

BATS, CITIES, AND TREES: THE RESPONSE OF MIDWESTERN BATS TO THE URBAN
FOREST GRADIENT

BY

SEAN MACLAINE OBROCHTA

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois Urbana-Champaign, 2024

Urbana, Illinois

Master's Committee:

Assistant Professor Joy O'Keefe, Adviser
Research Associate Professor T.J. Benson
Teaching Assistant Professor Sam Stickley
Assistant Professor Han Li, University of Nebraska at Omaha

ABSTRACT

The study of urban wildlife has grown within the past two decades. However, there are still significant gaps in our knowledge of the ecology of bats living in cities. Namely, we know very little about how urban bat assemblages respond to their environment across contrasting urban areas, as cities may have stark differences in vegetation and land use regimes. Variation in bat responses across cities, or “between-city differences,” has not been investigated in North America, as previous urban bat studies have been conducted at the scale of a single, large city. Additionally, few studies have sought to examine fine-scale responses of bats to LiDAR-derived tree metrics despite their demonstrated utility in quantifying canopy structure. We sought to fill these knowledge gaps through two research projects. The first was the Bats in Small Cities (BiSC) Project, a 36-city acoustic survey of urban areas in the Midwestern United States to ascertain how occupancy by different groups of bats is related to between-city differences. We also sought to overcome the large-city bias by focusing on smaller cities. We showed that for the big brown bat and silver-haired bat acoustic group, increasing local tree canopy cover within a 100-m buffer around our survey points strongly predicted occupancy; however, this local effect was more robust in urban areas with lower city-scale tree cover. Additionally, local hoary bat occupancy was lower in cities with higher city-scale tree cover. Together, our results show that bats respond differently to local habitat patches depending on habitat at the city-scale. We recommend more multi-city monitoring of urban bat activity and diversity using long-term, spatially distributed monitoring efforts, which would also capture temporal patterns.

In our second project, we placed acoustic monitoring devices on trees in the parks, forests, and neighborhoods of Champaign-Urbana, Illinois, to determine the effectiveness of LiDAR-derived metrics in predicting big brown bat and eastern red bat activity and documenting the bat species richness of the area. Both species responded positively to increasing horizontal canopy heterogeneity, defined as the standard deviation of the mean tree canopy cover, within a 50-m buffer around stationary survey points. However, this response depended upon interactions with other variables. For big brown bats, the positive effect of horizontal canopy heterogeneity was only significant within open park habitat or depended on the level of development within a 50-m buffer. For eastern red bats, the positive effect of horizontal canopy heterogeneity was only significant within forests. Additionally, we discovered that northern long-eared bats occur in the forests in the northeast part of the area. Modeling showed that northern long-eared bats were

more likely to occur farther from roads, but this effect was more intense in areas with lower canopy cover within a 500-m buffer. Monitoring a single urban area with stationary devices revealed that LiDAR-derived metrics quantifying tree structure are informative in predicting urban bat response at a fine scale and that the Champaign-Urbana area is home to a diversity of bat species, including the endangered northern long-eared bat. We recommend future experimental studies testing bats' responses to manipulated canopy heterogeneity in urban areas. Overall, we conclude that trees are crucial for supporting bat activity and occupancy in urban areas throughout the Midwest, and this emphasizes the importance of maintaining urban tree cover to support bat conservation. We recommend further study that investigates how bats respond to applied urban forestry management practices and also recommend future study examining urban bat ecology at a continental scale, using multi-city approaches to examine regional differences in bat responses to urbanization.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Joy O’Keefe, for guiding me throughout my time as a master’s student. Dr. O’Keefe introduced me to the world of bat research, and she was incredibly understanding while I bounced from research idea to research idea. I couldn’t have asked for a better mentor! I would also like to thank my committee members Dr. Han Li, Dr. T.J. Benson, and Dr. Sam Stickley for regularly meeting with me as I formulated my research methods and providing excellent advice. I also could not have successfully completed my thesis without the constant support of my lab colleagues: Reed Crawford, Dr. Elizabeth Beilke, Katie Fitzgerald, James Cox, Dr. Andrew Bennett, Josie Hoppenworth, Dr. Clarissa Starbuck, Melissa Bowman, Nicole Dobrosky, Katrina Cotten, and Johnny Baakliny. They helped me build so many different skills in stats, R coding, bat handling, and presentation making, and I am a more well-rounded scientist now because of it. I would also like to thank Johnny, as well as Joaquin Acevedo, Uriah Elliot, and Colin Dobson for working as technicians on my project. The data used in this thesis could not have been collected without their hard work! Thank you as well to Isabella Hubrich for volunteering to help me with acoustic deployments. I also would like to thank the NRES Support Staff, particularly Lisa and Jordyn for their help in shipping out detectors to Bats in Small Cities volunteers. I would also like to thank Karen for helping me throughout the formatting process.

I am immensely grateful to all the wonderful partners and collaborators who helped make this project happen. The City of Urbana and the Urbana Park District, the City of Champaign’s Public Works Department and Park District, and the University of Illinois at Urbana-Champaign all permitted me to collect data on their land and were incredibly helpful through the process. I would like to extend my warmest thanks to all the people of Urbana and Champaign who gave me permission to put bat detectors in front of their houses. I would also like to thank all the residents of the Holcomb and Raintree Woods neighborhoods for allowing me on their property to do the monitoring. I would like to thank the United States Department of Agriculture for funding my research through the McIntire-Stennis Grant, and for the NRES department at UIUC for providing my project with funding through the Graduate Student Research Improvement Award.

I thank my family for always supporting me through thick and thin. My mom, Connie, and late father, Wally, nurtured my love for wildlife from a very young age and did everything

they could to support my education so that I could end up where I am now. I will be forever grateful they took me to the nature center whenever they could! My siblings, Pat and Carleigh, have sent me many funny bat-related memes since I became a bat researcher, and they never cease to make me laugh! I want to thank my dog, Pistachio, for giving me an excuse to go for walks while I was glued to the computer doing analysis. Lastly, I want to thank Kala, the love of my life. Words cannot do justice at describing how much work she has put in the last two years supporting me, but I will do my best! After a year of long drives back and forth from Chicago and Urbana, while completing nursing school, she moved across the state for me. She's lifted me up when I was down, and she put up with me spending long nights writing my thesis and catching bats in the midst of her working 12-hour shifts. I am sure she is just as excited for me to be done with this thesis as I am!

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION	1
CHAPTER 2: URBAN BATS RESPOND TO LOCAL AND CITY-WIDE TREE COVER IN THE MIDWESTERN U.S.	6
Introduction.....	6
Methods.....	10
Results	30
Discussion.....	47
CHAPTER 3: URBAN BATS RESPOND TO FINE-SCALE HORIZONTAL CANOPY HETEROGENEITY	54
Introduction.....	54
Methods.....	58
Results	75
Discussion.....	97
CHAPTER 4: SUMMARY	105
LITERATURE CITED.....	107
APPENDIX A: SUPPLEMENTAL TABLE	127

CHAPTER 1: GENERAL INTRODUCTION

Bats live in cities throughout the world, bringing them into close proximity to people. Insectivorous bat species dwelling in cities benefit rural- and urban-residing humans by eating disease vectors such as mosquitos and preventing crop damage from other pests (Aguilar et al. 2021, Russo et al. 2022), with some evidence of top-down control of insect populations by bats (Villarroya-Villalba et al. 2021). However, the true magnitude of ecosystem services provided by bats in urban areas is hardly known. In contrast to ecosystem services, human-bat conflicts arise when both share living space, as bats sometimes act as disease vectors (Melaun et al. 2014). Urbanization has also been generally associated with fewer bats and lower bat diversity (Moretto and Francis 2017), resulting in fewer ecosystem services provided by bats (Brasileiro et al. 2022). With a better understanding of urban bat ecology, we can find ways to mitigate conflict and promote positive ecosystem services that bats may provide.

Despite the negative effect of human activity on bat populations in general, some bat species survive, and perhaps even thrive, in urban areas (Russo and Ancillotto 2015), and even imperiled bat species occur in cities (Thorne et al. 2021, Hernández-Brito et al. 2018). While cities have been heavily altered by humans, the presence of bats in cities suggests that urban areas offer roosting and foraging spaces that some bat species can exploit (Russo and Ancillotto 2015). Urban-associated species like the big brown bat (*Eptesicus fuscus*) often roost in human-built structures like house attics (Whitaker and Gummer 1992). For opportunistic roosters, cities may provide more abundant (Brigham 1991) and higher quality (Lausen and Barclay 2006) roosting habitat than in their natural environments. However, cities also harbor lower insect diversity and abundance (Fenoglio et al. 2021). As all bats in the temperate regions of North America are insectivores, there is a possible tradeoff between prey and roost availability in cities (Avila-Flores and Fenton 2005). Bats' ability to fly great distances also means that some bats may use city buildings for roosting and then commute to other areas to forage, though this is still an open question (Menzel et al. 2001). Tree-dwelling species also live in urban areas, roosting in trees in woodlots and residential areas (e.g., Mager and Nelson 2001).

While cities may have some habitat features attractive to bats, high-traffic roads act as barriers for commuting bats (Bennett and Zurcher 2013), and the artificial noise and light of cities negatively impact bats (Lehrer et al. 2021, Hale et al. 2015, Li and Wilkins 2022). Most urban bat research has found lower diversity and abundance in urban areas (Moretto and Francis

2017). While threatened species may occur in urban areas, the presence of large tracts of natural areas within the urban matrix, like forests, may be required to maintain their populations (Thorne et al. 2021). Additionally, it is generally unknown whether living in cities provides fitness advantages or disadvantages for bats and whether cities act as sources or sinks for bat populations (Russo and Ancillotto 2015, Threlfall and Jung 2023). Evidence suggests that urban bats roosting in dense aggregations in artificial roosts incur lower reproductive success and poorer body condition than bats in natural roosts (Coleman and Barclay 2011a), and both artificial- and natural-roosting species in urban areas can be exposed to introduced predators like cats (Vlaschenko et al. 2019) and parakeets (Tella et al. 2020). Overall, though, we know little about how cities are impacting bat conservation at large and whether they are ecological traps (Russo and Ancillotto 2015) or key habitats supporting populations.

Questions surrounding urban bat ecology and conservation are particularly important in North America as bats on the continent are experiencing population declines due to the anthropogenic threats of habitat loss, wind turbine fatalities, and human-mediated disease transmission (Park 2015, Romano et al. 2019, Frick et al. 2016). White-nose syndrome, a fungal disease likely brought from Europe through human action, has decimated little brown bat (*Myotis lucifugus*), northern long-eared myotis (*Myotis septentrionalis*), Indiana bat (*Myotis sodalis*), and tricolored bat (*Perimyotis subflavus*) populations across North America (Frick et al 2016), while other species such as big brown bats appear to be unaffected (Frank et al. 2014). Additionally, urban development and population density are increasing concurrently with reductions in urban tree cover in North America (Nowak and Greenfield 2020), but it is unknown whether this may drive further declines.

The response of bats to urbanization may be dependent on landscape-scale factors. It is possible that some cities provide better foraging habitats for bats than the surrounding landscape, e.g., when the area surrounding the city is dominated by agricultural crops rather than forests (Threlfall and Jung 2023). The Midwest region of the United States, in particular, provides an opportunity to investigate this dynamic. Many cities of the Midwestern United States, particularly the central “Corn Belt,” are surrounded by large-scale, pest-controlled, mono-crop agricultural fields that are not conducive to bat foraging due to a lack of insects and lack of cover from predators (Gehrt and Chelvsig 2003, Park 2015). In contrast to this hostile landscape, cities may provide foraging habitat for bats in greenspaces, such as forest preserves, parks, golf

courses, cemeteries, and gardens (Lehrer et al. 2021, Mimet et al. 2020), as well as water sources (Nystrom and Bennett 2019). For this reason, Midwestern cities could be hotspots for bat activity and diversity, as suggested in two studies across the Chicago area by Gehrt and Chelsvig (2003, 2004). Their work suggests urbanization effects may vary with landscape context, as some cities offer more forested habitat than the surrounding landscape. However, this link has not been firmly established, and the effects of urbanization may vary across species, with some showing positive or negative responses (Gallo et al. 2017). Most previous work has been unable to answer questions surrounding landscape-scale effects and has not examined between-city differences that may drive differential responses to urban habitat in bats.

In general, previous urban bat studies have been conducted at the scale of a single, large metropolitan area such as the Dallas-Fort Worth area (Bennett and Agpalo 2022), San Francisco-Oakland area (Krauel and LeBuhn 2016), Chicago (Lehrer et al. 2021), and New York City (Partridge et al. 2020)—all cities with populations of well over 1 million people (U.S. Census Bureau 2023a). Habitats vary by city (Magle et al. 2019), and work on terrestrial mammals has shown differences in responses to local urbanization depending on between-city differences in regional greenness and urbanization (Haight et al. 2023). Without multi-city urban bat studies, we have been unable to detect broad trends in bats' local and landscape-scale responses to urbanization. Furthermore, the urban-to-rural transition occurs over a shorter distance with decreasing city area (Kendal et al. 2020). Bat community dynamics may differ in small cities compared to nearby large cities (Luck et al. 2013). Nevertheless, few bat studies have been conducted in urban areas with populations < 500,000 (Li and Wilkins 2014), and this bias toward large cities could result in a skewed understanding of urban bat ecology if bats respond to habitat differently in small cities. Overall, this highlights the need for studies with city-level replication to elucidate the importance of both local and landscape-scale effects of urbanization on bats.

Greater knowledge of bat responses to urban environments would inform urban design practices to improve bat habitat. For example, wetland restoration in an urban environment increases bat activity compared to controls (Parker et al. 2019), showing this is a conservation tool available to urban land managers. Other actions, such as reducing light pollution (Laforge et al. 2019) and maintaining public and private green areas (Mimet et al. 2020), could also increase habitat connectivity for bats and reduce the hostility of the urban landscape.

Urban forestry has perhaps the greatest potential to affect bat presence and activity positively. Trees directly support insectivorous urban bats by providing habitat for their prey (Lumsden and Bennett 2005, Polyakov et al. 2019) and serve as natural roosts for some bats (Mager and Nelson 2001). Urban tree structure may benefit bats by mitigating negative factors, e.g., by dampening artificial light (Straka et al. 2019) and creating commuting corridors (de Oyarzabal Barba 2023). In Melbourne, Australia, bat activity and diversity is higher where there is a greater proportion of native vegetation and larger-diameter trees (Threlfall et al. 2016). Bats respond to fine-scale (25 m) tree cover in Toronto, Canada (Moretto et al. 2019), suggesting that urban forestry management can have positive effects even in backyards or small parks.

Bat responses to various metrics quantifying the availability of trees may differ by environmental context. In Zurich, Switzerland, vegetation structural and connectivity metrics do not affect bat diversity and activity but do increase insect diversity (Villarroya-Villalba et al. 2021), though bats respond positively to structural connectivity in Swiss agricultural landscapes (Frey-Ehrenhold et al. 2013). In some cases, too much tree cover can be detrimental to urban bat response, highlighting that there may be nuances in how to use urban forestry practices to aid in bat conservation. Increasing vegetation clutter reduced the activity of some species in Vienna, Austria (Suarez-Rubio et al. 2018), increasing canopy clutter above 43% reduced commuting activity in Fort Worth, TX (de Oyarzabal Barba 2023), and increasing discontinuous woodlands (tree cover 31–70%), rather than continuous woodland (tree cover >70%) demonstrated the greatest potential for mitigating negative effects of urban expansion in eastern England (Gili et al. 2020). In addition, two bat species showed varying and conflicting responses to canopy cover at 500-m and 1000-m scales (Gallo et al. 2017); these differing responses to canopy cover across species and scales highlight that urban bat conservation strategies may need to account for habitat availability and context and the goal of such actions.

Remote sensing technologies, such as LiDAR (Light Detection and Ranging), offer great potential to generate informative vegetation metrics to further parse out the nuances of bat responses to trees in urban contexts. LiDAR makes precise measurements of three-dimensional (3-D) canopy configurations that are less labor-intensive and more informative than traditional field measurements (Froidevaux et al. 2016). As bat flight requires navigation of complex 3-D environments, and bats respond differently to vegetation metrics at different levels of forest structure (Froidevaux et al. 2016), LiDAR data are valuable for testing bat responses to forest

management. However, few urban bat studies have used LiDAR-derived tree canopy metrics. Further use of high-resolution LiDAR data to quantify tree structure in cities could generate more targeted information for bat conservation strategies in urban areas.

Our study sought to address two research goals: 1) to uncover between-city differences in urban bat ecology and 2) to examine fine-scale responses of LiDAR-derived tree canopy metrics across the habitat matrix of a small city. To achieve the first goal, we launched a region-wide community science project to collect acoustic data from bats in 36 Midwestern cities, dubbed the “Bats in Small Cities Project”. To achieve the second goal, we deployed stationary acoustic recording devices throughout the parks, forests, and neighborhoods of Champaign-Urbana, Illinois, to assess bat activity in differing environments and levels of canopy cover. Our efforts represent the first step toward determining how bat ecology differs across urban areas in North America. It will be crucial to discover possible management solutions to make cities more bat friendly as bat populations contend with disease, development, and habitat loss.

CHAPTER 2: URBAN BATS RESPOND TO LOCAL AND CITY-WIDE TREE COVER IN THE MIDWESTERN U.S.

