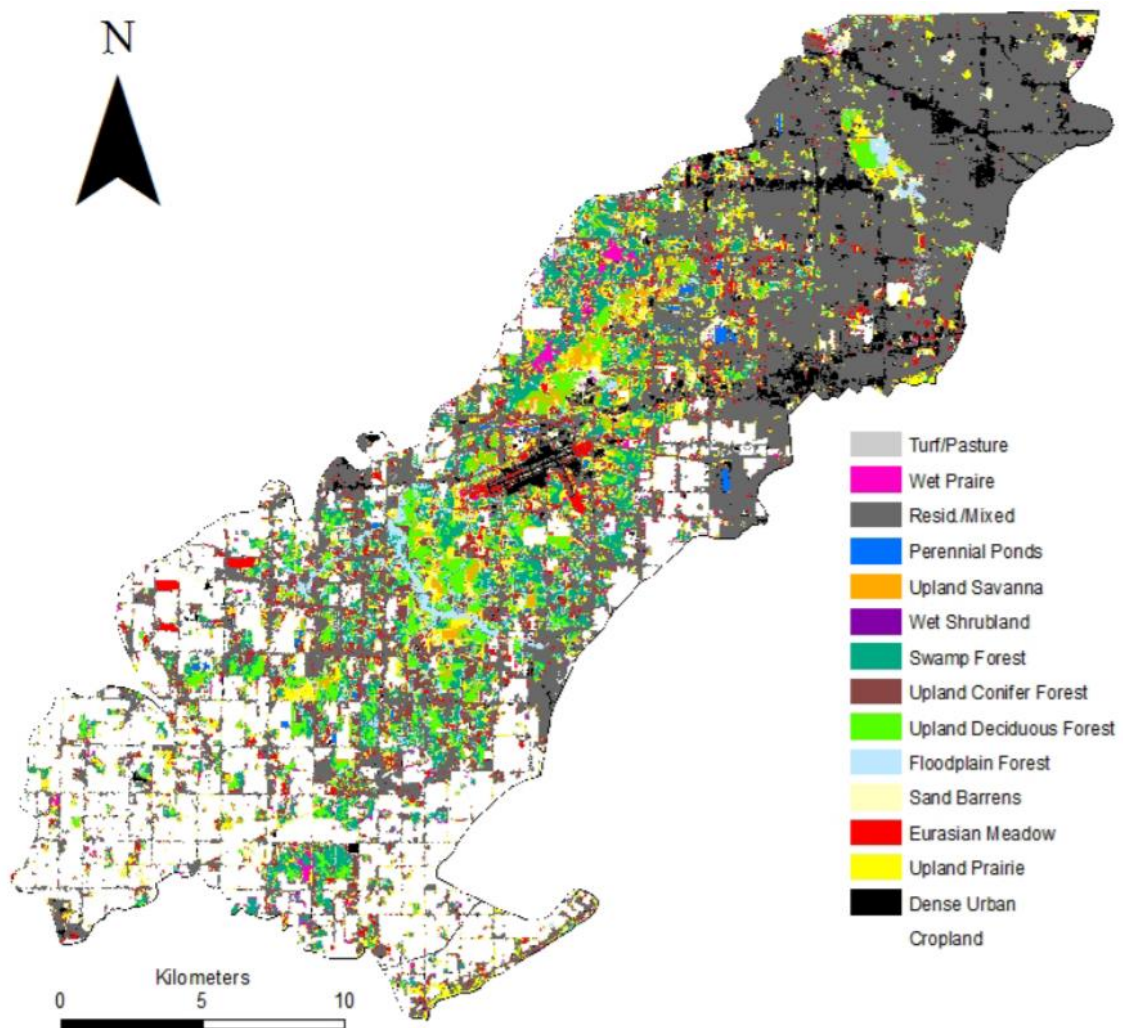


Figure 3.1. The Oak Openings Region land cover map of northwestern Ohio using the Brewer-Vankat boundary (Martin and Root 2020a).