Introduction

Increasing urbanization is a significant threat to hundreds of wildlife species as cities replace natural land cover with development (Simkin et al. 2022). For urban wildlife, the increased proximity to humans in cities can result in road mortalities (Riley et al. 2014), reduced health from disease transmission and pollution (Murray et al. 2019), disturbances from human activity (Markovchick-Nicholls et al. 2008), and behavioral changes (Ritzel and Gallo 2020). However, many wildlife species are able to exploit the urban environment, with generalist species tending to fare better than specialists (Ducatez et al. 2018, Sorace and Gustin 2009, Sol et al. 2014, Jung and Threlfall 2018, Wolf et al. 2022, Croci et al. 2008, Callaghan et al. 2019).

Though there has been an increase in urban wildlife studies in the past two decades (Collins et al. 2021), research has been biased toward sampling large cities (Kendal et al. 2020, and more than three-quarters of urban wildlife studies have been conducted at a single-city level (Rega-Brodsky et al. 2022). Wildlife in smaller cities may have easier access to rural landscapes due to a more compressed urban transitional gradient, which may result in different responses to urbanization compared with wildlife in large cities (Kendal et al. 2020). While single-city studies may be useful for understanding and managing wildlife in a particular urban area, they may have limited transferability due to the stark differences among many cities in terms of available habitat, climate, and wildlife community structure (Magle et al. 2019, Marsh et al. 2023). Urban wildlife studies that use the same methodology in multiple cities, or “multi-city studies,” are necessary to elucidate broad trends in wildlife ecology (Magle et al. 2019, Rega-Brodsky et al. 2022). Examining how regional, between-city, and within-city differences affect wildlife assemblages may be crucial for understanding what can be done through urban design or social change to reduce threats to urban species and enhance biodiversity (Magle et al. 2019). For example, one multi-city study found a decreasing diversity of terrestrial mammalian communities with increasing local urbanization, but this local response interacted with urbanization, greenness, and temperature at the regional scale (Haight et al. 2023). The negative impact of local urbanization was less acute in greener, cooler, and less urbanized cities, suggesting that city planning can impact biodiversity (Haight et al. 2023). Indeed, within-city disparities in wildlife assemblages often relate to historical socioeconomic development patterns

(Magle et al. 2021), further highlighting the potential for urban design to influence urban ecosystems.

While multi-city studies have been used to study herpetofauna (Marsh et al. 2023), avian (Ferenc et al. 2014, Aronson et al. 2014), and terrestrial mammal communities (Haight et al. 2023, Fidino et al. 2021, Magle et al. 2019, Magle et al. 2021), there has been little work on the regional and between-city factors influencing urban bat assemblages. Bats are commonly encountered in cities throughout the world, as many generalist roosting species (Jung and Threlfall 2018, Wolf et al. 2022) exploit anthropogenic structures like bridges and attics for roosting space (Kubista and Bruckner 2015). Despite the ubiquity of bats in cities, there have been few multi-city bat studies, and nearly all were conducted in Europe (Villarroya-Villalba et al. 2021, Andersson Skog 2021, Gili et al. 2020, Lintott et al. 2015, Lintott et al. 2016, but see Loeb et al. 2009 [North America] and Luck et al. 2013 [Australia]), though there have been meta-analyses of world-wide data (Wolf et al. 2022, Jung and Threlfall 2016, Jung and Threlfall 2018). Only Villarroya-Villalba et al. (2021), Lintott et al. (2015), and Lintott et al. (2016) examined between-city differences, with the others focusing on broader landscape effects across both rural and urban areas (Andersson Skog 2021, Gili et al. 2020, Loeb et al. 2009) or within-city differences (Luck et al. 2013). To date, there have been no studies in North America examining between-city differences in urban bat ecology.

Additionally, nearly all urban bat studies have been conducted in large metropolitan areas with urban populations > 500,000 (Li and Wilkins 2014). Examining U.S. Census data (2023a), we determined that there are only 84 cities with a population > 500,000, while there are 426 cities with a population of 50,000–500,000. Out of the few urban bat papers that sampled within these smaller cities, many have been focused on studying behavior or have been site-specific rather than sampling a broad area of the city (e.g., Menzel et al. 2001, Burrell and Bergeson 2022). Li and Wilkins (2014 and 2022 [Waco, TX]), Li et al. (2020 [Greensboro, NC]), and McGowan (2023, [Muncie, IN]) conducted city-wide studies that were spatially replicated, but we are unaware of any other published work in cities of this size that specifically documented their bat assemblages. American cities in this class are home to 64 million people spread across more than 85,000 km², representing a significant gap in both spatial coverage and community access. Luck et al. (2013) found greater bat activity in small cities and towns compared to

previous surveys in large cities within the same region of Australia, but it is not known whether this holds true in other parts of the world.

The lack of small or multi-city bat studies comes despite an increased focus on urban bats over the past two decades, an increase largely driven by the rising accessibility of acoustic devices to record bat echolocation calls (Rega-Brodsky et al. 2022). Acoustic methods allow researchers to generate large quantities of data from bats with relatively low sample effort compared to capture surveys, albeit with a greater risk of false-positive identification (Clement et al. 2014). The relative simplicity of acoustic data collection has allowed non-professionals to aid in data collection (Rodhouse et al. 2021); crowdsourcing acoustic data collection through community science may be one way to achieve a multi-city bat monitoring network (Lintott et al. 2015, Lintott et al. 2016).

Due to their high mobility and the propensity of many species to live in urban areas, chiropterans offer a great opportunity to study how large-scale differences between cities influence wildlife ecology. Some species, like the big brown bat (*Eptesicus fuscus*), respond positively to high levels of landscape-scale development (Loeb et al. 2009), which may be due to fitness benefits associated with artificial roosting habitat (Lausen and Barclay. 2006). However, urban big brown bats have been reported commuting up to 18.8 km in a single night from their artificial roosts to their foraging grounds (Everette et al. 2001), suggesting that bats exploiting human structures as roosts in cities could face a tradeoff of lengthy and energetically costly commutes (Geggie and Fenton 1985, Everette et al. 2001, Menzel et al. 2001). Alternatively, urban bats may congregate within fragmented foraging patches located closer to their roosts (Lintott et al. 2015), as bats do in mixed forest-agricultural landscapes (Fuentes-Montemayor et al. 2013), which may result in increased competition for resources. However, in cities with ample natural habitat and greenspaces, there might be less of a tradeoff, as bats will forage (Krauel and LeBuhn 2016) and use natural roosts (Kubista and Bruckner 2015) in greenspaces within city centers. Bats roosting in artificial structures could show positive responses with increased access to both natural habitat and human development, as they provide foraging and roosting habitat, respectively. Urban-associated rodents and carnivores (e.g., *Sciurus* and *Vulpes* spp.) respond positively to housing density in conjunction with increasing access to greenspaces (Fidino et al. 2021), but this interaction is unstudied in bats.

Urbanization may have differing effects on species that actively exploit urban areas compared to species that are merely tolerant of urban areas (Marsden et al. 2023). Cities are typically dominated by one common species (Russo and Ancillotto 2015) that is often pre-adapted (Marsden et al. 2023) to succeed in urban environments. Urban bats typically have generalist roosting requirements, open- or edge-space foraging strategies, high aspect-ratio wings with shorter forearms, and low-frequency calls with long durations (Jung and Threlfall 2018, Wolf et al. 2022). In North America, the Brazilian free-tailed bat (Avila-Flores and Fenton 2005 [Mexico City], Krauel and LeBuhn 2016 [California Bay Area], Li et al. 2020 [Greensboro, NC], Li and Wilkins 2014, 2022 [Waco, TX]), big brown bat (Gehrt and Chelsvig 2004, Gallo et al. 2017 [Chicago]; Kurta and Teramino 1992 [Detroit]; Moretto et al. 2019 [Toronto]); Johnson et al. 2008 [Washington, D.C.]; Dixon 2011 [Minneapolis]), eastern red bat (Parkins and Clark 2015 [New York City]), evening bat (Bienz 2016, de Oyarzabal Barba 2023 [Fort Worth]), and little brown bat (Coleman and Barclay 2011b [Calgary]) dominate different cities. Which species dominates an urban area may have to do with climatic differences, but the latitudes or landscape features where these shifts occur and why are mostly unknown.

Urban development reduces bat species evenness (Russo-Petrick and Root 2023) and diversity (Andersson Skog 2021, Duchamp and Swihart 2008), but it is not known how between-city differences in land cover may affect bat species richness. Some cities have more bat diversity than others (Villarroya-Villalba et al. 2021), and even cities within the same region can have vastly different rates of relative activity across species groupings (Luck et al. 2013). As some bat species are sensitive to landscape-scale deforestation and land disturbance (Meyer et al. 2016, Pauli et al. 2015, Henderson et al. 2008), it is possible that landscape-scale cover outside cities influences city-level species richness. Cities that host both rare and common species will have higher richness compared to cities that only host common urban-associated species. Imperiled species can occupy urban areas (Burrell and Bergeson 2022, Hernández-Brito et al. 2018), and they may need large patches of quality habitat, such as forested greenspaces, to survive in urban environments (Thorne et al. 2021). Bat diversity is often higher in large patches of urban greenspaces (Krauel and LeBuhn 2016, Tena et al. 2020), so it seems likely that city-wide bat diversity would be higher in cities with a greater proportion of natural habitat. Alternatively, the persistence of rare species—and higher richness—in some cities could reflect an “extinction debt,” where the urban populations of imperiled bats are unsustainable but have

not yet been extirpated (Caryl et al. 2016). If rare bats are only present in a city because of an extinction debt, then the availability of natural land cover would likely have little bearing on the current species richness. Understanding what factors, if any, influence bat diversity in cities will show managers whether changes to the urban environment could promote greater species diversity.

To answer questions surrounding regional, between-city, and within-city differences in urban bat assemblages and fill knowledge gaps within small cities, we launched a 36-city bat acoustic survey—the Bats in Small Cities (BiSC) Project—using a volunteer network across the Midwestern United States. As this was the first formal bat acoustic survey of many of these cities, we also aimed to identify which species were most dominant and to verify the presence of species of conservation concern. We sought to determine how individual urban bat groupings respond to local- and city-scale cover of tree and development and whether responses to local variables depended on city-scale variables. Lastly, we wanted to examine whether local or city-level bat species richness depends on local- and city-scale tree and development cover. The potential for context-specific effects of urbanization on bats has implications for seeking solutions to threats caused by urbanization and for making cities more “bat-friendly”.

Methods

Study Area

Our study area encompassed 36 urban conglomerations (Figure 2.1), which we will refer to as “cities”, across the Midwestern United States, which ranged in population from ~50,000 to ~500,000 people as defined by the Urban Area Criteria (U.S. Census Bureau 2023a). This population range allowed us to target many cities that had not been previously studied while limiting the amount of time volunteers would need to drive across their cities. We also only considered cities if most of their area was in one of 10 different states (Figure 2.1). We contacted government agencies, non-profits, organizations of nature enthusiasts, and existing volunteer networks to identify participants in our surveying efforts. Cities were opportunistically chosen based on volunteer interest and the number of bat detectors available. To classify the landscape of a city, we created 6 major land cover classes (Table 2.1) based on the 2021 National Land Cover Database (NLCD, Dewitz 2023). We created these major classes to represent broad habitat features known to be important to bats. Using the Raster to Polygon tool in ArcGIS Pro (v. 3.2.2, Esri Inc. 2023), we merged contiguous raster cells of the same major class into distinct features.

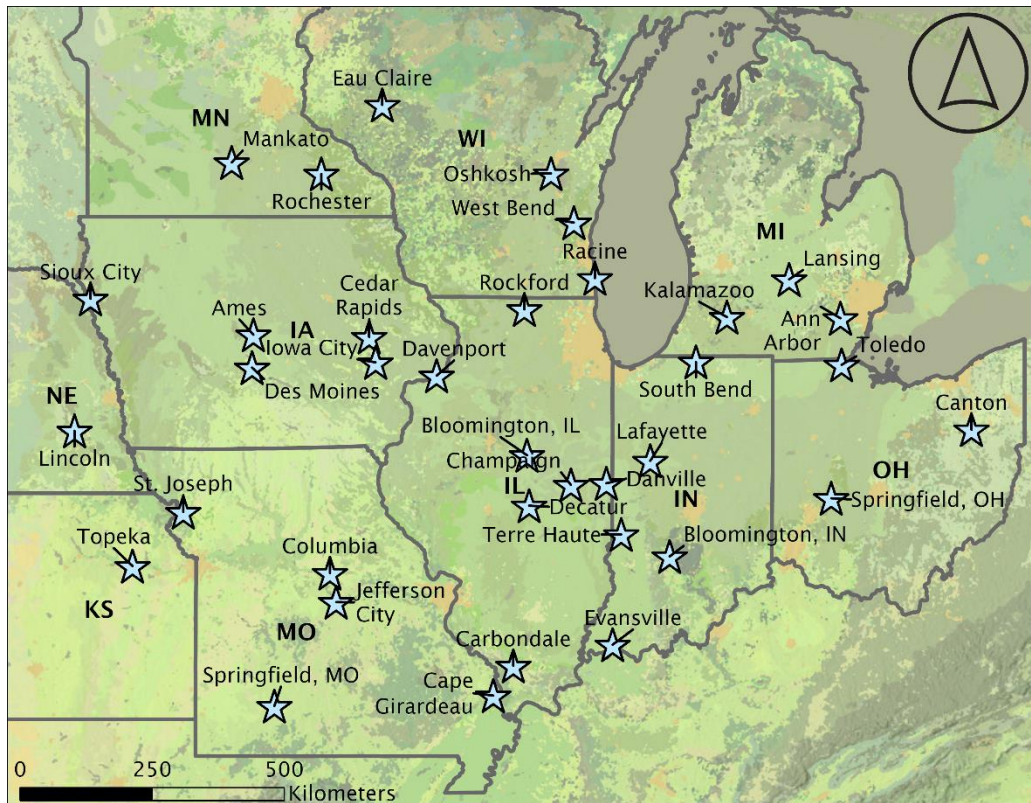


Figure 2.1: A map of the 36 cities and 10 states sampled during the Bats in Small Cities Project.

Table 2.1: Major land cover classes used to generate sample points, National Landcover Database (NLCD) classes included within each major class, and the rationale for the importance of each major class to bats.

Major Class	NLCD Classes Included	Rationale
Forest	Deciduous Forest, Evergreen Forest, Mixed Forest, Woody Wetlands	Provides roosting and foraging habitat for many species (Brigham 2007)
Open Vegetation	Open Space Developed, Shrub/Scrub, Grassland/Herbaceous, Emergent Herbaceous Wetlands	Provides foraging habitat but limited tree roost availability (Adams et al. 2009)
Low Development	Low Intensity Developed	Tends to comprise neighborhoods of single-family housing (such as those commonly found in suburban areas), which may provide artificial roosting for some species and some foraging habitat (Threlfall et al. 2012a)
High/Med. Development	High-Intensity Developed, Medium Intensity Developed	Tends to comprise heavily built-up areas, such as the urban core, which may provide artificial roosting but limited foraging opportunities (Everette et al. 2001)
Crops	Cultivated Crops, Pasture/Hay	Typically, monoculture systems that may provide roosting in barns, but limited foraging opportunities compared to natural areas due to anti-pest measures (Olimpi and Philpott 2018)
Open Water	Open Water	Provides water, a limiting resource for bats, and foraging opportunities (Nystrom and Bennett 2019)

We defined the sampling boundaries for each city using the Urban Area Criteria (UAC, U.S. Census Bureau 2023a). We removed noncontiguous outlier settlements, or “jumps” (U.S. Census Bureau 2023a), from the UAC shapefile to minimize travel times for surveyors and ensure that the final city polygons represented continuous urban development. Jumps from the UAC shapefiles were isolated by the “Identify Narrow Polygons” tool (with a minimum width of 400 m) in ArcGIS Pro (purple lines in Figure 2.2) and removed if not connected to the core urban area by Low, Medium, or High Intensity Developed landcover beyond a single road (Dewitz 2023), resulting in a final corrected UAC polygon.

Bloomington, IN

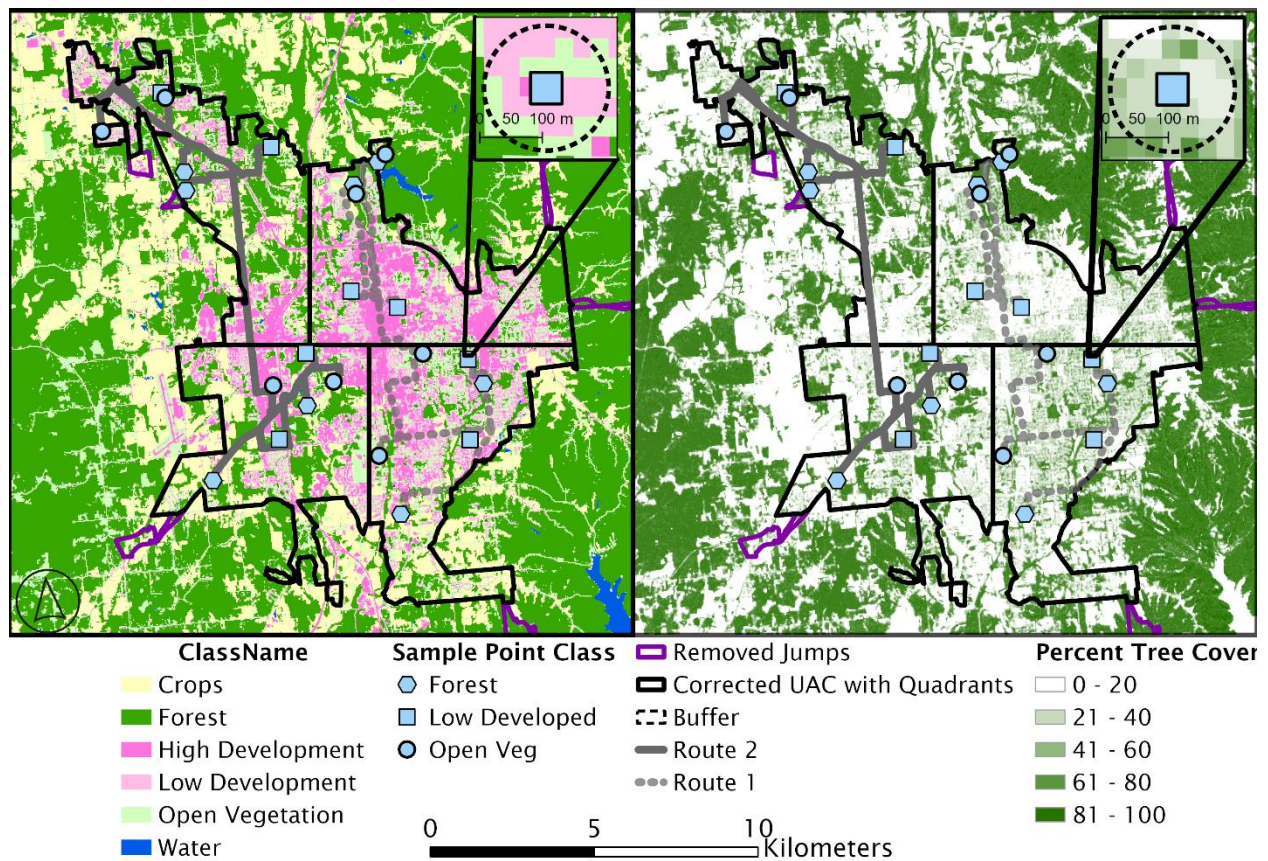


Figure 2.2: Example of the sampling scheme in the Bloomington, IN Urban Area Criteria (UAC) overlaid with the major landcover classes—**left**—and NLCD Tree Canopy Cover values (Housman et al. 2023)—**right**. Two routes with 12 points each were surveyed twice during the four survey nights. Habitat variables were summarized within buffers around the points or by measuring the distance to habitat features.

The corrected polygons of each city were divided into 4 equal area quadrants. Each quadrant received 6 sample points (24 sample sites per city) stratified by major class to survey a variety of urban habitats. After removing all high/med. development, crop, and water polygons, as well as all polygons < 1 ha, we clipped our major class polygon layer with a 30-m buffer of local low-traffic roads (MAF/TIGER Feature Class Code S1400, U.S. Census Bureau 2023b). Then, we randomly generated 2 points each in forest, open vegetation, and LID classes within each quadrant of every city (Figure 2.3) using the Create Random Points feature in ArcGIS Pro. We sought to avoid collecting data directly within the high/med. development and crop classes, as these are the most anthropogenically altered systems and were not expected to generate as many bat calls as the other classes; we also avoided open water, as bat call quality decreases when echoing off the water. We excluded all polygons < 1 hectare to filter out small features that may have otherwise been dominated by other surrounding land cover classes. It was impossible to generate 2 points for the forest and open vegetation classes in every single city quadrant. When this was the case, we randomly generated 24 backup points within the forest, open vegetation, or low development major classes and selected the backup point(s) closest to the missing landcover class(es) for sampling (Figure 2.3D). Due to our use of these backup points and because points placed in one major class could be directly adjacent to one or more other classes, we did not use the major class of sample points in our models. Surveyors reviewed all points in their city beforehand to determine the feasibility and safety of sampling. If any points were deemed unsuitable, we selected the closest backup point for sampling. Due to differences in urban area size and shape, some cities had longer driving distances between sample points, which resulted in longer survey nights (minimum survey length = 67 minutes, maximum length = 306 minutes, mean = 203 minutes).

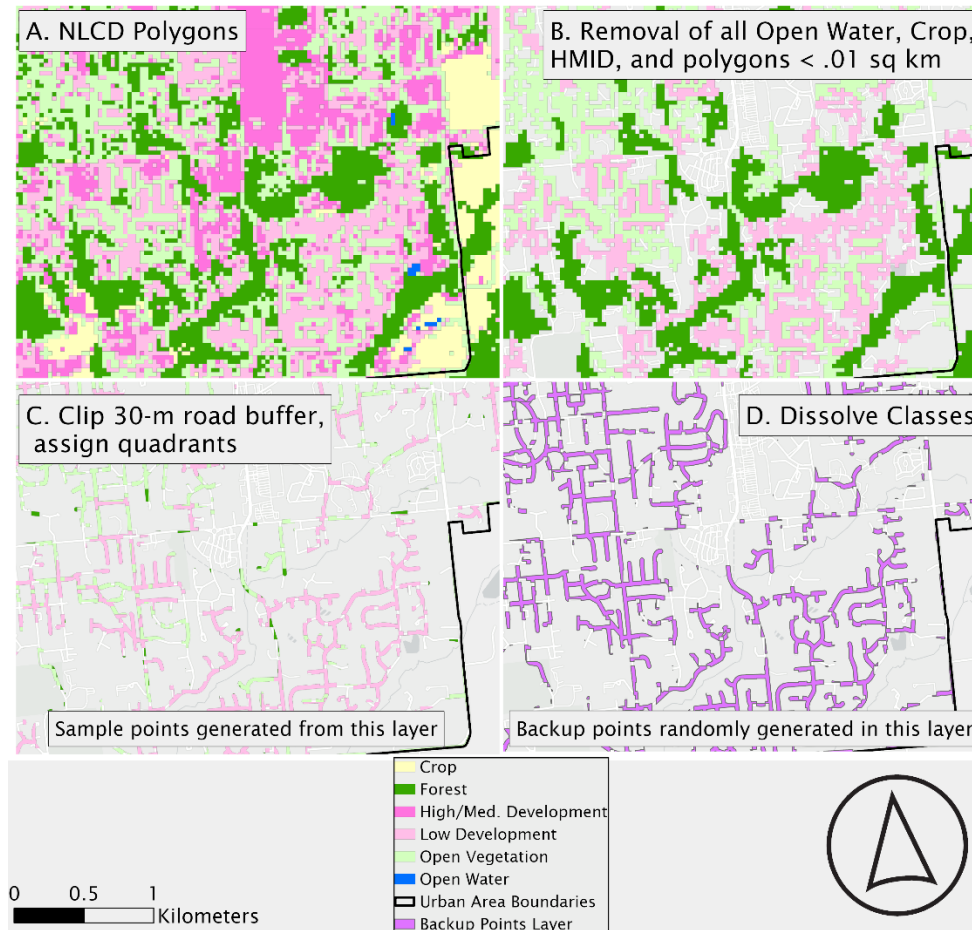


Figure 2.3. Maps showing the criteria for sample point selection. Land cover polygons were converted from NLCD raster to single-part polygons. All streets considered are local low-traffic roads (MAF/TIGER Feature Class Code S1400, U.S. Census Bureau 2023b) due to their lower estimated traffic levels. Random points were $\geq 100\text{-m}$ apart to avoid detection range overlap.

Acoustic Monitoring

We implemented active acoustic sampling protocols to maximize our spatial coverage within cities. Acoustic transects involve continuous monitoring from a device in motion, and driving transects have been used to increase the spatial coverage of bat surveys (Hogue and McGowan 2018). However, driving transects are difficult to conduct in cities because frequent stops prevent surveyors from maintaining constant speeds (Loeb et al. 2015), and continuous recording from a moving vehicle can reduce call quality and detection rates due to noise (Hogue and McGowan 2018). Instead, we conducted 10-minute acoustic point counts at our sample locations. While not frequently used in bat acoustic surveys (but see Johnson et al. 2010 and Mimet et al. 2020), point counts can result in wide spatial coverage that captures comparable

amounts of bat activity and diversity as driving surveys, and point counts are preferable to driving surveys when testing hypotheses about bat ecology (Hogue and McGowan 2018).

Surveyors drove to each sample point and turned off their cars upon arrival. Then, they stuck out a 1-m long pole with a Titley Scientific Chorus (Firmware Version 2.4.6) bat detector attached to it (Figure 2.4). The Chorus was set to record ultrasonic noises between 10–250 kHz with a sampling frequency of 320 kHz, a sensitivity of 16, a minimum file length of 2 seconds, and a maximum of 15 seconds. The microphone was pointed upwards, and the unit recorded for 10 minutes at each point. We refer to each 10-minute point count as a “sampling event”. While recording, the surveyor tracked how many cars drove down the street they were parked on as an estimate of traffic. To ensure optimal conditions for bat activity and acoustic recording, we instructed surveyors not to conduct the transects on days with rain or fog, wind $\geq 24\text{km/h}$, a temperature $\leq 21^{\circ}\text{C}$ at the time of sunset, or if the temperature was projected to drop below 13°C within 3 hours of sunset. Sampling began 30 minutes after sunset, with each point sampled immediately after the previous one, driving the route with the fastest travel time. During each of the four nights of sampling, volunteers recorded data at one of two different groups of 12 points (Figure 2.3). Each group of points was sampled twice over the course of the survey and was sampled in the same order when repeated.



Figure 2.4: Example of acoustic recording method, with surveyors remaining in the car while holding a Titley Scientific Chorus out their car window.

The whole sampling effort was limited to a three-week period between 12 June and 3 July 2023 to control known seasonal patterns of bat activity while still giving volunteers flexibility on which nights they would sample. We chose this period because 1) it is when bat activity is typically near its peak, increasing our likelihood of bat detection at any given point; 2) juveniles are typically not yet volant, preventing skewed activity levels; and 3) this avoided migratory periods in late spring and late summer (Gorman et al. 2021). In addition, most American universities and secondary schools are out of session, which opened up our volunteer pool. Of note, the tail end of our survey occurred amidst severe air quality issues associated with the 2023 Canadian wildfires (Wang et al. 2024).

Predictor variables

Sampling-event-level covariates

To account for the effects of weather on bat detection, we gathered historical weather station data from the Weather Underground website (Weather History and Data Archive) for each city. For each survey night, we recorded the most recent temperature before the start of the sampling (Temp., °C), the maximum 24-hr wind speed (Wind) in m/s (Table 2.2). We applied the same Temp. and Wind values for all sampling events on a given night. We also recorded the time after sunset at which a given 10-minute sampling event began (Time), as bat activity typically decreases later in the night (Gorman et al. 2021), and the number of cars (Traffic) that passed during a sampling event, as traffic may impact bat behavior (Bennett et al. 2013) and car noise may reduce audio quality.

Point-level covariates

We calculated several environmental variables for each sample point to quantify the local habitat (Table 2.2). We were interested in three local variable groupings: tree habitat (Tree), as trees can support natural roosting and foraging (Brigham 2007); development (Development), as buildings, roads, and parking lots reduce natural foraging space, while buildings may provide artificial roosting habitat (Threlfall et al. 2011, Threlfall et al. 2012a); and water (Water), as bats are often drawn to water for foraging and drinking (Lehrer et al. 2021). Some bats respond to environmental factors in different ways across spatial scales (Gallo et al. 2017); so, for each sample point, we calculated Tree, Development, and Water variables within 100-m, 250-m, 500-

m, and 1000-m buffers using the “Summarize Within” tool in ArcGIS Pro, and also the distance to habitat features in meters with the “Near” tool.

Our Tree variables included mean percent tree canopy cover (Canopy), proportion forest (Forest), and distance to forest (Forest Dist.). The Canopy metric was derived from the NLCD Tree Canopy Cover product (Housman et al. 2023). Forest was taken from the NLCD class groupings. Forest Dist. measures the distance to the nearest patch of NLCD-defined forest. Our Development variables consisted of the proportion of NLCD-derived High/Medium Development and mean nightly radiance in $\text{nW/cm}^2/\text{sr}$ (Radiance). Radiance data was taken from the Earth Observation Group (2023, June) Visible and Infrared Imaging Suite (VIIRS) Monthly Cloud-free DNB Composite using the vcm (stray-light excluded) files. As the VIIRS data is comprised of 750-m raster cells, we did not calculate the Radiance variable for buffers ≤ 750 m. We also measured the distance to High/Med. Development (High/Med. Development Dist.) but excluded it from our analysis because roads are typically classified as High/Med. Development and all our sample points were along roads, resulting in very little variation. Our Water variables consisted of the proportion of NLCD Open Water (Water) and distance to the nearest National Hydrological Dataset Plus Version 2 (NHDPlusV2, U.S. Environmental Protection Agency 2014) area features (e.g., ponds, lakes, streams, and rivers,) in meters (Water Dist.).

City-level covariates

For each sample city, we used the “Summarize Within” feature to determine the proportion of our Tree, Development, and Water variables within the corrected UAC boundaries to quantify habitat at the intracity-scale (Intracity) and within a 10-km buffer around the UAC to quantify habitat at the landscape-scale (Landscape) (Table 2.2). For cities bordering lakes or large rivers, we excluded open water from the 10-km buffer area so that calculations for other landcover types were made across only areas of land. For city-level covariates, the Tree and Development variables were correlated, so they were combined into a single grouping, Tree/Development. We also recorded latitude (Lat.), taken as the mean latitude of all sample points within a city.

Table 2.2: Predictor variables by group and individual data type at the sampling-event-level (underlined), sample-point-level, and city-level used in analyses. Included is the ecological justification for variable groupings (rationale), abbreviation (Abbr.), definition, and scales at which they were used.

Group	Rationale	Data Type	Abbr.	Definition	Sample Unit	Scales ¹
Detection	Sampling-event-level variables with likely impacts on detection	Temperature	<u>Temp.</u>	Temperature at survey start, in °C (Weather Underground)	<u>Sampling event</u>	E
					Point	P%
					City	C [#]
		Wind	<u>Wind</u>	Maximum 24-hr wind speed in m/s (Weather Underground)	<u>Sampling event</u>	E
		Time	<u>Time</u>	Time of the start of a sampling event, in minutes after sunset.	<u>Sampling event</u>	E
					Point	P%
					City	C [#]
Tree	Trees provide natural roosting and foraging habitat	Tree Canopy Cover	Canopy	Mean percent tree canopy cover from the National Landcover Database (Housman et al. 2023) within boundary	Point	100 m
						250 m
						500 m
						1000 m
					City	Intracity [^] Landscape [^]
		Proportion Forest	Forest	Proportion of forest cover from the National Landcover Database (NLCD) (Dewitz 2023) within boundary	Point	100 m
						250 m
						500 m
						1000 m
					City	Intracity [^] Landscape [^]
Development	Buildings and roads decrease available natural habitat, while buildings can hold artificial roosts	Proportion High and Medium Intensity Development	High/Med. Development	Proportion of High and Medium Intensity Developed cover from the National Landcover Database (NLCD) (Dewitz 2023) within boundary	Point	100 m
						250 m
						500 m
						1000 m
					City	Intracity [^]
		Distance to Forest	Forest Dist.	Distance from sample point to NLCD forest patch (Dewitz 2023) in meters	Point	Dist.

Table 2.2 (cont.)

Group	Rationale	Data Type	Abbr.	Definition	Sample Unit	Scales ¹
						Landscape [^]
		Mean Nightly Radiance	Radiance	Mean nightly radiance (Earth Observation Group, 2023) in nW/cm ² /sr within boundary	Point	1000 m
					City	Intracity [^]
						Landscape [^]
						100 m
		Proportion Open Water	Water	Proportion Open Water cover from the National Landcover Database (NLCD) (Dewitz 2023) within boundary	Point	250 m
						500 m
						1000 m
					City	Intracity
						Landscape
Water	Water is necessary for bat survival and can provide natural foraging habitat					
		Distance to Water	Water Dist.	Distance from sample point to National Hydrological Database Plus Version 2 features (NHDPlusV2, U.S. Environmental Protection Agency 2014) in meters.	Point	Dist.
Lat.	Regional climate changes occur as latitude changes	Latitude	Lat.	Mean latitude, in decimal degrees of sample points within a city	City	C [#]

¹E = discrete detection variable for each sampling event, P = summarized detection variable by sample point, C = summarized variable by city; 100 m = summarized within a 100-m buffer, 250 m = summarized within a 250-m buffer, 500 m = summarized within a 500-m buffer, 1000 m = summarized within a 1000-m buffer, Dist. = measured distance to nearest feature; *Intracity* = Intracity-scale variables summarized within the corrected Urban Area Criteria (UAC) boundary for a city; Landscape = Landscape-scale variables summarized within a 10-km buffer around a city, excluding landcover within the UAC boundary and Open Water; [^] City-level variables (Intracity and Landscape) in the Tree and Development groupings are combined in the same Tree/Development grouping; * For Water (Landscape), Open Water was included in proportion calculations; # Only included for city-level richness analysis; % Only included for point-level richness analysis

Response variables

We considered each individual recorded file recorded by the Chorus as one “bat call”. Each call had a duration of 2–15 seconds, with differing numbers of individual echolocation pulses. The device started to record once a sound between 10–250 kHz was detected and automatically stopped recording when it failed to detect sounds in its range. The device automatically started recording a new file every time a call exceeded 15 seconds. We processed all acoustic data through the Kaleidoscope Pro AutoID software (v. 5.6.6; Wildlife Acoustics, Inc.) with the Bats of North America 5.4.0 classifier to identify calls to bat species. We used the book *Bats of the United States and Canada* (Harvey et al. 2011) to determine which species ranges overlapped with our cities, resulting in 10 cohorts of cities with the same list of potential species (Appendix A, Supplemental Table A.1). Each cohort’s recorded files were analyzed separately in the AutoID software, and we analyzed only the listed potential species. After AutoID, we manually vetted every recorded file, updating file IDs as appropriate. For each of our sampling events, a species or grouping was considered present if there was at least one manually vetted call sequence with ≥ 3 pulses, and we used this as our estimate for naïve occupancy.