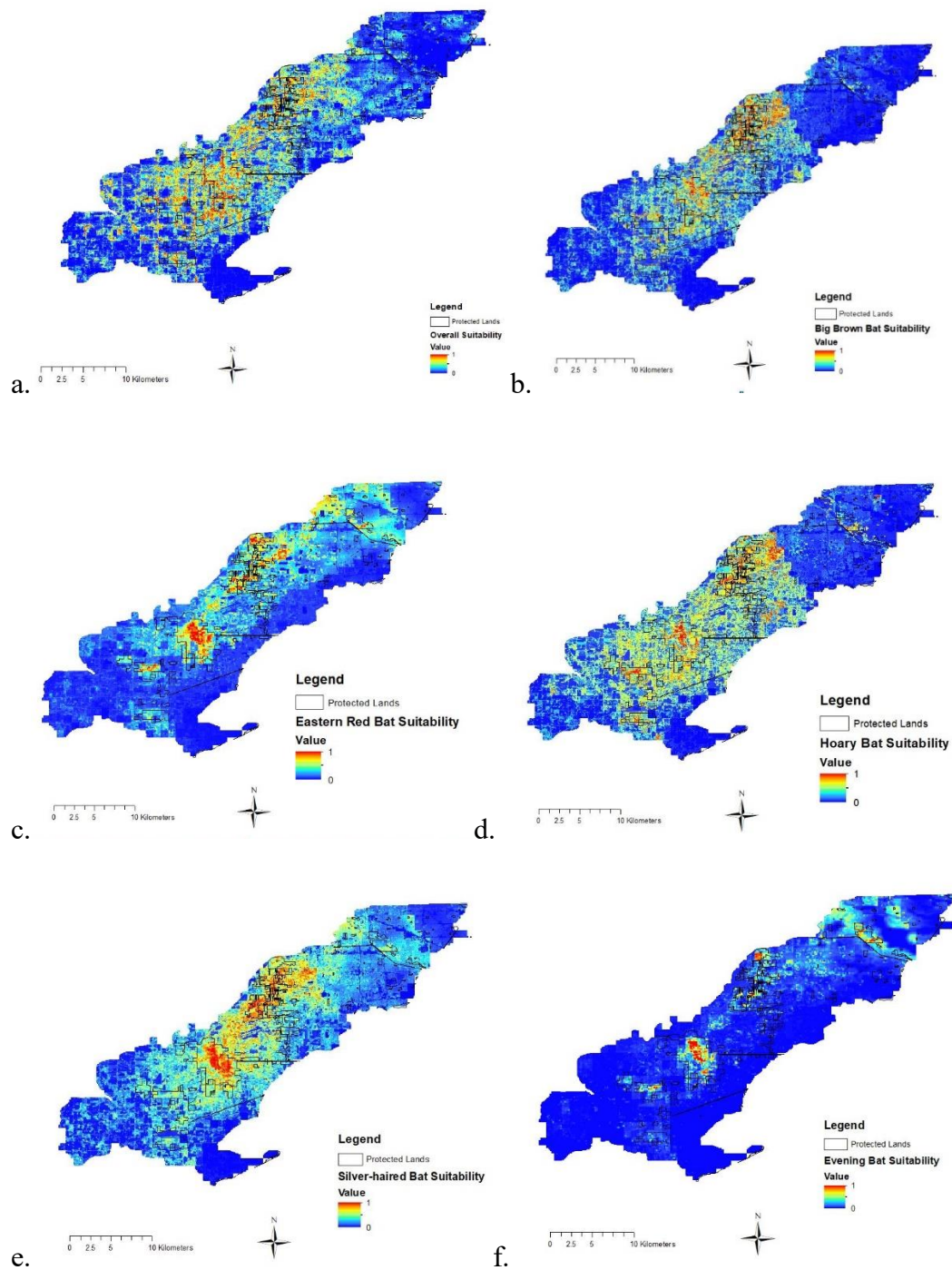


Figure 3.2. Continuous Maxent model results for (a.) total bat activity individual bat species in the Oak Openings Region of Northwest Ohio. Species modelled were the (b.) big brown bat, (c.) eastern red bat, (d.) hoary bat, (e.) silver-haired bat, and (f.) evening bat. Protected parks are outlined in black.

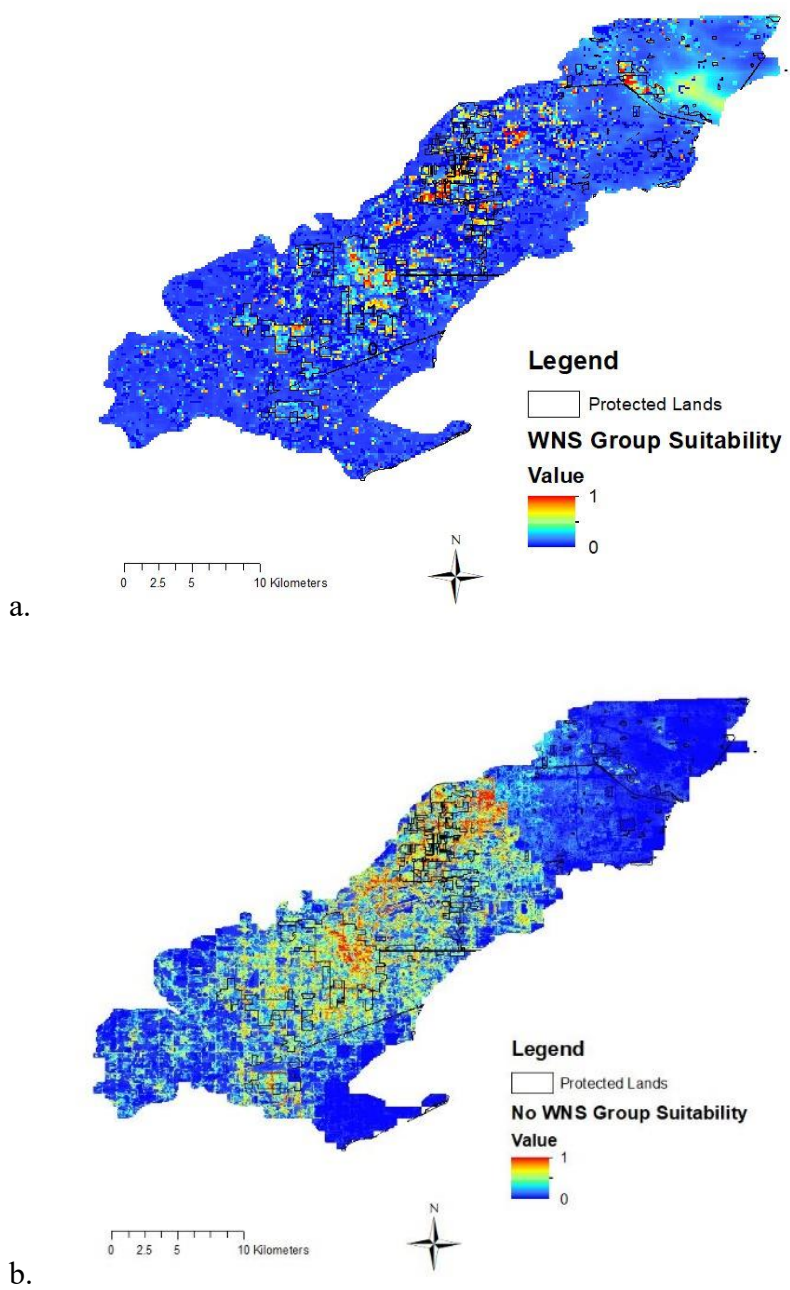


Figure 3.3. Continuous Maxent model results for bat species affected by WNS (a.) and not affected by it (b.) in the Oak Openings Region of Northwest Ohio. Protected parks are outlined in black.