Due to uncertainty surrounding acoustic ID for many calls, we classified species that had very similar call structures into 6 acoustic groupings (Table 2.3) for our analyses. The Brazilian free-tailed bat (TABR) emits calls similar to bats in the big brown + silver-haired bat acoustic grouping (Lausen et al. 2023). We kept the Brazilian free-tailed bat separate because only two cities in our dataset were within its known range (Topeka and Lincoln), and we sought to enhance the transferability of the data from these two cities to the other 34 cities. Excluding these two cities from our analysis did not change our top big brown + silver-haired bat occupancy model. While the effect sizes changed slightly, there were no changes in which parameters we determined were significant, so we included both cities in our final analysis.

Table 2.3: List of species recorded from the Bats in Small Cities Project that had positive identification for at least one call by common name, scientific name, four-digit species code, acoustic grouping used in analysis, and associated code.

Common Name	Scientific Name	Species Code	Acoustic Grouping	Grouping Code
Big brown bat*^	<i>Eptesicus fuscus</i>	EPFU	Big brown + silver-haired bat	EPFULANO
Eastern red bat*^	<i>Lasiurus borealis</i>	LABO	Eastern red + evening bat	LABONYHU
Hoary bat*	<i>Lasiurus cinereus</i>	LACI	Hoary bat	LACI
Silver-haired Bat*^	<i>Lasionycteris noctivagans</i>	LANO	Big brown + silver-haired bat	EPFULANO
Evening bat*	<i>Nycticeius humeralis</i>	NYHU	Eastern red + evening bat	LABONYHU
Little brown bat*#	<i>Myotis lucifugus</i>	MYLU	<i>Myotis</i>	MYO
Gray bat#	<i>Myotis sodalis</i>	MYGR	<i>Myotis</i>	MYO
Tricolored bat	<i>Perimyotis subflavus</i>	PESU	Tricolored bat	PESU
Brazilian free-tailed bat	<i>Tadarida brasiliensis</i>	TABR	Brazilian free-tailed bat	TABR

Statistical Analyses

Analysis 1: Occupancy Modeling

We used a multiscale occupancy approach (Nichols et al. 2008) similar to that of Pavlacky et al. 2012, wherein R small-scale subsamples are nested within N large-scale sample sites, with a certain number of repeated sampling occasions represented by K . For our study, $N = 36$ cities, $K = 24$ sample points (per city), and $L = 2$ sample events of 10 minutes (per point). Four sampling points had no sampling events, resulting in 860 successfully sampled points, and there were 22 missing sampling events in total, meaning we had 1704 successful sampling events. We substituted a “.” wherever missing data were found within the encounter history. In the model structure, the p parameter represents the probability of detection during a sampling event. The θ (*theta*) parameter, or point-level occupancy, is the proportion of sample points occupied. The ψ (*psi*) parameter, or city-level occupancy, signifies the proportion of cities occupied.

We conducted our multiscale occupancy modeling in Program MARK (White and Burnham 1999) within R (R Core Team 2023) using the RMark package (v.3.0.0, Laake 2013). With RMark, we followed the methods outlined in the “larksparrow” example (Pavlacky 2022), with model = “MultScaleOcc” and mixtures = 2. We evaluated occupancy for big brown bat + silver-haired bat (EPFULANO), eastern red bat + evening bat (LABONYHU), and hoary bat (LACI). We held ψ constant for all models, as we recorded a 100% naïve city-level occupancy rate for the EPFULANO and eastern red + evening bat (LABONYHU) acoustic groups and assumed 100% city-level occupancy for hoary bats (LACI, city-level naïve occupancy = 89%).

We used a three-step approach to arrive at our top model(s) for each group (Tables 2.4, 2.5, 2.6). For each of these steps, we ranked a suite of models with different combinations of covariates to assess which was the most plausible for explaining bat occupancy using Akaike's Information Criterion corrected (AICc) for small sample size (Hurvich and Tsai 1989, Burnham and Anderson 2004). We considered all models with $\Delta\text{AICc} \leq 2$ to be competitive, and all parameters with 85% confidence intervals that did not overlap with zero were considered ecologically significant (Arnold 2010).

First, we ranked models predicting the effects of our sampling-event-level covariates on p , while holding θ constant (Table 2.4). If there was model selection uncertainty with 2 or more p models with $\Delta\text{AICc} \leq 2$, we defaulted to using the highest ranked model to simplify future steps.

We questioned the reliability of the traffic data due to inconsistencies in effort between cities, so it was excluded from our analysis. Second, we tested univariate θ models for all point- and city-level covariates (Table 2.5), contingent upon the top p model from step one. The top-ranked covariate within each variable grouping (Tree [Point-level], Development [Point-level], Water [Point-level], Tree/Development [City-level], Water [City-level]) was retained for the final analysis. In cases of model-selection uncertainty with the same variable grouping, we defaulted to the variable representing the finest scale or resolution (e.g., 100-m buffer chosen over 250-m buffer; see Table 2.5). Third, we ranked a suite of hypothesis-based θ models, contingent upon the top-ranked p model (Table 2.6), built from combinations of point and city-level variables to find the most plausible model for predicting point-level occupancy. After identifying the top model(s), we examined the coefficient estimates (β s) to examine the effects of individual covariates. Each model also generated 24 estimates of true point-level occupancy (θ , one for each K) after accounting for imperfect detection and 48 estimates of detection probability (p , one for each L * K). We averaged both of these estimates ($\hat{\theta}$, $\hat{p}$) across all competitive models.

Table 2.4: List of detection models tested during Step 1 of multiscale occupancy modeling and the hypothesized effect of variables on the probability of detecting bats (p). The model with the lowest AICc was retained for future steps. Ψ and θ are held constant in all Step 1 models.

Step 1: p modeling		
Model Name	Detection Hypothesis	p
Null	Detection is random	Constant
Temperature	Detection is more likely as temperature increases	<u>Temp_E</u>
Time	Detection is less likely as time after sunset increases	<u>Time_E</u>
Wind	Detection is less likely as wind speed increases	<u>Wind</u>
Temperature + Time	Detection is more likely with increasing temperature and less likely with increasing time after sunset	<u>Temp_E</u> + <u>Time_E</u>
Temperature + Wind	Detection is more likely with increasing temperature and as wind speed increases	<u>Temp_E</u> + <u>Wind_E</u>
Temperature + Time + Wind	Detection is more likely with increasing temperature and less likely with increasing time after sunset and as wind speed increases	<u>Temp_E</u> + <u>Time_E</u> + <u>Wind_E</u>

Table 2.5: Univariate point-level occupancy models tested to prune each variable grouping to one variable during Step 2 of multiscale occupancy modeling. The model with the lowest AICc in each group was retained, except in cases with model selection uncertainty. When multiple models were competitive, the model with the highest level of priority (with higher priority variables placed at the top of the table) based on data resolution and predicted ecological relevance was retained. For all models, p covariates were those in the best model from Step 1 and Ψ was held constant.

Step 2: Univariate θ modeling					
	Tree (Point-level)	Development (Point-level)	Water (Point-level)	Tree/Development (City-level)	Water (City-level)
Higher Priority	Forest Dist.	High/Med. Devel. (100 m)	Water Dist.	Canopy (Intracity)	Water (Intracity)
	Canopy (100 m)	High/Med. Devel. (250 m)	Water (100 m)	Canopy (Landscape)	Water (Landscape)
	Canopy (250 m)	High/Med. Devel. (500 m)	Water (250 m)	Forest (Intracity)	
	Canopy (500 m)	High/Med. Devel. (1000 m)	Water (500 m)	Forest (Landscape)	
	Canopy (1000 m)	Radiance (1000 m)	Water (1000 m)	High/Med. Devel. (Intracity)	
	Forest (100 m)			High/Med. Devel. (Landscape)	
	Forest (250 m)			Radiance (Intracity)	
	Forest (500 m)			Radiance (Landscape)	
Lower Priority	Forest (1000 m)				

Table 2.6: Hypothesis-driven point-level models tested during Step 3, along with hypothesized effects of variables on the probability of point-level occupancy (θ) for urban bats. For each model, the p covariates are the same as the top model from Step 1, and Ψ is held constant. City-level covariates are italicized.

Model Name	Occupancy Hypothesis	θ
Null	Occupancy is random	Constant
Water landscape	Occupancy is more likely at points with greater access to water at the landscape scale.	<i>Water (City-level)</i>
Tree affinity	Occupancy is more likely at points with greater access to local and landscape-scale access to natural foraging and roosting habitats.	Tree + <i>Tree/Development</i>
Anthropogenic avoidance	Occupancy is less likely at points with increasing heavy/medium development, traffic, and surrounding crop cover.	Development+ <i>Tree/Development</i>
Water affinity	Occupancy is more likely at points with greater access and proximity to local and landscape-scale water features.	Water (Point-level) + <i>Water (City-level)</i>
Tree + Development	Occupancy is more likely with increasing tree cover and less likely with increasing development.	Development + Tree
Water Interaction	Occupancy is more likely at points with greater access and proximity to local and water features, but this effect is lower with greater water at the landscape scale.	Water (Point-level) * <i>Water (City-level)</i>
Tree Double Interaction	Occupancy is more likely at points with increasing tree local tree cover, which mitigates the negative effect of development. However, in cities with high tree cover, this local effect is muted.	Development * Tree + Tree * <i>Tree/Development</i>
Tree-Tree Interaction	Occupancy is more likely at points with higher tree local tree cover, but this effect is lower in cities with higher tree cover.	Tree * <i>Tree/Development</i> + Water (Point-level)
Tree-Development Interaction	Occupancy is more likely at points with higher tree local tree cover, which mitigates the negative effect of development.	Tree * Development+ Water (Point-level)
Local	Occupancy is more likely at points with higher local access to foraging and roosting habitat, lower development and traffic, and increasing proximity to water features.	Tree + Development + Water (Point-level)
Landscape	Occupancy is more likely at points with higher access to foraging and roosting habitats at a landscape scale and increasing access to water features.	<i>Tree/Development</i> + <i>Water (City-level)</i>
Global Additive	Occupancy is more likely at points with higher local and landscape access to habitat, lower development and traffic, and increasing proximity to water features.	Tree + Development + Water (Point-level) + <i>Water (City-level)</i> + <i>Tree/Development</i>

Analysis 2: Species Richness Modeling

We also conducted species richness analyses using point-level and city-level richness as response variables in generalized linear models. Point-level species richness was the total number of different species recorded at a sample point across both survey nights. Calls manually vetted to acoustic or frequency grouping were counted toward the richness tally when species-level identification was not possible. City-level richness was calculated using the same methods but was undertaken cumulatively for all the sampling events within a city.

For point-level richness, we fitted a suite of generalized linear mixed hurdle models with zero-truncated negative binomial distributions using the glmmTMB package (v.1.1.9, Brooks et al. 2024) in R. We used a hurdle approach as for most points (63%) species richness was 0 or 1, and we wanted to ensure our richness analysis was not skewed by mere presence-absence responses already accounted for in our occupancy analysis. In hurdle models, the data are analyzed in a model with the original response variable reduced to a binary system (0 or 1, where 1 represents any sampling event with ≥ 1 call) and a conditional model that predicts only responses ≥ 1 .

We implemented the same 3-step modeling approach as in Analysis 1 (Table 2.6), with the variable groupings as fixed effects. As we were measuring the cumulative richness across two sampling events at a sample point, we averaged the time after sunset (Time_p), temperature (Temp_p), and (Wind_p) across both sampling events and included them as fixed effects in every non-null model to account for their effects on detection. We used the same variable list from the univariate pruning Step 2 in the occupancy modeling process (Table 2.5). We excluded the 20 points missing a sampling event, and the sample city was included as a random effect to account for potential within-city spatial autocorrelation. This resulted in sampling units of 844 points within 36 cities.

We fitted generalized linear models to predict the response of city-level richness, with $n = 36$. We used the glmmTMB package with a Poisson distribution, as our response was count data, and there was no evidence of overdispersion ($\hat{c} = 0.30$). As every city had a species richness of at least 2, we did not have the same issue with zero inflation as we did with point-level richness. We scaled and centered all variables prior to conducting the same three-step modeling process as Analysis 1. We selected our detection variables by ranking a combination of models, including the start time (Time_c), temperature (Temp_c), and wind speed (Wind_c) averaged across

all sample events in a city as fixed effects. For univariate and hypothesis modeling, we incorporated only city-wide habitat characteristics used in the other analyses (Table 2.7). We also examined the effect of an additional variable, the city-averaged latitude (Lat.), as cooler climates at more northern latitudes may have lower activity and richness. We did not test longitude as a variable because there is no easily discernible east-west factor affecting bat richness or abundance within our study range of the Midwestern U.S., though this presents an opportunity for future research.

Table 2.7: Models and hypothesized effects of variables used in the analysis of city-level bat species richness.

Model Name	Richness Hypothesis	Model
Null	Occupancy is constant	Constant
Water landscape	Species richness is higher in cities with greater access to water at the landscape scale	<i>Water (Intracity)</i>
Tree landscape	Species richness is higher in cities with greater access landscape scale access to natural foraging and roosting habitat	<i>Canopy (Intracity)</i>
Water + Latitude	Species richness is higher in the south and cities with greater access to water at the landscape scale	<i>Water (Intracity) + Lat.</i>
Tree + Latitude	Species richness is higher in the south and cities with greater access landscape scale access to natural foraging and roosting habitat	<i>Canopy (Intracity) + Lat. (Intracity)</i>
Water * Latitude	Species richness is higher with greater access to water at the landscape scale, and this response depends on latitude	<i>Water (Intracity) * Lat.</i>
Tree * Latitude	Species richness is higher in cities with greater access landscape scale access to natural foraging and roosting habitat, and this effect is greater in the south	<i>Canopy (Intracity) * Lat.</i>
Global	Species richness is higher in the south and cities with greater access to water and foraging habitat at the landscape scale	<i>Water (Intracity) + Canopy (Intracity) + Lat.</i>

Results

Summary statistics

Across the 36 cities we sampled, we recorded 6,929 bat call files during our 1,705 total successful sampling events for an average of 192.5 calls per city, 8.1 calls per sample point, and 4.1 calls per sampling event. We manually vetted voucher calls from 9 different species across all our files (see Table 2.3), averaging 4.4 confirmed species per city (Figure 2.5). Cedar Rapids, IA had the highest richness, with 7 species (Figure 2.5A). Two cities—Lincoln, NE and Des Moines, IA—also stood out for having the highest bat activity, totaling >500 call files across all survey points (Figure 2.5B), in addition to both having 6 species.

At least one bat call was recorded in 705 of 860 successfully sampled point locations, resulting in a naïve bat occupancy of 82.0%. The big brown + silver-haired bat acoustic grouping (EPFULANO) was encountered most often, both in number of sites occupied (n=600) and total number of calls recorded (n=4359), representing 62.9% of all bat calls recorded (Figure 2.6). The EPFULANO group occupied the most sites in 33 of 36 cities. In comparison, the eastern red + evening bat acoustic group (LABONYHU) occupied more sites in 3 cities located at the southern extent of our survey (Figure 2.7). The LABONYHU group was the second most frequently encountered overall (332 sites, 1612 calls), followed by hoary bats (LACI, 129 sites, 242 calls). We recorded relatively few calls from the *Myotis* group (MYO, n=11), tricolored bat (PESU, n=7), and Brazilian free-tailed bat (TABR, n=4); due to the low sample size, occupancy models for these species did not converge so we excluded them from the analyses.

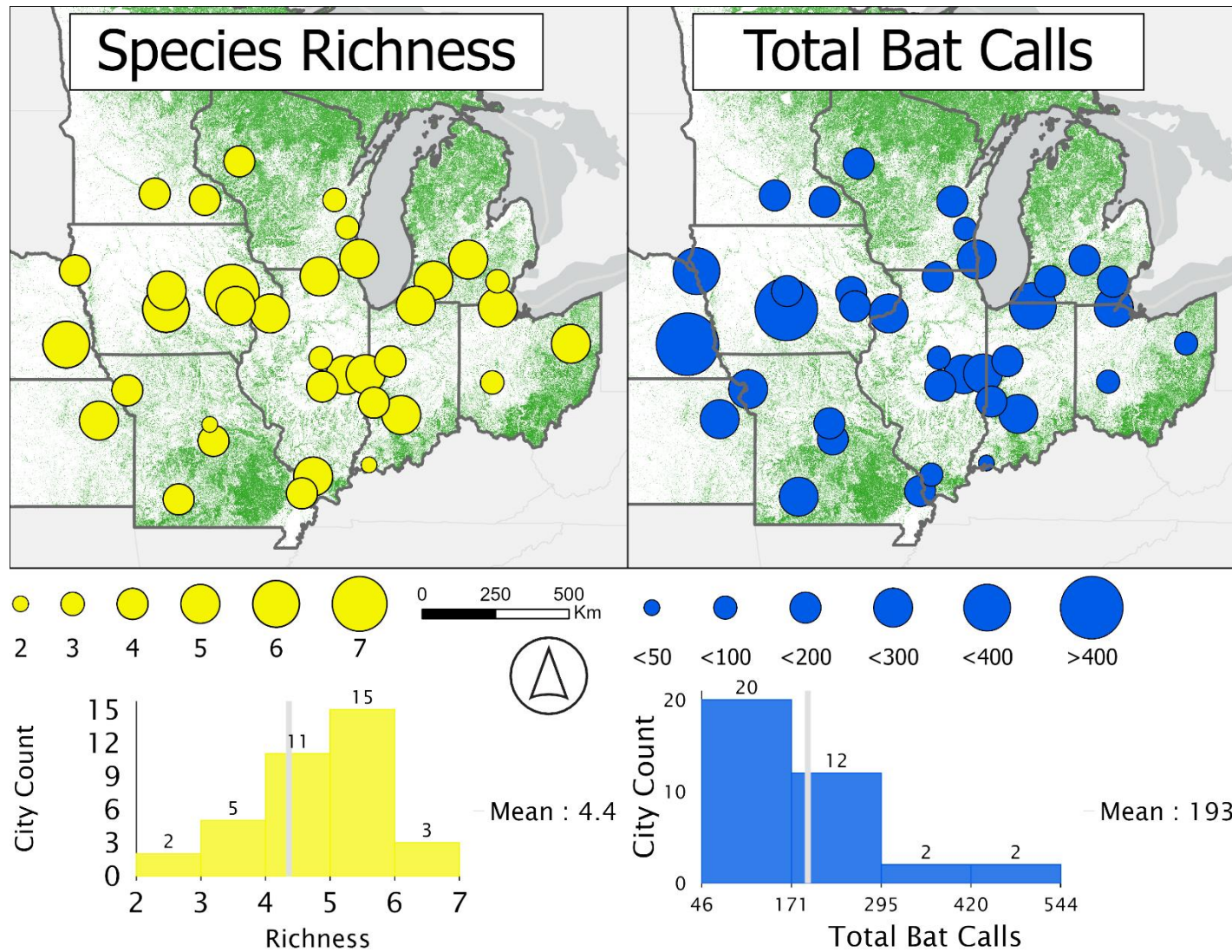


Figure 2.5: Left, a map and histogram of confirmed species richness for the cities surveyed in the Bats in Small Cities Project. Right a map and histogram of total bat calls for each city sampled. The gray lines in the histograms represent the mean across all cities.

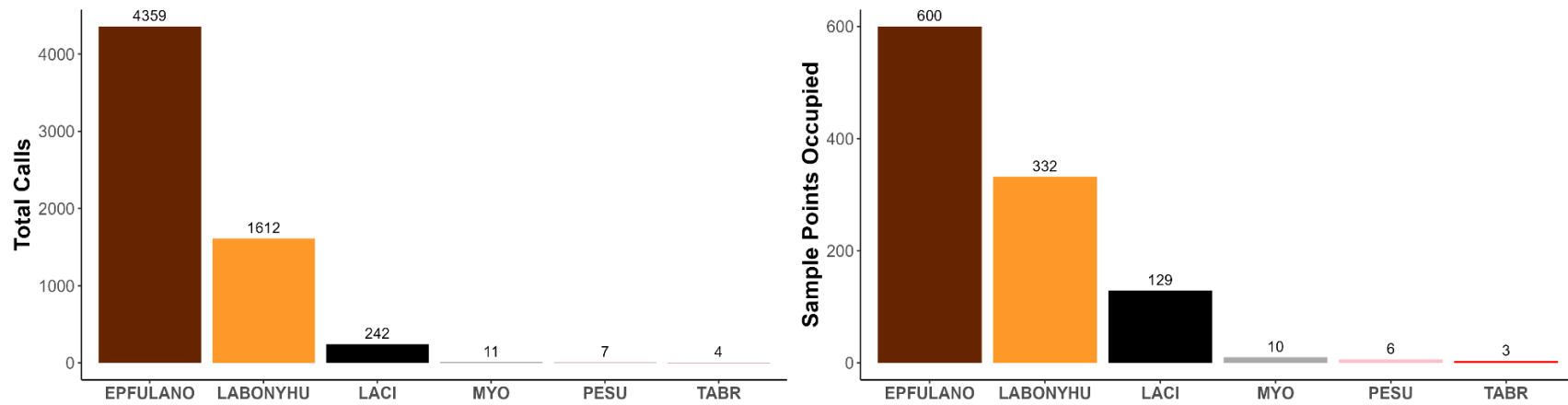


Figure 2.6: Left, bar plot of total calls per acoustic grouping across Midwestern cities, showing that the big brown + silver-haired bat (EPFULANO) grouping generated the largest number of calls, followed by the eastern red + evening bat grouping (LABONYHU), hoary bat (LACI), calls from the *Myotis* genus (MYO), tricolored bat (PESU), and Brazilian free-tailed bat (TABR). Right, bar plot of total sites, or sample points, occupied for each acoustic grouping across Midwestern cities, showing that the EPFULANO grouping occupied the largest number of sites.

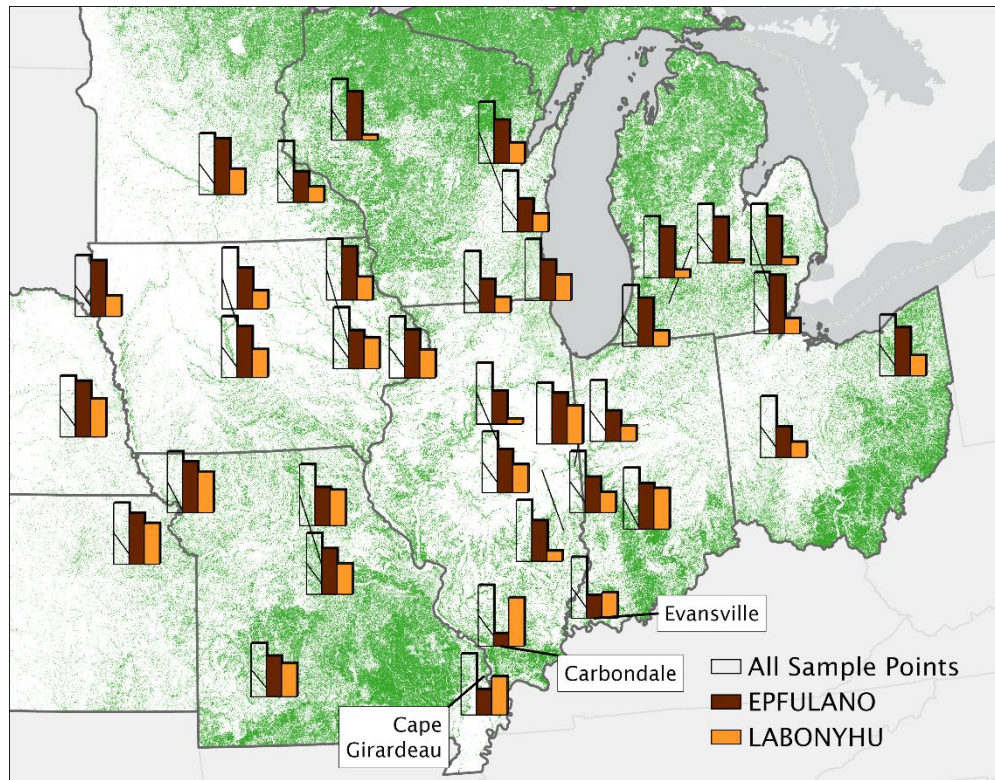


Figure 2.7: A map comparing the number of sample points occupied by the big brown + silver-haired bat acoustic grouping (EPFULANO) and eastern red + evening bat grouping (LABONYHU) compared to the total number of sample points in each city surveyed during the Bats in Small Cities Project ($n = 24$ except Lansing, MI and Springfield, MO). The three cities with higher LABONYHU occupancy than EPFULANO occupancy—Cape Girardeau, Carbondale, and Evansville—are labeled.

Analysis 1: Multiscale Occupancy Modeling

For our big brown + silver-haired bat group (EPFULANO) occupancy modeling, the Tree Double Interaction Model was the best fit (Table 2.8). Within this model, the averaged point-level occupancy estimate ($\hat{\theta}$) was 0.89 (θ range = 0.84–0.97, $\widehat{SE} = 0.028$, SE range = 0.026–0.034), which was moderately higher than the naïve occupancy rate of 0.70. The averaged detection probability ($\hat{p}$) was 0.64 (p range = 0.58–0.69, $\widehat{SE} = 0.019$, SE range = 0.018–0.20). EPFULANO was more likely to occupy points with higher mean tree canopy cover within 100 m (Canopy [100 m]) and further from water features (Water Dist.) and less likely to occupy points with great local high-intensity development (High/Med. Development [100 m]) (Table 2.9, Figure 2.8). There was a significant interaction between local tree cover and average tree cover within the city UAC boundary (Canopy [100 m] * Canopy [Intracity]), as EPFULANO were more likely to occupy points with high local tree cover in cities with lower overall intracity tree cover. For p covariates, time after sunset (Time_E) negatively predicted EPFULANO detection, while temperature (Temp_E) at sunset had a positive effect on detection.

Table 2.8: AICc rankings, number of parameters (K), and weights (w_i) for 12 hypothesis-based multi-scale models and the null model predicting occupancy of the big brown + silver-haired bat acoustic group (EPFULANO) across 36 Midwestern U.S. cities. The Tree Double Interaction Model, in **bold**, was the only competitive model. For all models, $p = \text{Time}_E + \text{Temp}_E$ and ψ held constant.

Hypothesis Model	θ	K	ΔAICc	w_i
Tree Double Interaction	Canopy (100 m) * Canopy (Intracity) + Canopy (100 m) * High/Med. Devel. (100 m) + Water Dist.	10	0.00	0.95
Tree -Tree Interaction	Canopy (100 m) * Canopy (Intracity) + Water Dist.	8	7.26	0.03
Global Additive	Canopy (100 m) + Water (Intracity) + Canopy (Intracity) + High/Med. Devel. (100 m) + Water Dist.	9	7.59	0.02
Anthropogenic Avoidance	High/Med. Devel. (100 m) + Canopy (Intracity)	7	20.31	< 0.01
Tree Affinity	Canopy (100 m) + Canopy (Intracity)	6	24.50	< 0.01
Tree-Development Interaction	Canopy (100 m) * High/Med. Devel. (100 m) + Water Dist.	8	25.08	< 0.01
Local	Canopy (100 m) + High/Med. Devel. (100 m) + Water Dist.	7	25.40	< 0.01
Tree + Development	High/Med. Devel. (100 m) + Canopy (100 m)	6	37.48	< 0.01
Landscape	Canopy (Intracity) + Water (Intracity)	6	39.01	< 0.01
Water	Water Dist. + Water (Intracity)	6	50.18	< 0.01
Water Landscape	Water (Intracity)	5	52.47	< 0.01
Water Interaction	Water Dist. * Water (Intracity)	7	53.02	< 0.01
Null	Constant	4	54.56	< 0.01

Table 2.9: Parameters, estimates, standard errors (SE), lower (LCL) and upper (UCL) 85% confidence limits for variables included in the top multi-scale occupancy model (Tree-Interaction Model) predicting big brown + silver-haired bat acoustic group (EPFULANO) detection probability (p), point-level occupancy (θ), and city-level occupancy (ψ , held constant) across 36 Midwestern cities. Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant.

Model	Parameter	Estimate	SE	LCL	UCL
p	Intercept	-2.24	0.47	-2.92	-1.56
	Time_E	-0.0042	0.0010	-0.0056	-0.0028
	Temp_E	0.15	0.021	0.12	0.17
θ	Intercept	1.33	0.82	0.15	2.52
	Canopy (100 m)	0.12	0.048	0.052	0.19
	Canopy (Intracity)	-0.024	0.034	-0.073	0.026
	High/Med. Development (100 m)	-0.037	0.011	-0.052	-0.021
	Water Dist.	0.0019	0.00070	0.0009	0.0029
	Canopy (100 m) * Canopy (Intracity)	-0.0046	0.0018	-0.0072	-0.0020
	Canopy (100 m) * High/Med. Development (100 m)	0.00081	0.00058	-0.000024	0.0016
ψ	Intercept	24.48	5649.09	-8110.20	8159.16

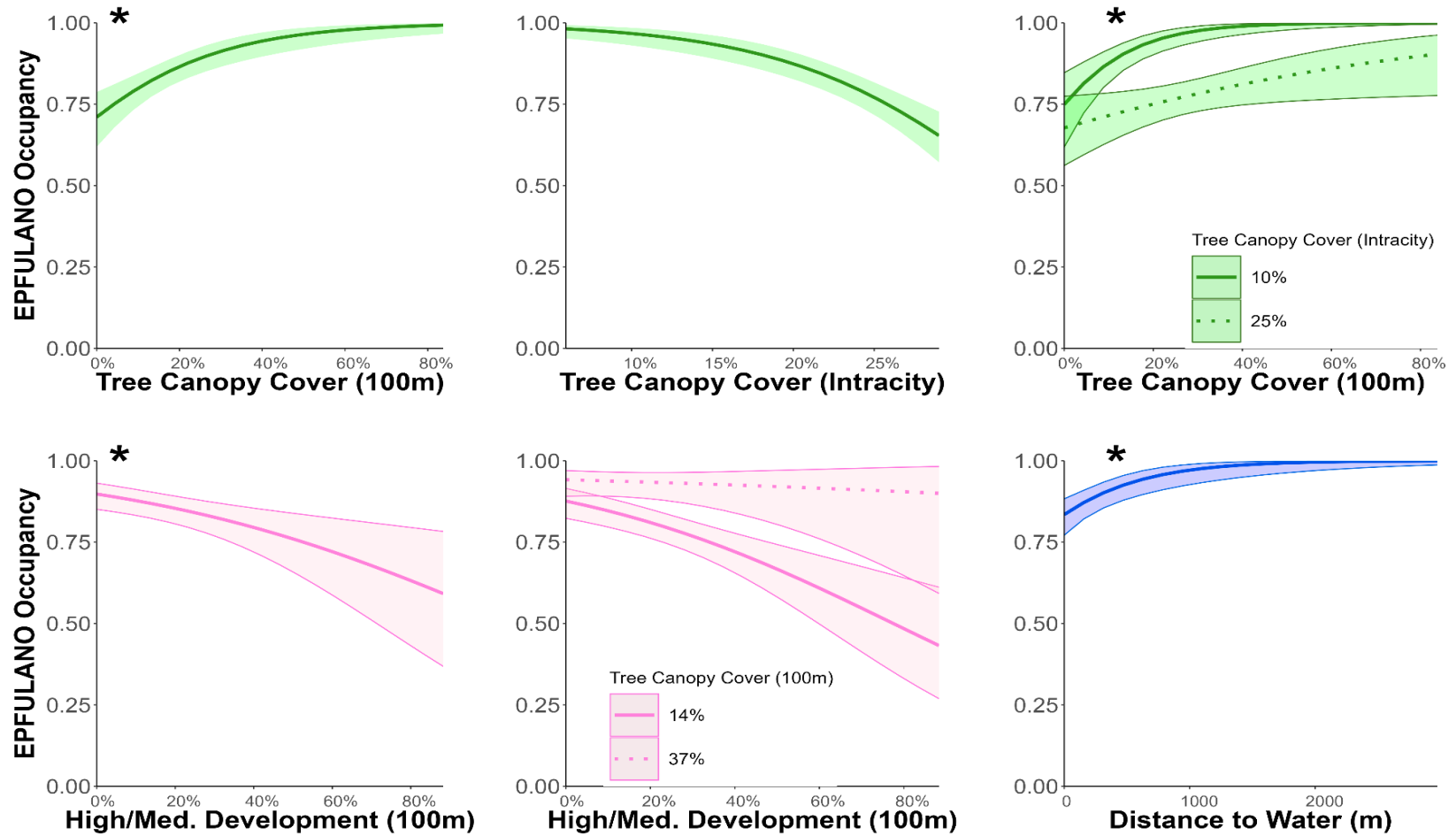


Figure 2.8: Predicted point-level (θ) big brown + silver-haired bat acoustic group (EPFULANO) occupancy for all covariates in top performing Tree Double Interaction Model, with all other variables held at mean values. Going clockwise, from the top left: Canopy (100 m), Canopy (Intracity), Canopy (100 m) * Canopy (100 m), Water Dist., High/Med. Devel. (100 m), High/Med. Devel. (100 m) * Canopy (100 m). An * indicates ecologically significant parameter estimates with 85% confidence intervals that do not overlap with zero.

For the eastern red + evening bat acoustic group (LABONYHU), three models were competitive (Table 2.10). The point-level occupancy estimate ($\hat{\theta}$), averaged across all three models, was 0.62 (θ range = 0.58–0.66, $\widehat{SE} = 0.045$, SE range = 0.044–0.055). $\hat{\theta}$ was substantially higher than the naïve occupancy rate of 0.39, and the average probability of detection ($\hat{p}$) was 0.39 (p range = 0.35–0.42, $\widehat{SE} = 0.029$, SE range = 0.028–0.031). LABONYHU occupancy was less likely farther from forest (Forest Dist.) in all competitive models (Table 2.11, Figure 2.9). An increasing proportion of local open water (Water [500 m]) negatively predicted occupancy in two of the models, while increasing average tree cover outside of the urban areas (Canopy [Landscape]) positively predicted occupancy in one model. LABONYHU detections were more likely with increasing temperature (Temp._E) at sunset and less likely with increasing time after sunset (Time_E).

Table 2.10: AICc rankings, number of parameters (K), and weights (w_i) for 12 hypothesis-based multi-scale models and the null model predicting occupancy of the eastern red + evening bat acoustic group (LABONYHU) across 36 Midwestern U.S. cities. The Local, Tree Interaction, and Tree Affinity models, in **bold**, were all competitive models. For all models, $p = \text{Time}_E + \text{Temp}_E$ and ψ held constant.