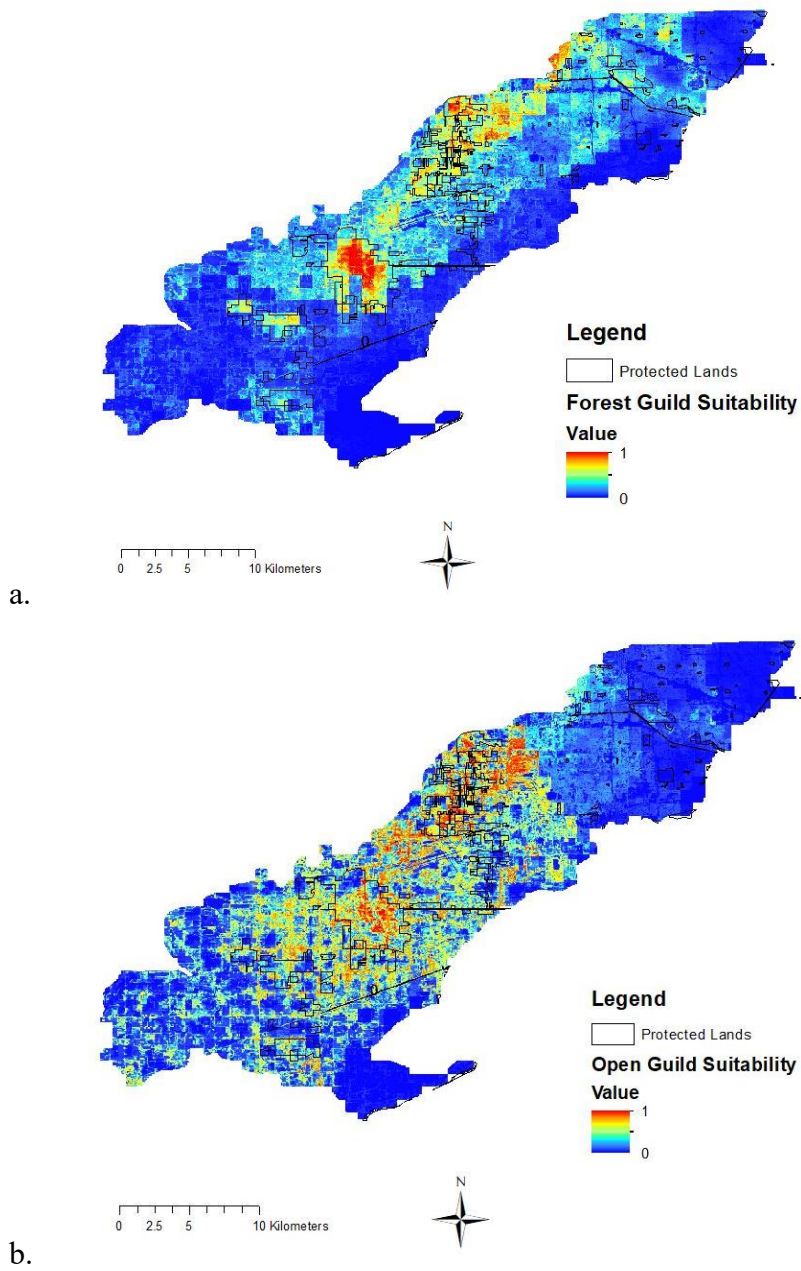


Figure 3.4. Continuous Maxent model results for forested (a.) and open (b.) guilds in the Oak Openings Region of Northwest Ohio. Protected parks are outlined in black.