Hypothesis Model	θ	K	ΔAICc	w_i
Local	Forest Dist. + High/Med. Devel. (100 m) + Water (500 m)	7	0.00	0.34
Tree Interaction	Forest Dist. * Canopy (Landscape) + Water (500 m)	8	0.31	0.29
Tree Affinity	Forest Dist. + Canopy (Landscape)	6	1.07	0.20
Tree-Development Interaction	Forest Dist. * High/Med. Devel. (100 m) + Water (500 m)	8	2.94	0.08
Global Additive	Forest Dist. + Water (Intracity) + Canopy (Landscape) + High/Med. Devel. (100 m) + Water (500 m)	9	4.00	0.05
Tree + Development	High/Med. Devel. (100 m) + Forest Dist.	6	4.63	0.03
Tree Double Interaction	Forest Dist. * Canopy (Landscape) + Forest Dist. * High/Med. Devel. (100 m) + Water (500 m)	10	6.35	0.01
Landscape	Canopy (Landscape) + Water (Intracity)	6	9.65	< 0.01
Anthropogenic Avoidance	High/Med. Devel. (100 m) + Canopy (Landscape)	6	12.51	< 0.01
Water	Water (500 m) + Water (Intracity)	6	12.59	< 0.01
Water Interaction	Water (500 m) * Water (Intracity)	7	13.48	< 0.01
Water Landscape	Water (Intracity)	5	14.53	< 0.01
Null	Constant	4	16.16	< 0.01

Table 2.11: Parameters, estimates (Est.), lower (LCL), and upper (UCL) 85% confidence limits for variables included in the three competitive multi-scale occupancy models (Local, Tree Interaction, Tree Affinity) predicting eastern red + evening bat acoustic group (LABONYHU) detection probability (p), point-level occupancy (θ), and city-level occupancy (ψ , held constant) across Midwestern cities. The variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. Forest Dist. was the only ecologically significant variable across all θ models, while Time and Temp. were ecologically significant across all p models.

	ψ	θ						p		
				Forest Dist. * Canopy (Landscape)	High/Med. Devel. (100 m)	Canopy Landscape	Water (500 m)			
Parameter	Intercept	Intercept	Forest Dist.					Intercept	Time	Temp
Model	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL	Est., LCL, UCL
Local	20.2 -4775, 4815	0.95 0.59, 1.30	-0.00057 -0.00080, -0.00034		-0.0073 -0.018, 0.0030		-0.058 -0.087, -0.029	-2.11 -2.90, -1.33	-0.0042 -0.0058, -0.0026	0.094 0.063, 0.13
Tree	21.72, -9850, 9893	0.47 -0.070, 1.01	-0.00057, -0.00097, -0.00017	9.31 E ⁻⁶ , -2.86 E ⁻⁵ , 4.72 E ⁻⁵		0.017 -0.0038, 0.038	-0.054, -0.084, -0.025	-2.01 -3.08, -0.94	-0.0044 -0.0066, -0.0022	0.092 0.048, 0.14
Tree Affinity	19.34, -5083, 5122	0.35 -0.18, 0.88	-0.00048 -0.00079, -0.00017			0.020 0.00016, 0.040		-2.03 -3.11, -0.96	-0.0044, -0.0065, -0.0022	0.092, 0.049, 0.14

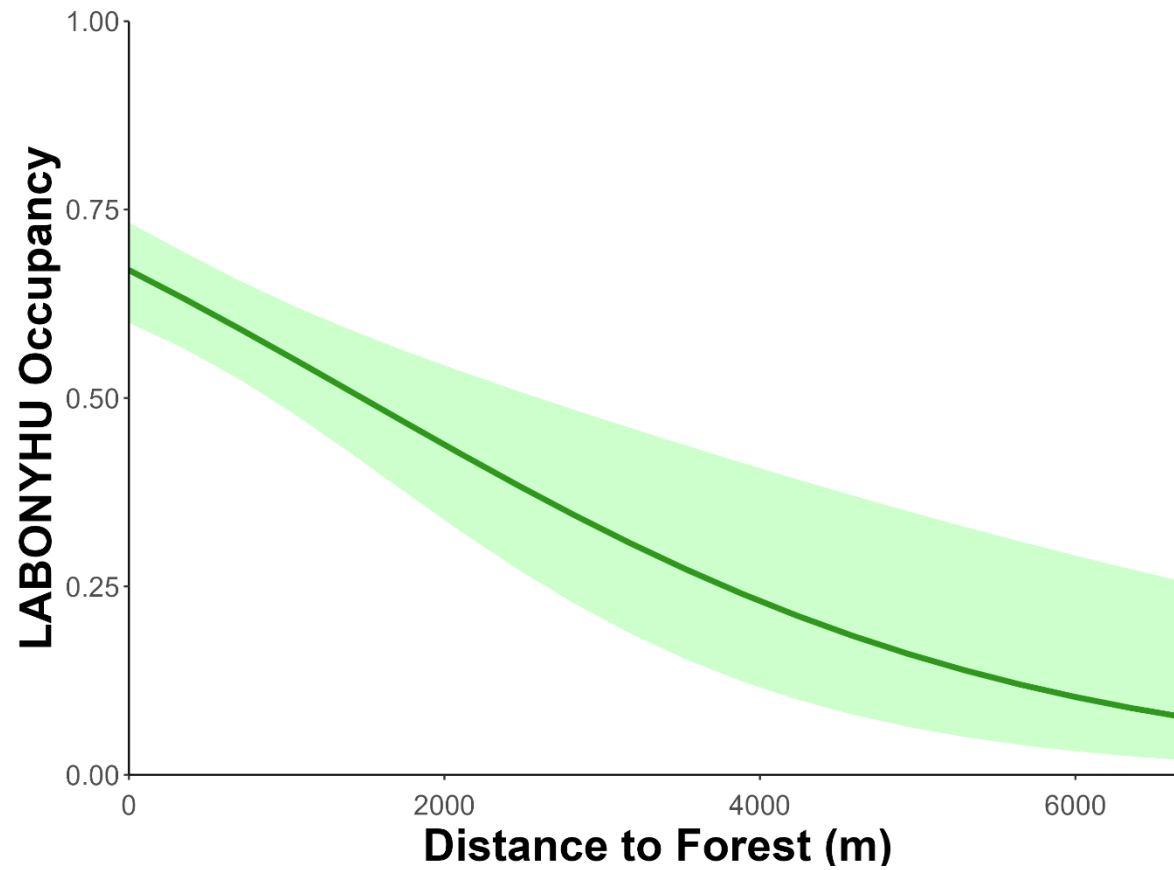


Figure 2.9: Predicted point-level (θ) eastern red + evening bat acoustic group (LABONYHU) occupancy for Forest Dist. in the competitive Tree Affinity Model, with all other variables held at mean values. The probability of point-level LABONYHU occupancy decreases at distances further from forest patches, and this effect is considered ecologically significant as the 85% confidence interval does not overlap with zero.

For the hoary bat (LACI), only the Tree Affinity model was competitive (Table 2.12). Within this model, the averaged point-level occupancy estimate ($\hat{\theta}$) was 0.54 (θ range = 0.44–0.60, $\widehat{SE} = 0.15$, SE range = 0.12–0.16), substantially higher than the naïve occupancy rate of 0.15. The large difference between $\hat{\theta}$ and the naïve occupancy was likely driven by the very low probability of detection, as the average ($\hat{p}$) was 0.15 (p range = 0.13–0.17, $\widehat{SE} = 0.036$, SE range = 0.031–0.039). LACI were less likely to occupy points with more mean tree cover within the UAC boundary (Canopy [Intracity]) but more likely to occupy points closer to forest (Forest Dist., Table 2.13, Figure 2.10).

Table 2.12: AICc rankings, number of parameters (K), and weights (w_i) for 12 hypothesis-based multi-scale models and the null model predicting occupancy of the hoary bat (LACI) across 36 Midwestern U.S. cities. The Tree Affinity model, in **bold**, was the only competitive model. For all models, $p = \text{Time}_E + \text{Temp}_E$ and ψ held constant.

Hypothesis Model	ψ	K	ΔAICc	w_i
Tree Affinity	Forest Dist. + Canopy (Intracity)	7	0.00	0.86
Anthropogenic Avoidance	High/Med. Devel. (100 m) + Canopy (Intracity)	7	5.79	0.05
Canopy Interaction	Forest Dist. * Canopy (Intracity) + Water Dist.	9	6.48	0.03
Landscape	Canopy (Intracity) + Water (Landscape)	7	6.67	0.03
Global Additive	Forest Dist. + Water (Landscape) + Canopy (Intracity) + High/Med. Devel. (100 m) + Water Dist.	10	8.62	0.01
Canopy Double Interaction	Forest Dist. * Canopy (Intracity) + Forest Dist. * High/Med. Devel. (100 m) + Water Dist.	11	8.83	0.01
Water Landscape	Water (Landscape)	6	12.80	< 0.01
Water Interaction	Water Dist. * Water (Landscape)	8	14.05	< 0.01
Water	Water Dist. + Water (Landscape)	7	14.48	< 0.01
Null	Constant	5	18.68	< 0.01
Canopy + Development	High/Med. Devel. (100 m) + Forest Dist.	7	20.75	< 0.01
Canopy-Development Interaction	Forest Dist. * High/Med. Devel. (100 m) + Water Dist.	9	21.82	< 0.01
Local	Forest Dist. + High/Med. Devel. (100 m) + Water Dist.	8	23.97	< 0.01

Table 2.13: Parameters, estimates, standard errors (SE), lower (LCL) and upper (UCL) 85% confidence limits for variables included in the top multi-scale occupancy model (Tree Affinity model) predicting hoary bat detection probability (p), point-level occupancy (θ), and city-level occupancy (ψ , held constant) across Midwestern cities. Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant.

Model	Parameter	Estimate	SE	LCL	UCL
p	Intercept	0.074	0.80	-1.50	1.65
	Time_E	-0.0064	0.0016	-0.010	-0.0033
	Temp _E	-0.043	0.030	-0.10	0.016
θ	Intercept	4.55	2.16	0.32	8.78
	Forest Dist.	-0.0011	0.00053	-0.0022	-0.0001
	Canopy (Intracity)	-0.21	0.080	-0.37	-0.057
ψ	Intercept	3.36	1.21	0.99	5.74

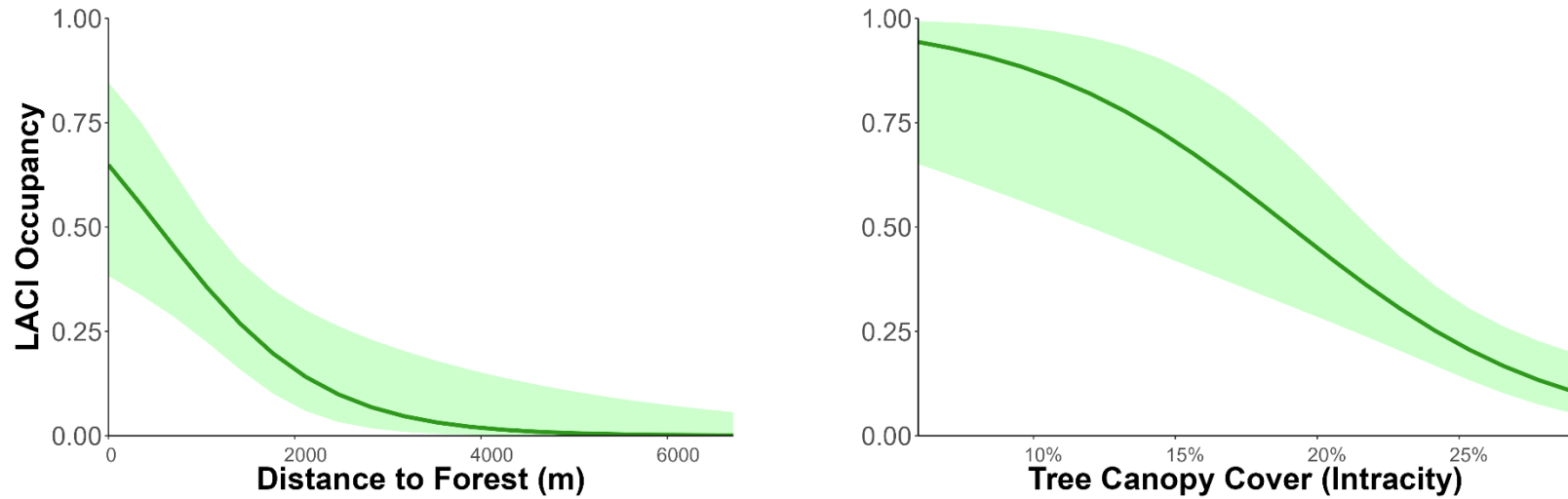


Figure 2.10: Predicted point-level (θ) hoary bat (LACI) occupancy for Forest Dist.—**Left**, and Canopy (Intracity)—**Right**, in the top performing Tree Affinity Model, with all other variables held at mean values. The probability of point-level hoary bat occupancy decreases at distances further from forest patches and decreases with increasing intracity tree cover; these effects are considered ecologically significant as their 85% confidence intervals do not overlap with zero.

Analysis 2: Species Richness Modeling

For our modeling of species richness at the point level, there were three competitive models (Table 2.14). Within the zero-truncated models, temperature (Temp.p) and the proportion of local canopy cover (Canopy [100 m]) were ecologically significant across all three models, with increasing temperature and increasing canopy cover positively predicting bat presence (Table 2.15). In the conditional model, point-level species richness decreased with increasing time after sunset (Time_p) (Figure 2.11). For city-level richness, no model outperformed the null (Table 2.16), indicating that none of the models we tested were strong predictors of overall richness.

Table 2.14 AICc rankings for generalized linear mixed “hurdle” models predicting point-level bat richness, with City included as a random effect. All models included a binary component with a binomial distribution and a conditional component with a negative binomial distribution. All models marked in **bold** (Global Additive, Tree-Development Interaction, Tree + Development) were competitive.

Hypothesis Model	Fixed Effects	K	ΔAIC_c	w_i
Global Additive	Canopy (100 m) + High/Med. Devel. (100 m) + Water Dist. + Canopy (Intracity) + Water (Intracity) + Time_p + Temp._p	19	0.00	0.29
Tree-Development Interaction	Canopy (100 m) * High/Med. Devel. (100 m) + Time_p + Temp._p	17	0.13	0.27
Tree + Development	Canopy (100 m) + High/Med. Devel. (100 m) + Time_p + Temp._p	13	1.14	0.16
Anthropogenic Avoidance	High/Med. Devel. (100 m) + Canopy (Intracity) + Time _p + Temp. _p	13	2.28	0.09
Local	Canopy (100 m) + High/Med. Devel. (100 m) + Water Dist. + Time _p + Temp. _p	15	2.33	0.09
Tree Double Interaction	Canopy (100 m) * High/Med. Devel. (100 m) + Canopy (100 m)* Canopy (Intracity) + Water Dist. + Time _p + Temp. _p	21	2.56	0.08
Tree Affinity	Canopy (100 m) + Canopy (Intracity) + Time _p + Temp. _p	13	10.65	< 0.01
Tree Interaction	Canopy (100 m) * Canopy (Intracity) + Time _p + Temp. _p	17	13.19	< 0.01
Water Landscape	Water (Intracity) + Time _p + Temp. _p	11	20.42	< 0.01
Water	Water Dist. + Water (Intracity) + Time _p + Temp. _p	13	22.40	< 0.01
Landscape	Canopy (Intracity) + Water (Intracity) + Time _p + Temp. _p	13	22.41	< 0.01
Detection (Null)	Time _p + Temp. _p	9	23.05	< 0.01
Water Interaction	Water Dist. * Water (Intracity) + Time _p + Temp. _p	15	25.86	< 0.01

Table 2.15: Parameters, estimates (Est.), lower (LCL), and upper (UCL) 85% confidence limits for variables included in the three competitive hurdle models (Global Additive, Tree-Development Interaction, Tree + Development) predicting point-level bat presence (binary component, binomial distribution) and species richness (conditional component, negative binomial distribution) across Midwestern cities. The variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. Canopy (100 m) and Temp_p positively predicted bat presence and were the only ecologically significant variables across all binary models. Increasing Time_p negatively predicted bat species richness and was the only significant variable in the conditional models.

Component	Parameter	Global Additive Model				Tree-Development Interaction				Tree + Development			
		Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
Binary	Intercept	1.80	0.16	1.56	2.04	1.95	0.19	1.68	2.22	1.79	0.18	1.54	2.04
	Temp_p	0.28	0.12	0.10	0.46	0.28	0.13	0.10	0.47	0.26	0.13	0.08	0.45
	Time _p	0.05	0.10	-0.10	0.19	0.05	0.10	-0.10	0.19	0.06	0.10	-0.09	0.20
	High/Med. Devel. (100 m)	-0.37	0.10	-0.52	-0.22	-0.13	0.15	-0.34	0.09	-0.37	0.10	-0.52	-0.22
	Water Dist.	0.15	0.12	-0.03	0.32	0.17	0.12	-0.01	0.34				
	Water (Intracity)	0.32	0.17	0.07	0.56								
	Canopy (100 m)	0.20	0.12	0.02	0.38	0.31	0.13	0.12	0.50	0.17	0.12	0.001	0.35
	Canopy (Intracity)	-0.16	0.16	-0.39	0.07								
	Canopy (100 m) * High/Med. Devel. (100 m)					0.32	-0.13	0.13	0.51				
Conditional	Intercept	0.01	0.06	0.10	-0.08	0.004	0.07	0.11	-0.10	0.003	0.07	0.10	-0.09
	Temp _p	0.05	0.05	0.13	-0.02	0.04	0.06	0.12	-0.04	0.04	0.06	0.13	-0.04
	Time_p	-0.17	0.05	-0.10	-0.24	-0.18	0.05	-0.11	-0.25	-0.18	0.05	-0.11	-0.25
	High/Med. Devel. (100 m)	-0.05	0.06	0.04	-0.13	-0.05	0.07	0.04	-0.15	-0.06	0.06	0.03	-0.14
	Water Dist.	-0.05	0.05	0.02	-0.13	-0.05	0.05	0.03	-0.13				
	Water (Intracity)	-0.10	0.06	-0.01	-0.19								
	Canopy (100 m)	0.09	0.05	0.16	0.01	0.07	0.06	0.16	-0.02	0.07	0.05	0.15	-0.002
	Canopy (Intracity)	-0.12	0.06	-0.03	-0.20								
	Canopy (100 m) * High/Med. Devel. (100 m)					-0.002	0.07	0.09	-0.10				

Table 2.16: AICc rankings, number of parameters (K), and weights (w_i) for generalized linear models predicting city-level bat richness. Models were fitted under a Poisson distribution. Only the Detection (Null) model was competitive.