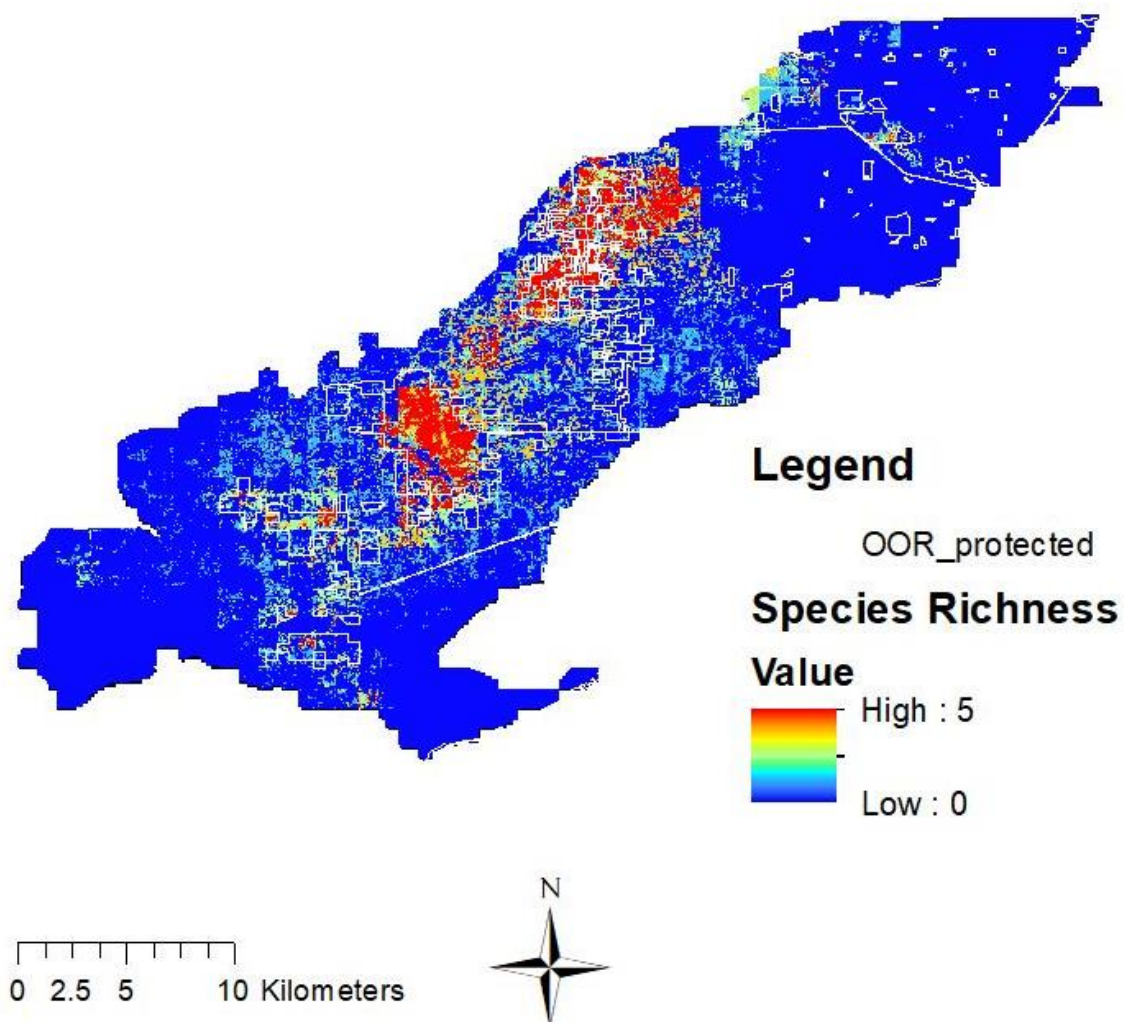


Figure 3.5. Species richness map for the Oak Openings Region of Northwest Ohio. Protected parks are outlined in white.

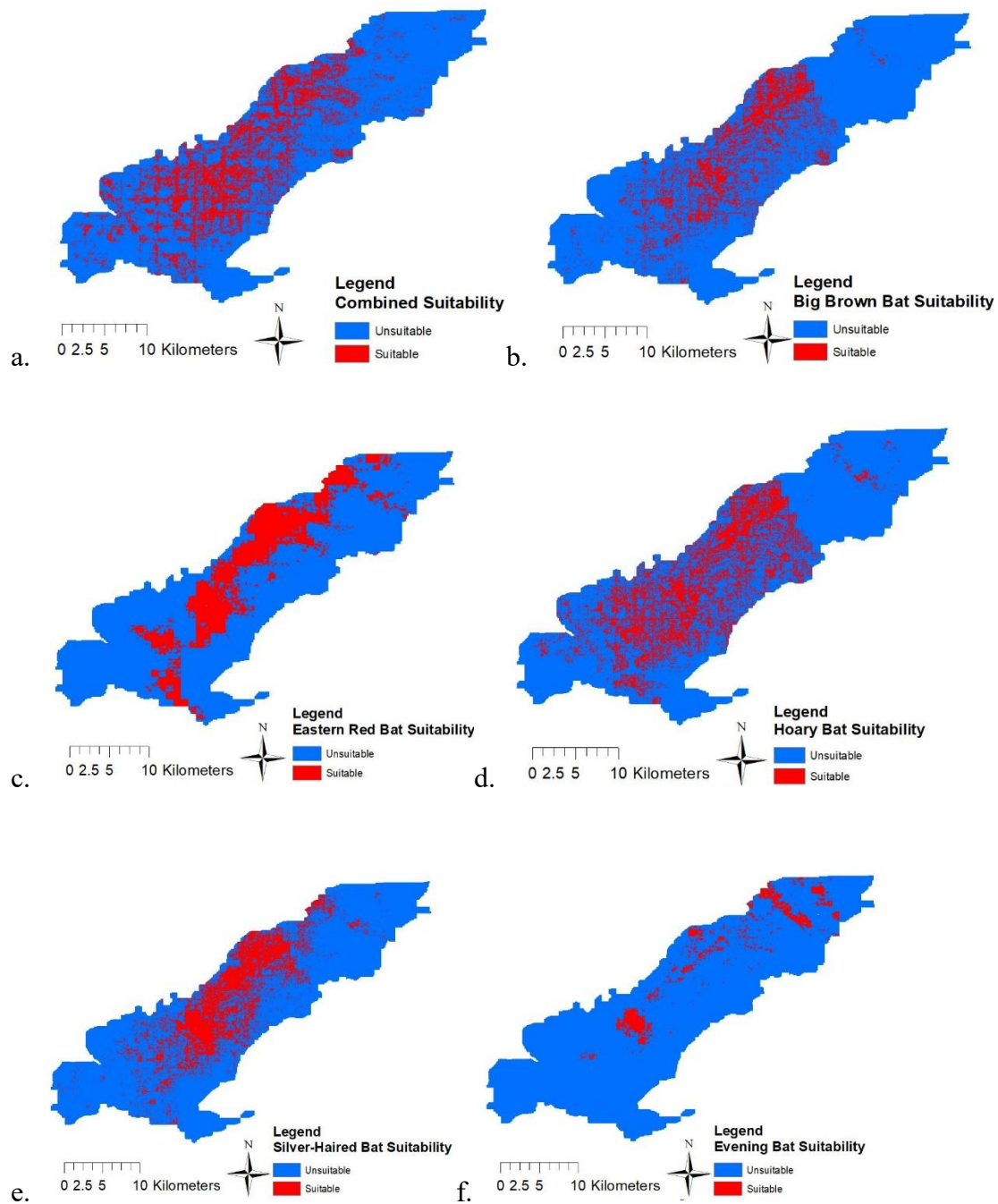


Figure 3.6. Binary Suitability maps for (a.) total activity and (b.) big brown, (c.) eastern red, (d.) hoary, (e.) silver-haired, and (f.) evening bats.

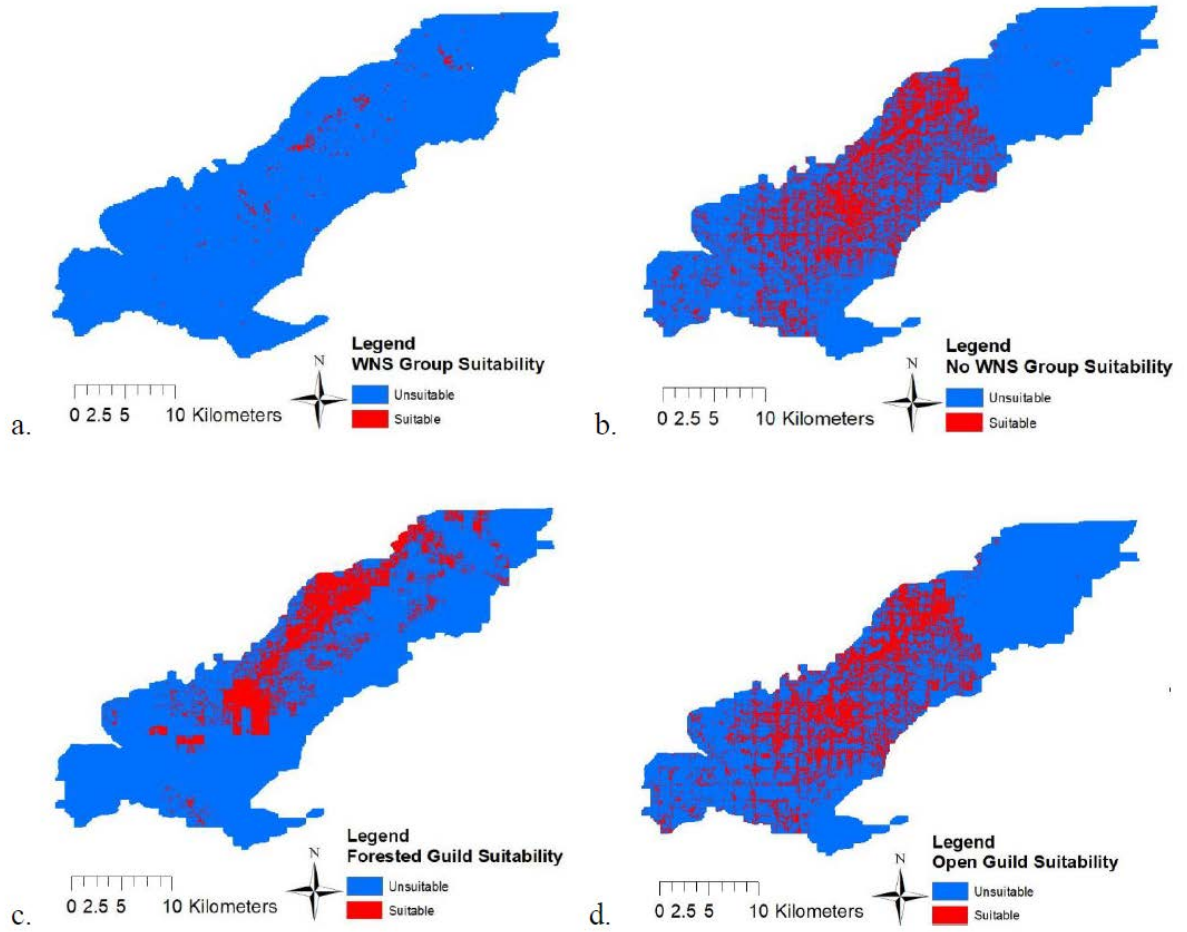


Figure 3.7. Binary Suitability maps for the (a.) WNS group, (b.) no WNS group, (c.) forest guild, and (d.) open guild.