Hypothesis Model	Covariates	K	$\Delta AICc$	w_i
Detection (Null)	Time_C + Temp._C	3	0	0.62
Natural Affinity	Canopy (Intracity) + Time _C + Temp. _C	4	2.01	0.22
Tree + Latitude	Canopy (Intracity) + Lat. + Time _C + Temp. _C	5	4.64	0.06
Water + Latitude	Water (Intracity) + Lat. + Time _C + Temp. _C	5	4.98	0.05
Water-Latitude Interaction	Water (Intracity) * Lat. + Time _C + Temp. _C	6	7.00	0.02
Tree-Latitude Interaction	Canopy (Intracity) * Lat. + Time _C + Temp. _C	6	7.37	0.02
Global	Canopy (Intracity) + Water (Intracity) + Lat. + Time _C + Temp. _C	6	7.52	0.01

Discussion

The expansion of cities threatens wildlife populations and brings them closer to human contact (Simkin et al. 2022). Understanding how the urban environment influences city-dwelling animals across different landscapes is crucial for developing management solutions to promote wildlife conservation successfully. While responses to between-city differences have been reported for terrestrial mammal species (Fidino et al. 2021, Magle et al. 2021, Haight et al. 2023), this dynamic had not yet been explored for North American bat assemblages. Our research demonstrates the importance of considering between-city differences when studying urban ecology of wildlife generally and bats specifically. By harnessing a multi-city community science network, we identified that some urban bats respond to tree cover at local- and city-wide scales and in differing ways. Our results emphasize the importance of urban trees for supporting bats in cities. In addition, we found that some bats respond differently to their local environment depending on the overall landscape of their city. This finding highlights the value in using a multi-city approach because such studies may detect between-city differences driving ecological responses. We recommend more multi-city studies to inform tailored land management strategies by city type.

Bats' responses to tree cover varied with city and landscape context and by species. Locally, bat presence and occupancy of every individual bat grouping responded positively to either increasing tree cover or proximity to forests, though for big brown + silver-haired bats, this effect was only important in cities with low city-wide tree cover. Our results indicate that trees are a crucial resource for urban bats, which is logical because trees provide foraging habitat (Lumsden and Bennett 2005, Polyakov et al. 2019) and natural roosting habitat (Brigham et al. 2007). Previous studies have found positive effects of canopy cover on urban bat activity (Dixon 2011, Moretto et al. 2019, Straka et al. 2019), and our results corroborate these findings. However, responses to tree cover may differ among species (Li and Wilkins 2014) and at different spatial scales (Gallo et al. 2017). The fact that tree cover is decreasing in urban areas across North America (Nowak and Greenfield 2020) presents added challenges for urban bat populations that depend upon trees as foraging and natural roosting habitat.

Reductions in tree cover could reduce foraging habitat for urban bat populations. The positive effects of local tree cover were higher in cities with low tree cover, suggesting that bats may concentrate their foraging in tree-dense areas when there is little tree cover in the overall

city landscape. Within rural agricultural landscapes, trees may be rare on a landscape scale, driving bats to forage more intensely and thus be perceived as more active at survey points within small and fragmented forest patches, whereas activity may be more distributed across larger fragments (Fuentes-Montemayor et al. 2013). Illustrative of a similar dynamic for bats to seek out a scarce resource, *Nyctalus* sp., a riparian specialist, is less active over urban streams when there is a high proportion of water within 200m (Lintott et al. 2015). For cities with low canopy cover, tree-dense pockets like forest preserves may function like forest patches in agricultural landscapes as a congregating point for dense clusters of foraging big brown + silver-haired bats; in cities with high canopy cover, bats may spread out more evenly across the urban area.

Alternatively, the observed positive effect of tree cover on big brown + silver-haired bat occupancy in tree-sparse cities could be due to other mechanisms. This acoustic grouping could have greater true population density in cities with low tree cover due to greater artificial roost availability, as tree cover and development are often negatively correlated at a landscape scale (Moretto et al. 2019). For big brown bats, buildings may provide higher quality roosting habitat than some natural roosts (Lausen and Barclay 2006). Populations and occupancy rates may be higher in development-rich cities. American cities with high tree cover are often surrounded by more forested landscapes (Nowak and Greenfield 2020). Urban big brown bats will travel long distances to forage (Everette et al. 2001, Menzel et al. 2001), so it is possible that big brown + silver-haired bats may leave cities entirely to forage in large, high-quality rural forests, which may have more diverse insect populations compared to cities (Fenoglio et al. 2021). Lastly, bats may respond through a combination of the proposed mechanisms. Further research is needed to understand the dynamics between urban bat populations, distance to foraging habitat, and artificial roost availability to determine how best to conserve urban bat species.

While local access to tree cover and forests had a generally positive effect on bat occupancy, city-scale tree cover negatively affected hoary bat occupancy. As hoary bats roost in trees (Perry and Thill 2007), this negative response to tree cover was surprising. The most logical explanation is that tree cover reduced the detectability of echolocation calls, as detection rates were low for hoary bats overall. Like all bats, hoary bats increase call frequency in more cluttered environments (Barclay et al. 1999) like forests, and these high-frequency calls may have been misidentified or labeled only as “low-frequency bats”. In addition, hoary bats are

highfliers (up to 2,438 m, Peurach 2003), so their calls might be blocked by high tree canopy cover (Patriquin et al. 2003). Hoary bats have relatively larger foraging ranges than most other North American bats (Bonaccorso et al. 2015) and can travel distances up to 20 km in one night (Barclay 1989), so it is possible that hoary bats prefer to forage in rural areas less accessible to smaller bats, possibly to avoid within-city competition from the urban-associated big brown bat.

Anthropogenic features appear to negatively impact some bat groups, such as the big brown + silver-haired bats. While big brown bats respond positively to development at a 5000-m scale (Loeb et al. 2009), we saw the opposite response for big brown + silver-haired bats within a 100-m buffer. As highly urbanized areas typically support little insect biomass (Threlfall et al. 2012b), even synurban bats likely have fewer foraging opportunities in areas of locally high development. While bats may tolerate cities on a broad scale, they may prefer the less urbanized parts of cities, resulting in an uneven distribution of their valuable ecosystem services (Wang et al. 2023). Areas of intense development may thus suffer from reduced pest control (Schell et al. 2020). However, even in intensely developed areas, big brown + silver-haired occupancy is predicted to be ~50%; bats may be attracted to these spaces for reasons not accounted for in our models, such as nearby artificial roosts, hyper-local foraging sources (such as congregating insects at a streetlight, Jung and Kalko 2010), or the presence of commuting corridors (de Oyarzabal Barba 2023).

While water is an important resource for bats, it appears there is a complex relationship between urban-associated bats and water. We unexpectedly discovered lower big brown + silver-haired bat occupancy closer to water sources, which went against our hypothesis. A previous study found positive responses of these bats with proximity to water in Chicago (Lehrer et al. 2021). However, other urban studies have found no significant effect of proximity to water (Li and Wilkins 2014) or lower activity in some species with greater proportions of water in the landscape (Lintott et al. 2015). Placing sample points >30 m from water may have lessened our ability to detect bats that were flying directly over water bodies in cities. Alternatively, it is possible that bats meet water needs through smaller sources of drinking water in cities, such as puddles, fountains, or pools (Li and Wilkins 2014), and that urban bats are less dependent on larger water bodies.

Our analysis demonstrates that prescriptions for urban land management should be adapted to particular landscapes. For instance, we predict that increasing local tree cover by

planting trees in cities with very little intracity tree cover would increase big brown + silver-haired bat occupancy and may benefit their conservation. However, in an urban area with high intracity cover, improving forest conditions for bats may be a better strategy to support bat conservation. Nevertheless, we also found that some habitat variables can influence urban bat ecology regardless of landscape, suggesting there are some broader trends to keep in mind when assessing potential conservation actions. Converting highly developed areas into forested greenspaces should increase bat occupancy in cities, regardless of the landscape. While widespread land use change in this manner is unfeasible due to the competing needs of a city's human population, local replacement of unused developed plots, like abandoned parking lots or warehouses, with treed greenspaces could offer benefits to both people and bats. Trees offer benefits to people by filtering out air pollution (Sæbø et al. 2012), providing cooling effects (Kong et al. 2014), and improving mental health (Wolf et al. 2020). While we would predict higher bat occupancy in reforested urban spaces, we cannot know how individual bats would respond to these land management prescriptions or if these changes would increase bat fitness. It is unclear whether our occupancy results were driven by differences in bat behavior (e.g., bats in cities with low tree cover concentrate in small patches or commute to rural areas) or abundance (e.g., bats in cities with low tree cover have higher population densities of bats) between cities. While likely difficult to achieve, research examining how bat fitness responds to habitat restoration across different urban areas could illuminate what cities can do to better support chiropterans.

Preventing the loss of biodiversity is a cornerstone of the broader conservation movement (Williams et al. 2020). To support biodiversity in cities, we must understand how the urban environment shapes species richness; further work will be needed to investigate these dynamics in bats. While we found that Midwestern cities host a diversity of bat species, with an average of 4.4 species per city and a high of 7, we cannot make firm conclusions on what factors influence species richness, as both our point-level conditional and city-level models failed to produce ecologically significant covariates besides known detection variables.

The fact that no hypothesis-driven models explained city-level richness could be attributable to the temporal constraints of our survey. At each point we recorded only 20 minutes in total across both sampling events, meaning each city only had 480 minutes of data spread across 24 points. To detect rare species in an area as large as a city, several full nights of

acoustics at multiple sites is typically necessary to gain a more complete picture of bat species (Skalak et al. 2012). As bat species partition temporal niches, with some species being more active later in the night (Beilke et al. 2021), our short recording window might have missed some species that were actually present. While our surveys captured the peak period for bat activity, we would be less likely to record the rarer *Myotis* species (Beilke et al. 2021). We also did not survey during the spring or fall migratory periods for bats in the Midwest; species richness might have been higher had we recorded during the time when long-distance migrant's stopover in cities (e.g., Vlaschenko 2023b). Even with ephemeral use, cities may be vital for migratory bats, as some individuals, particularly juveniles, appear to be drawn to cities during migration (Vlaschenko 2023b). Future studies seeking to analyze what drives bat species richness within and between cities should aim for both spatial and temporal replication through long-term research.

Overall, we found relatively high naïve bat occupancy at a local level (82%), supporting previous work showing that bats, as a clade, are encountered even in highly developed parts of urban areas (Krauel and LeBuhn 2016). However, as is typical of urban bat assemblages (Russo and Ancillotto 2015), the occupancy rate varied greatly by acoustic grouping and was dominated by the big brown + silver-haired bat group, which occupied most survey sites and produced most of the recorded calls. These results align with previous studies that specifically found the big brown bat to be the dominant urban bat throughout the Midwest (Gehrt and Chelsvig 2004, Gallo et al. 2017, Kurta and Teramino 1992, Dixon 2011). For these reasons, we suspect the majority of the calls in the big brown + silver-haired grouping were generated by the big brown bat. Its large size and generalist habitat requirements (Agosta 2002) likely allow the big brown bat to dominate Midwestern cities. In addition, its relative resistance to the *Pseudogymnoascus destructans* fungus, the cause of white-nose syndrome (WNS), has allowed big brown populations to increase at hibernacula in which the little brown bat has experienced precipitous declines (Frank et al. 2014).

We showed that the eastern red + evening bats acoustic group may dominate certain cities, all clustered along the Ohio and Mississippi Rivers in the southern part of our study area. These results provide further support that the eastern red bat and evening bat are common urban residents. The eastern red bat has a similar degree of urban affinity as big brown bats (Wolf et al. 2022), and evening bats are commonly encountered in some urban areas (Hall and Bennett 2021)

and known to occasionally roost in buildings (Watkins 1972). This pattern extends beyond the southern portion of the Midwest. In the Bronx (Parkins 2015) and on green roofs in New York City, NY (Parkins and Clark 2015, Partridge et al. 2020), the eastern red bat is the dominant species, while in Fort Worth, TX, the evening bat is the most common (Bienz 2016, de Oyarzabal Barba 2023).

The apparent regional clustering of the eastern red + evening bat-dominated cities and the fact that the three cities all have relatively high tree canopy covers (mean = 26.7%, compared to the study-wide mean of 18.4%) suggest that there may be habitat or climatic factors driving this effect. In general, identifying what bat species dominate the cities across North America and the mechanisms influencing these assemblages may be important as climate change is expected to facilitate northward range expansion of species like the Brazilian free-tailed bat (McCracken et al. 2018). Expanding species may colonize cities first, as the heat island effect may make colder latitudes tolerable (Vlaschenko 2023a). As the Brazilian free-tailed bat is highly synurban, it seems likely that it will continue to expand northward into new cities, potentially resulting in competition with big brown and eastern red bats. Cities within the southern Midwest should be studied to determine if this dynamic will manifest. As little brown bats are known to dominate some northern cities like Calgary (Coleman and Barclay 2011b) and are already imperiled due to WNS (Frank et al. 2014), these should be monitored for increasing dominance of big brown bats, which may present an additional conservation threat.

Multi-city studies offer opportunities for insights into broad-scale trends in urban bat ecology, and future research using this approach should consider full-season, and preferably multi-year, monitoring to detect changes in bat assemblages over time. Expanding multi-city studies across continents would also allow for investigation into between-region differences (Magle et al. 2019) in urban bat assemblages. Our study was also limited to cities with populations between 50,000–500,000, and we could not compare the ecology of bats in these cities to those in larger metropolitan areas. Future work could incorporate a mixture of small and large cities to investigate the effects of urban area size. Additionally, a more comprehensive approach should also employ capture surveys and evaluation of potential roost sites, as there are some limitations to using only acoustic data. For example, call identification presents challenges (Goodwin and Gillam 2021, Fraser 2018), and we can only estimate but not know the exact population sizes from acoustics (Hoggatt et al. 2024). Lastly, further investigation might reveal

the variables we tested in our analyses were more important to detection rather than occupancy; we only included habitat variables as occupancy covariates.

In conclusion, we found that local tree cover and access to forests support city-dwelling bat occupancy. But importantly, the response of some bats to local or within-city habitat varies depending on the overall landscape or between-city context. Future urban bat research studies and land managers should take landscape context into account when designing studies and implementing management actions. In cities where forests are scarce, preservation and restoration of existing forest tracts may be particularly important for sustaining urban bat populations. We found bat assemblages in the Midwest to mostly be dominated by the big brown bat + silver-haired acoustic group, but there are exceptions where the eastern red + evening bat group may be more dominant. Lastly, the local and landscape scale factors influencing species richness and community composition are still unknown, but longer-duration studies may be revealing. Long-term endeavors are also needed to answer deeper questions surrounding the importance of urban areas for bat conservation, including whether cities act as ecological traps or potential refuges and how to increase bat diversity and activity in cities while reducing sources of mortality.

CHAPTER 3: URBAN BATS RESPOND TO FINE-SCALE HORIZONTAL CANOPY HETEROGENEITY

Introduction

Urban trees benefit people and wildlife by providing local cooling effects in urban heat islands (Kong et al. 2014) and filtering out air pollution (Sæbø et al. 2012). Trees also support wildlife in cities by providing food and structural habitat for a variety of taxa, including insects, birds, and mammals, including bats (Threlfall et al. 2017). Bats use tree cavities, foliage, and bark for roosting habitat (Brigham et al. 2007), and trees sustain insect prey of temperate bats (Lumsden and Bennett 2005, Polyakov et al. 2019). However, some bat species may be less reliant on trees – e.g., the big brown bat (*Eptesicus fuscus*) readily roosts in artificial structures and is frequently found in highly urbanized environments (Lausen and Barclay 2006, Neubaum et al. 2007). However, urban artificial roosting bats may still be dependent on trees in other ways. Some urban bats commute up to 5 km each way to forage in forests (Menzel et al. 2001), suggesting that tree-dense areas provide food resources worthy of the energetic cost of long flights. Nevertheless, cities are often a mosaic of areas with varying intensities of human development and tree cover, and bats still forage within urban areas (Li and Wilkins 2014). Urban trees are likely important for supporting bat foraging within cities, as increasing tree cover often promotes urban bat activity (Moretto et al. 2019). Furthermore, trees provide structural benefits to bats by buffering the negative effects of urbanization, such as artificial light at night (Straka et al. 2019). Urban trees also provide natural roosting habitat (Mager and Nelson 2001) and may be key to promoting bat diversity beyond synanthropic artificial roosting species (Moretto and Francis 2017). However, our knowledge of the link between bats and urban trees is incomplete, as fine-scale effects are poorly understood.