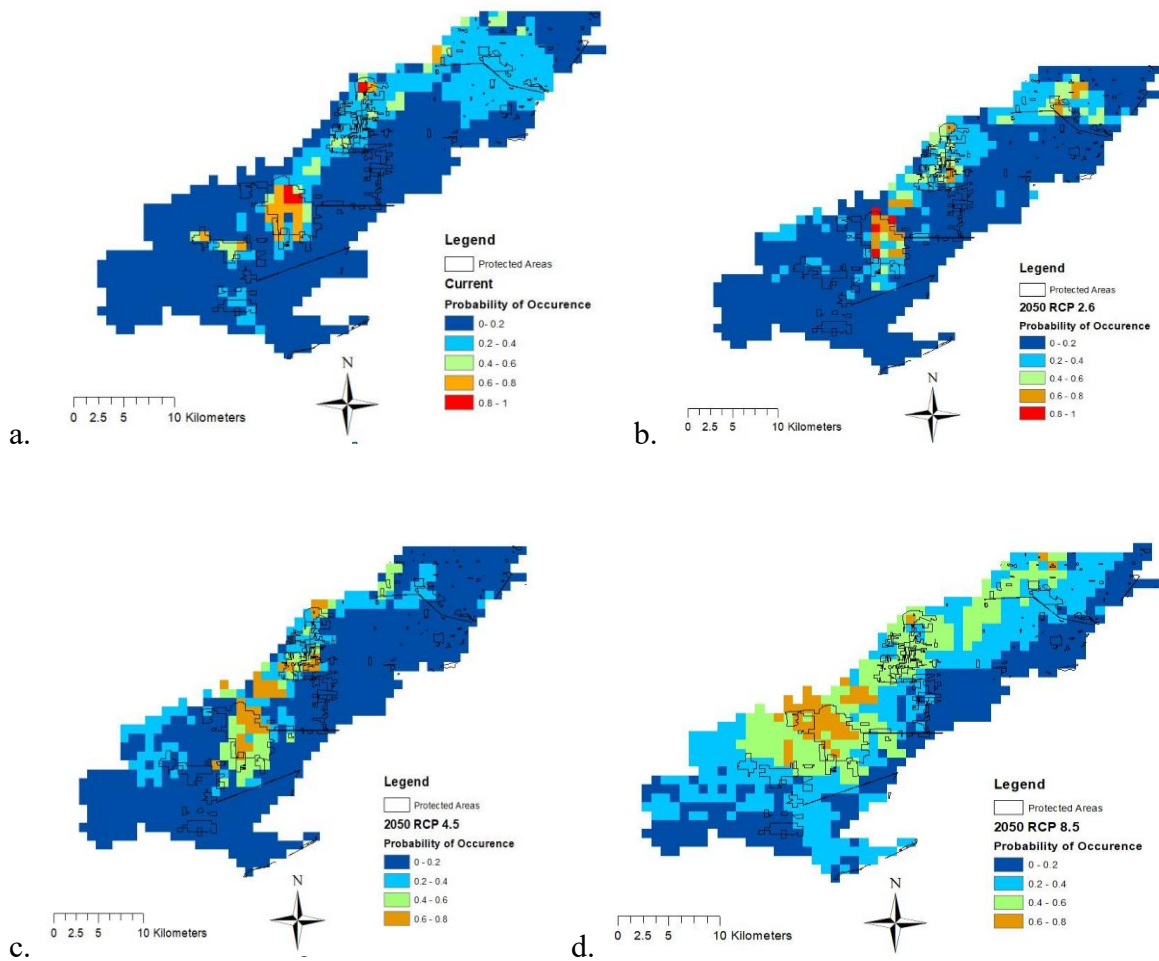


Figure 3.8. Climatic habitat suitability continuous probability maps for evening bats for four different scenarios: (a) Current (1979-2013), (b) 2050 Representative Concentration Pathway (RCP) 2.6, (c) 2050 RCP 4.5, (d) 2050 RCP 8.5. Color changes indicate probability of suitability, with blue indicating low to no probability and red indicating high probability.

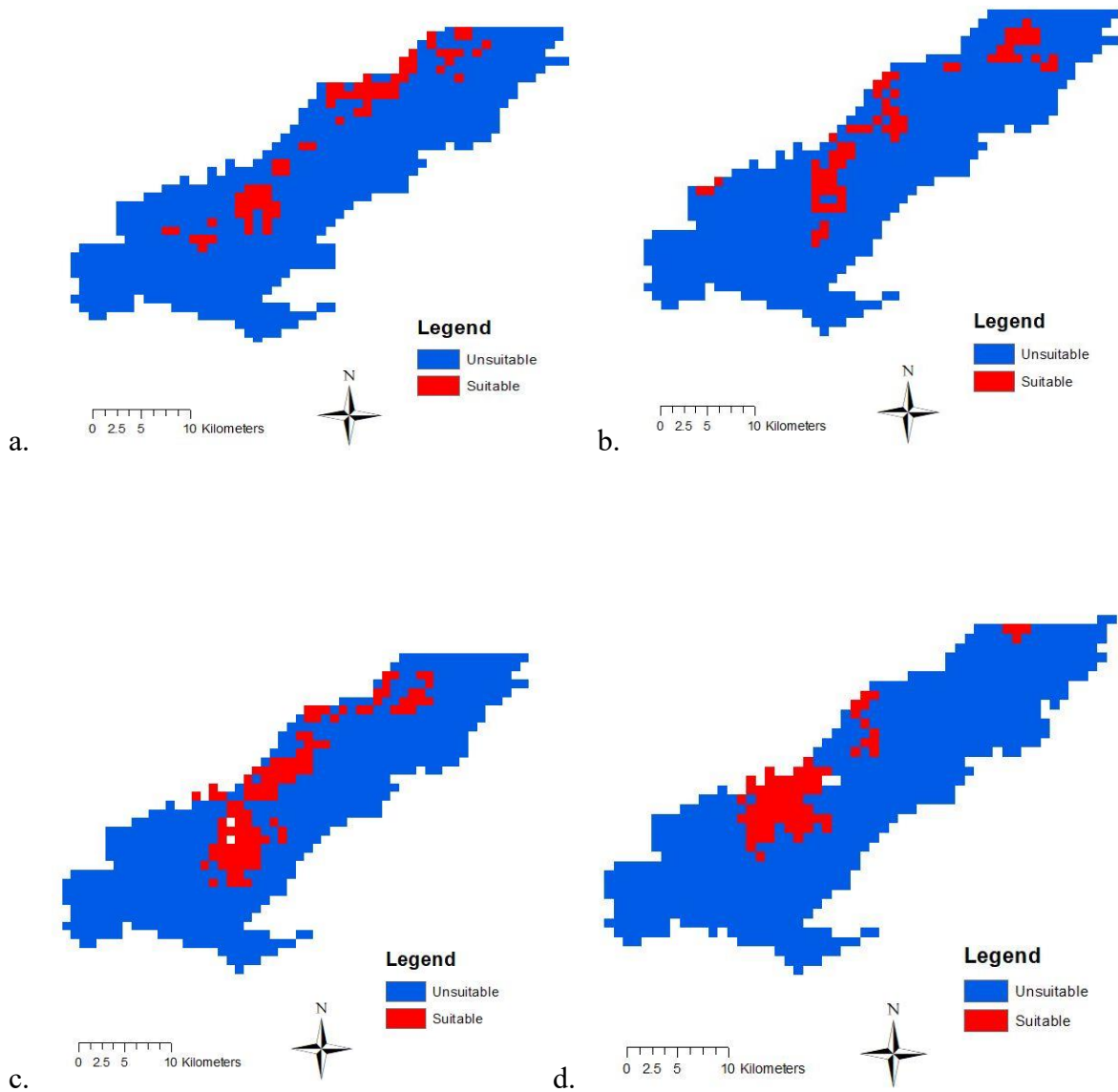


Figure 3.9. Binary climate suitability maps for evening bats for four different scenarios: (a) Current (1979-2013), (b) 2050 Representative Concentration Pathway (RCP) 2.6, (c) 2050 RCP 4.5, (d) 2050 RCP 8.5.

CONCLUSIONS

In my dissertation, I explored temporal changes in bat activity and species richness and what habitat factors had the biggest impact on bat activity, species richness, and habitat suitability. I examined these factors with a combination of field surveys, remote sensing data, and species distribution modeling. My first chapter examines how bat species richness and activity have changed in the Oak Openings Region of Northwest Ohio over the past decade. Using volunteer collected data from 2011-2021, I found that overall bat activity, species richness, and activity for multiple species decreased since 2011. However, overall activity and that for most individual species increased since 2019. My results demonstrate changes in overall bat activity detected over the last decade and notable community shifts due to changes in individual species activity. These year-to-year differences may explain some of the differences in short and long-term results. It also shows the value of volunteer collected data for recording temporal changes in bat activity.

In the second chapter, I examined what point, local, and landscape scale habitat factors have the most impact on bat activity and species richness. Data were collected through a combination of field surveys, ArcGIS, and FRAGSTATS. Bat activity and species richness were significantly higher at stationary points (e.g. within parks) than along transects (e.g. along roads), even when accounting for recording time. Higher bat activity and species richness were associated with higher percentages of sand barrens, savanna, ponds and upland prairie, higher canopy height, natural habitat along roads, more months with water present, and higher percent structural clutter 0-3 m. Bat activity and species richness were negatively associated with higher understory height, clutter from 3-6.5, and percent floodplain forest, conifer forest, and wet prairie. Patch richness was negatively associated with activity at stationary points, but positively associated with it along transects, while the opposite was true for percent cropland. Ideal bat

habitat would therefore have plenty of dry and open habitats such as savanna or sand barrens, a lack of mid-level clutter, tall trees, available water, and more undeveloped (i.e. untouched fields and forests) areas. My findings can be used by land managers to determine what habitat factors to prioritize for bat habitat.

In the third chapter, I created species distribution models to determine the areas of most suitable habitat for bats overall, individual species, open and forested guilds, and species affected and not affected by white-nose syndrome (WNS). Maxent was used to create models with habitat and environmental data. The most important factors in the best-fitting models were percent savanna, distance to agriculture, May NDVI, annual precipitation, mean diurnal range, and annual mean temperature, while upland forest was especially important for species affected by WNS. No groups had more than 25% of the available habitat considered suitable, with the WNS group able to use the least habitat. Protected areas were especially high in bat habitat suitability. Predictive models were also created using expected climate changes for 2050. In evening bat models (the single species models with the highest AUC), suitable habitat moved north and the most suitable areas decreased in suitability in the highest emission scenarios, but the amount of total suitable habitat didn't change. This chapter gives land managers a guide on which areas to prioritize for protection, as the highest suitability areas not currently protected should be focused on.

This work contributes to the current knowledge of spatial ecology and long-term monitoring of bats. The models created in chapter 2 and 3 can also be applied to other temperate regions as well and the importance of many of the same variables in prior studies supports the generalizability of my findings. Those managing bat habitats should focus on continuing to monitor bat calls, increasing savanna and tree cover, decreasing mid-level understory cover, and

increasing natural habitat along roads. This is especially important since urbanization and habitat fragmentation is continuing to increase.

APPENDIX A: SUPPLEMENTAL FIGURES

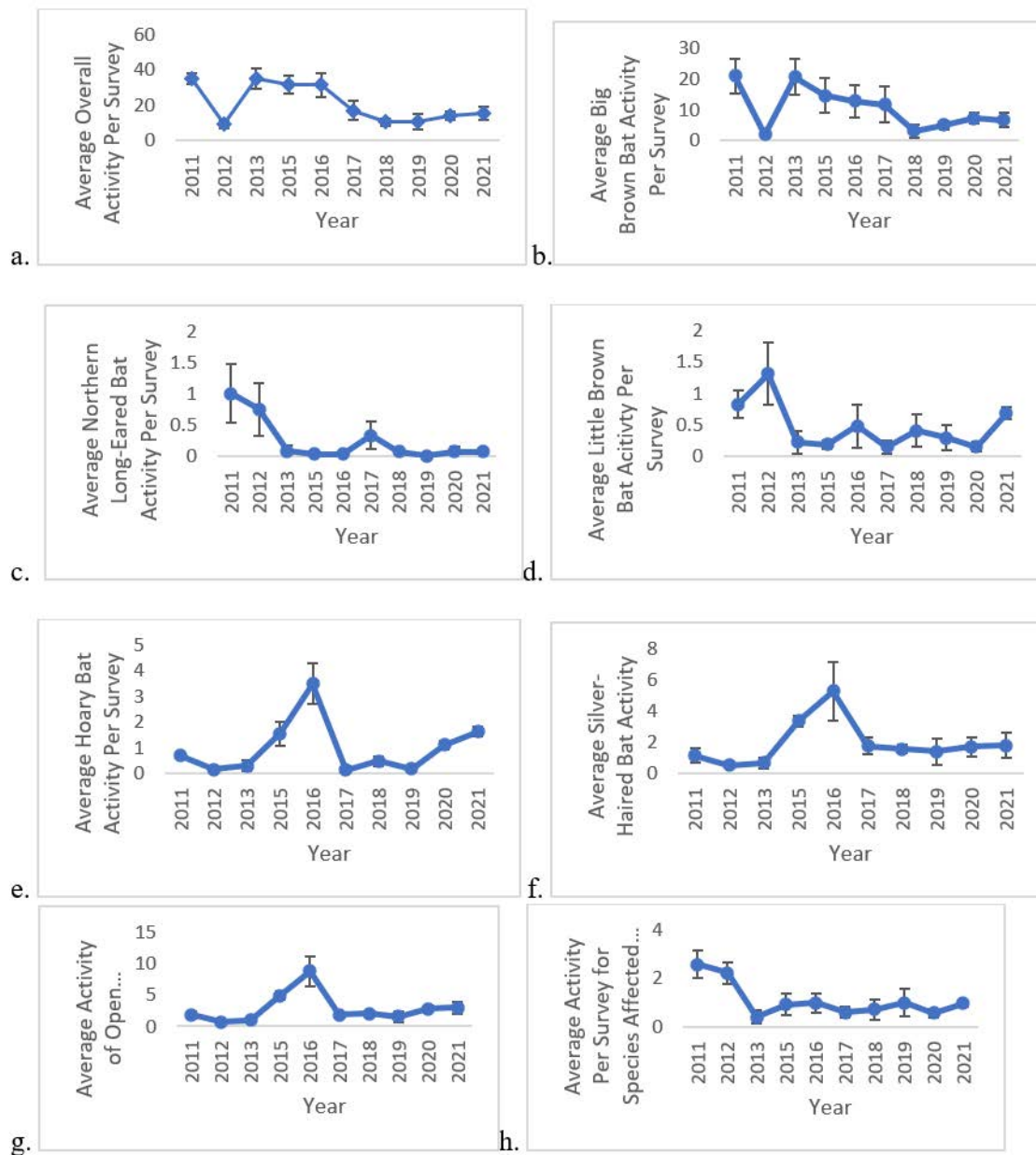


Figure 1.S1. Long term trends in a. average overall bat activity per volunteer survey, b. average big brown bat activity per volunteer survey, c. average northern long-eared bat activity per volunteer survey, d. average little brown bat activity per volunteer survey, e. average hoary bat activity per volunteer survey, f. average silver-haired bat activity per volunteer survey, g. average open guild species minus big brown bats per volunteer survey, and h. average species impacted most by white-nose syndrome per volunteer survey from 2011-2021. Error bars represent standard error. All the results graphed were significant.

APPENDIX B: SUPPLEMENTAL TABLES

Table 2.S1. AICc table for variables in best model for species richness at stationary points.

Variable	Rsquare	AICc
% Sand barrens in 500 m	0.422	331.488
% Savanna in 500 m	0.450	328.979
% Upland prairie in 500 m	0.486	327.121
Max. temperature °F	0.379	336.177
% Wet prairie in 100 m	0.468	328.135

Table 2.S2. AICc table for variables in best model for total activity at stationary points.

Variable	Rsquare	AICc
Understory height m.	0.450	280.782
% Deciduous forest in 500 m	0.514	273.500
% Floodplain forest in 500 m	0.490	275.792
% Cropland in 500 m	0.578	267,160
Max. temperature °F	0.597	265.352
% Wet prairie in 500 m	0.542	270.022
Patch richness in 500 m	0.371	291.391
Min % clutter in 3-6.5 m	0.556	269.517
Min. humidity %	0.276	302.666

Table 2.S3. AICc table for variables in best model for open guild at stationary points.

Variable	Rsquare	AICc
Understory height m.	0.503	287.029
% Deciduous forest in 500 m	0.541	281.795
% Floodplain forest in 500 m	0.446	292.873
% Sand barrens in 100 m	0.361	289.790
Min % clutter 0-3 m	0.574	279.429
% Wet prairie in 500 m	0.567	278.560
Patch richness in 500 m	0.477	289.576
Min % clutter in 3-6.5 m	0.599	276.392
Min. humidity %	0.276	314.103

Table 2.S4. AICc table for variables in best model for forest guild at stationary points.

Variable	Rsquare	AICc
Canopy height m.	0.075	788.528
% Upland prairie in 500 m	0.308	774.572
% Floodplain forest in 500 m	0.260	776.142
Mean area ha.	0.286	775.136
Maximum wind speed mph	0.189	780.259
Maximum barometric pressure	0.228	777.887
Max. humidity %	0.153	782.275

Table 2.S5. AICc table for variables in best model for species richness at transect points.

Variable	Rsquare	AICc
Canopy height m.	0.331	1314.30
% Savanna 250/500 m	0.287	1325.42
% Conifer forest in 250/500 m	0.301	1320.71
% Cropland in 250/500 m	0.254	1338.85
Min. temperature °F	0.149	1394.76
% Wet prairie in 500 m	0.319	1317.32
Patch richness in 500 m	0.294	1323.04
Avg % clutter in 3-6.5 m	0.315	1317.91
Avg % clutter in 0-3 m	0.270	1331.20
Months water present	0.324	1316.17
Min. barometric pressure	0.333	1315.05
Max. barometric pressure	0.339	1313.22
Habitat type	0.311	1318.62
% Ponds in 100 m	0.307	1319.14
% Upland prairie in 100 m	0.279	1327.74

Table 2.S6. AICc table for variables in best model for total activity at transect points.

Variable	Rsquare	AICc
Avg. % canopy cover	0.286	-36.139
% Floodplain forest in 250/500 m	0.288	-35.689
% Conifer forest in 250/500 m	0.249	-11.276
% Total forest in 250/500 m	0.217	-11.776
Max. temperature °F	0.274	-32.902
% Cropland in 250/500 m	0.265	-29.836
Avg % clutter in 3-6.5 m	0.182	5.413
Avg % clutter in 0-3 m	0.123	32.499
Max. humidity %	0.281	-35.449
M. of road in 250/500 m	0.227	34.921
Max. barometric pressure	0.239	-20.362
Habitat type	0.257	23.037
Number of habitat types in 250/500 m	0.155	17.729