The magnitude and scale at which bats respond to urban tree cover have been the subject of much work. Overall, research points to a general positive effect of canopy cover within a 25–1000-m buffer on urban bat richness (Bailey et al. 2019, Caryl et al. 2014) and species-specific bat activity across the world (Dixon 2011, Moretto et al. 2019, Straka et al. 2019), though there is interspecific variation (Li and Wilkins 2014) and intraspecific variation across spatial scales (Gallo et al. 2017). With the exception of Moretto et al. (2019), the examples above examine covariates at scales >100 m and often make use of widely available products such as the 30-m resolution National Landcover Database Tree Canopy Cover (NLCD Canopy) raster (Housman

et al. 2023). While larger-scale parameters may be ecologically relevant, they offer no insights into the fine-scale responses of bats to urban tree cover (Moretto et al. 2019), which can vary dramatically from one city block to the next. In addition, it is difficult to disentangle the effects of urbanization and tree cover on bats as the two are often inversely correlated (Moretto et al. 2019).

Understanding fine-scale effects may be critical to making informed decisions regarding land management for bats in urban environments (Moretto et al. 2019). City lot sizes can be as small as < 0.2 ha (Kopits et al. 2009), and urban green patches are often much smaller than large public and privately owned patches of agricultural or forested land. Furthermore, in cities, it is highly improbable that large-scale conservation actions can be implemented across parcels with different ownership, zoning, and use. Discerning the practices that could improve bat habitat on smaller scales would then allow landowners, such as municipal parks departments or even private individuals, to take steps toward bat conservation on a per-site basis. Fine-scale habitat management, when repeated across a wide enough area, could then positively affect urban bat populations at a larger scale (Mimet et al. 2020). However, very few studies have assessed a spatial scale <100 m when using remote-sensed methods to predict the response of urban bats to canopy cover, canopy heterogeneity, or other variables describing urban trees (Moretto et al. 2019).

The increasing availability of high-resolution LiDAR (Light Detection and Ranging) and imagery datasets, which allows for precise quantification of tree and forest structure (Fisher et al. 2016), offers opportunities to generate precise 3-D maps of tree canopies and can be used to generate environmental data that outperforms more labor-intensive field measurements when predicting bat activity in forests (Froidevaux et al. 2016). Few urban bat studies have used remote-sensed data (LiDAR or imagery) to measure variables of interest (Villarroya-Villalba et al. 2021, Moretto et al. 2019, Mimet et al. 2020, Suarez-Rubio et al. 2018). Moretto et al. (2019) sought to determine the scale at which bats in Toronto, Ontario, Canada, exhibit the most intense response to tree cover, or “scale of effect,” finding that eastern red bats (*Lasiurus borealis*) responded at the 25-m scale, whereas larger bats (big brown bats, silver-haired bats [*Lasionycteris noctivagans*], and hoary bats [*Lasiurus cinereus*]) responded at 100–250-m scales. Mimet et al. (2020) found increasing presence and activity of *P. pipistrellus* with increasing vegetation cover and height heterogeneity within a 20-m buffer across the urban

mosaic of Paris, France. However, Villarroya-Villalba et al. (2021) found woody vegetation cover and height heterogeneity within 50-m buffers were not informative predictors of bat diversity in three European cities, though land-use heterogeneity within 50 m of sample points negatively predicted insect abundance. Suarez-Rubio et al. (2018) found that an imagery-derived canopy complexity metric had a mostly negative impact on bat activity within a 20-m radius of acoustic devices placed in the greenspaces of Vienna, Austria.

The evidence from these studies suggests that fine-scale trees and vegetation cover are important, but more research is needed to discern their effects in different urban areas. In addition, previous work has only examined metrics relating to tree abundance, canopy cover, or vertical structure, but horizontal canopy heterogeneity can also be important for bats (Erasmy 2021). Some species respond positively to horizontal heterogeneity within forests in the form of gaps (Brooks et al. 2017, Loeb and O’Keefe 2011) or edges (Morris et al. 2010), presumably due to more efficient foraging. We do not know how bats respond to gaps in urban forests, but earlier work showed that bats are more active closer to urban forest edges (Gehrt and Chelsvig 2004) or use forest edges more than other habitats (Everette et al. 2001). However, different bat species may respond differently to gaps and edges depending on their ecomorphological and habitat context. Bats that are more forest-associated tend to have high-frequency echolocation calls and broader wings with higher body mass-to-wing area ratios adapted to navigate clutter, while bats that are less forest-associated tend to have low-frequency echolocation calls, narrower wings, and higher body mass to wing area ratios adapted to navigating open spaces (Siemers and Schnitzler 2004, Crome and Richards 1988). Fine-scale measures of horizontal heterogeneity derived from LiDAR may unearth more nuanced effects of gaps and edges between species and across urban habitat types; in turn, this could provide urban land managers with more targeted recommendations to promote bat conservation.

While LiDAR-derived structural measures of tree cover offer great potential in the study of urban bat ecology, they do not take into account tree diversity. Bat activity and occupancy in Melbourne, Australia, is higher, with greater proportions of native plants relative to non-native vegetation (Threlfall et al. 2016 and 2017), which highlights the potential importance of plant taxonomic identity for bat assemblages. The relationship between bats and total tree diversity (e.g., including both native and non-native trees) has seldom been studied, and the only research on this question found no significant impact of diversity but a positive effect of tree species

evenness on activity (Ampoorter et al. 2020). One reason that few studies have attempted to investigate the relationship between bats and tree diversity is the labor-intensive nature of identifying a significant number of individual trees in dense forests; urban environments may be more suitable study sites, as many cities maintain public tree inventories providing the location and species of municipal-owned trees along streets or in parks (Ma et al. 2021). While tree inventories typically do not include privately owned trees and thus do not capture the complete tree diversity of a city, they still present an incredibly rich resource for analyses. Coupling LiDAR data and tree inventory data at a fine scale could reveal precise habitat associations of urban bats, thus informing recommendations for urban forest management to better support bat populations.

Even though cities tend to have low bat diversity (Duchamp and Swihart 2008), patches of forest and other greenspaces within cities support high bat activity and diversity compared to the surrounding urban matrix (Avila-Flores and Fenton 2005, Oprea et al. 2009, Krauel and LeBuhn 2016). Some urban spaces even support endangered bats (Burrell and Bergeson 2022, Hernández-Brito et al. 2018), provided that there is sufficient suitable habitat (Thorne et al. 2021). However, cities may serve as “ecological traps” for imperiled species by reducing fitness (Russo and Ancillotto 2015, Vlaschenko et al. 2019, Tella et al. 2020, Coleman and Barclay 2011a). As bats in cities may be exposed to a variety of threats like invasive species (Hernández-Brito et al. 2018), human disturbance (Li et al. 2020), and disease (Coleman and Barclay 2011a), studying how bats use urban forests of varying structures and composition is an important first step toward identifying management strategies to promote their health and conservation.

To answer questions regarding the effect of fine-scale tree metrics on urban bat activity, we conducted a 6-month acoustic survey in Champaign-Urbana, IL. As this was the first formal bat acoustic survey of this urban area, we also aimed to identify which species were most dominant and document the presence of any species of conservation concern. We aimed to determine whether LiDAR- or tree inventory-derived metrics predicted bat activity and presence and whether any of these metrics exhibited interactions with other environmental variables. We intend for this research to demonstrate the potential importance of cities as an arena for bat conservation and the utility of LiDAR and tree inventory data in classifying urban tree landscapes to generate future management strategies.

Methods

Study Area

We conducted our study across the twin cities of Champaign and Urbana, IL (Figure 3.1), the two largest cities in an urban conglomeration with a population of approximately 150,000 people and a footprint of 120.5 km² (U.S. Census Bureau 2023a). According to U.S. Census data (2023a), it is the third most densely populated urban area (1,224 people/km²) in the Midwest, with a population >50,000 behind only Chicago, IL, and Lawrence, KS. The twin cities have different land-use histories and management practices in their greenspaces, resulting in differences in the availability of forested habitats and biodiversity (Pollock et al. 2024). Forests are rare in the area, though the northeast part of Urbana was once dominated by a large hardwood forest known as the “Big Grove” (Pollock et al. 2024). The city of Champaign lacks forests entirely, while the Urbana Parks Department manages a few patches of forest along the Saline Branch Drainage Ditch. Also, along and near the Saline Branch are two privately owned patches of forest, Holcomb Woods and Raintree Woods, that incorporate residential neighborhoods and three forests managed by The University of Illinois. Two of these, Trelease Woods and Brownfield Woods, are old-growth remnants of the original Big Grove. The university also manages three patches of forest adjacent to southwest Urbana, which are the only forests not along the Saline Branch.

Besides the forests, both cities maintain dozens of public parks, which typically have trees but are generally dominated by turf grass. Some of the parks have natural areas, such as riparian habitat and restored prairie. Both cities also have trees in neighborhoods and on university grounds, along public rights-of-way adjacent to streets, and in private yards. Champaign, Urbana, and the University of Illinois maintain publicly available inventories of all trees in parks and along rights-of-way, excluding forest areas (City of Urbana, City of Champaign Public Works, Champaign Park District, Welch et al. 2022).

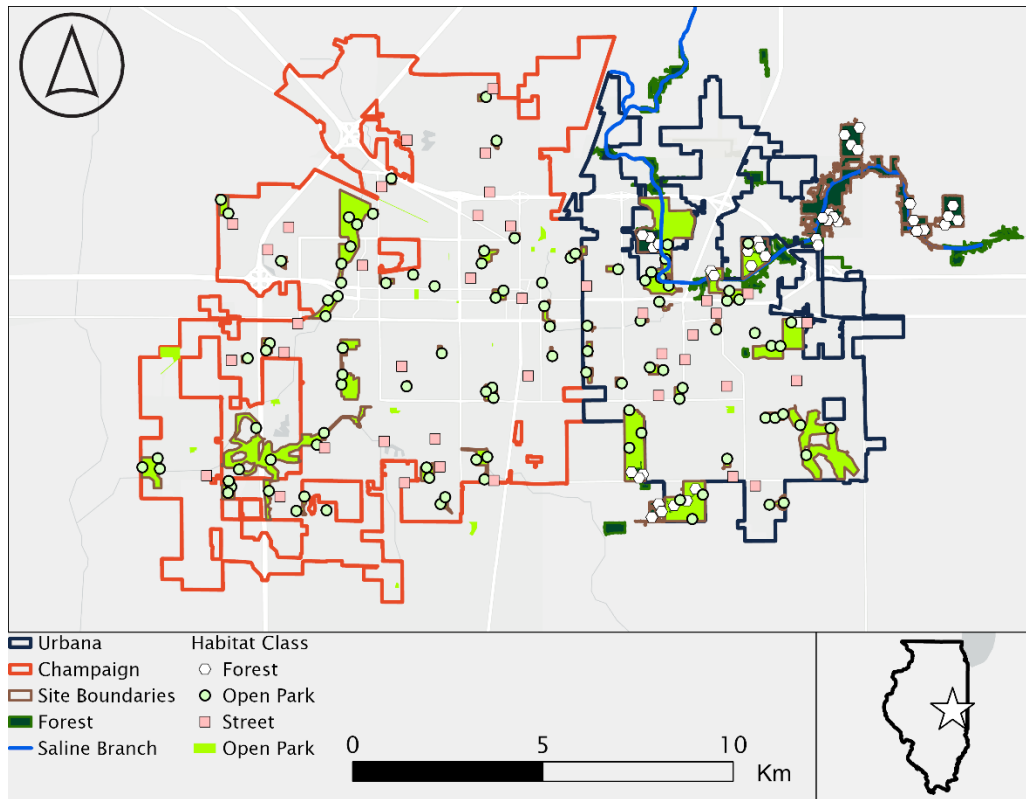


Figure 3.1: Map of our sample points, with habitat class marked, and sites in and around the cities of Champaign and Urbana, IL. Forest patches and the Saline Brach Drainage Ditch are pictured.

The Champaign-Urbana area is within the range of 9 species of bats (Romano et al. 2019, Table 3.1). The northern long-eared (*Myotis septentrionalis*) and Indiana bat (*Myotis sodalis*) are currently federally endangered (U.S. Fish and Wildlife Service 2023a and 1973), while the tricolored bat (*Perimyotis subflavus*) has been proposed to be listed as federally endangered (U.S. Fish and Wildlife Service 2022). The status of the little brown bat (*Myotis lucifugus*) is currently under review (U.S. Fish and Wildlife Service 2023b). A study of bat mortality at a nearby wind farm has confirmed the presence of at least seven of these bat species in Champaign County and the adjacent Vermilion County (Romano et al. 2019, Table 3.1) from 2014–2016. iNaturalist observations have also confirmed the presence of three species in the Champaign-Urbana area proper between the discovery of white-nose syndrome (WNS; Hoyt et al. 2021) in Illinois in 2012 (Langwig et al. 2015) and the beginning of our study in 2022 (GBIF.org 2024). However, whether these species are residents or passing migrants in Champaign-Urbana is unknown, as is the post-WNS species richness.

Table 3.1: List of bat species with possible ranges in Champaign County, IL. Common name, scientific name, and 4-letter species code for each species are listed.

Common Name	Scientific name	Species Code
Big Brown Bat*^	<i>Eptesicus fuscus</i>	EFPU
Eastern Red Bat*^	<i>Lasiurus borealis</i>	LABO
Hoary Bat*	<i>Lasiurus cinereus</i>	LACI
Silver-haired Bat*^	<i>Lasionycteris noctivagans</i>	LANO
Evening Bat*	<i>Nycticeius humeralis</i>	NYHU
Little Brown Bat*#	<i>Myotis lucifugus</i>	MYLU
Indiana Bat#	<i>Myotis sodalis</i>	MYSO
Northern Long-eared Bat#	<i>Myotis septentrionalis</i>	MYSE
Tricolored Bat*#	<i>Perimyotis subflavus</i>	PESU

*Species found in Champaign and Vermillion counties by Romano et al. 2019

^Species with iNaturalist observations in the cities of Champaign or Urbana between 2013–2022

#Species of conservation concern

Sampling Scheme

We used Titley Scientific Chorus bat detectors (Firmware Version 2.4.6) to record the ultrasonic calls (10–250 kHz) of bats. The Choruses were set to a maximum sampling frequency of 320 kHz and a sensitivity of 16, with allowable file lengths of 2–15 seconds. We deployed bat detectors by securing them to trees at our sample sites 3–5 m off the ground with cable locks and paracord (Figure 3.2). We used trees for deployments to make detectors less conspicuous in public parks, though the clutter of tree canopies may have resulted in fewer recorded calls compared to detectors attached to free-standing poles. We targeted medium-sized trees for deployment, with the microphone facing an opening in the canopy to minimize the muffling of bat calls from leaves and branches. Detectors were deployed for a minimum of 3 nights to capture night-to-night variability, but when detectors were left for >3 nights due to logistic or weather-related reasons, these extra nights of data were included in the final dataset. We placed detectors >100 m apart so that two different detectors did not record the same bat call.



Figure 3.2: Left, an example of a detector placement on a tree in Urbana's Prairie Park, considered an "open park" habitat. Right, a close-up of a Chorus attached to a tree.

From 10 April to 3 October 2023, we placed detectors on 183 trees in Champaign and Urbana, hereafter referred to as "sample points" (Figure 3.1); these were categorized as one of three discrete habitat classes: open park, forest, or street nested into "sites" (Figure 3.3). Open parks were defined as all polygons included in the Open Spaces Layer of the Champaign County, IL Geodatabase (Champaign County GIS Consortium), which mostly includes public parks, university quads, and golf courses dominated by turf grass (see Figure 3.2) with varying degrees of tree cover; some of these polygons contained forest patches, which we excluded when calculating amount or location of open park habitat. Forest patches were identified from LiDAR data from the Illinois Height Modernization Project's (ILHMP) City of Champaign-Urbana Special Area Collection (Illinois Geospatial Data Clearinghouse 2019). The ILHMP dataset had a nominal point spacing of 0.354 m, with a vertical root mean square error of 0.019 m and horizontal accuracy of 0.18 m. We created a tree canopy cover raster in ArcGIS Pro (v.3.2.2, Esri Inc. 2023) by dividing the number of points with classifications of Low (0.15–1.5 m), Medium (1.5–6.1 m), and High (> 6.1 m) Vegetation by the number of all classified, non-noise points per 3.048-m raster pixel (see Esri Inc. 2021 for all steps and tools used to create the tree canopy cover raster). This calculation of tree canopy cover includes cover from all levels of vegetation (e.g., understory and midstory cover in addition to canopy cover) so that it is analogous to other remotely sensed derivations of horizontal tree canopy cover view from above, such as satellite imagery (Housman et al. 2021). To create polygons of forest patches, we used the "Reclassify" tool to convert our Canopy raster from a decimal value (0–1 proportion of total points being marked as vegetation) to a binary raster with a threshold of 70% (cells with vegetation density $\geq 70\% = 1$, cells with $< 70\% = 0$). The 70% density value corresponds to a dense woodland (Gili et al. 2020) containing mature tree crowns, so the binary raster we created represents areas of intense canopy overlap. After this, we used the Raster to Polygon tool to create a polygon shapefile of all cells with value = 1, merging contiguous patches, eliminating patches < 0.8 hectares, and manually filtering out the remaining patches (< 5) within the urban street grid as they were highly perforated. We then used the "Aggregate Polygons" tool in ArcGIS Pro to fill holes < 0.025 hectares to form our final forest class patches.

We defined street habitat as all sites not in forest or open park habitat. When sampling forest or open park points < 50 m from the nearest street, we angled the detector toward the interior of the park or forest to avoid recording bats flying along streets. We treated all forest and

open park sites within 100 m of each other as one site when delineating sample points to mitigate potential spatial autocorrelation (Figure 3.3). However, we treated all non-contiguous forest patches as separate sites regardless of the distance between them, as they often had distinct management practices and histories. The forest patches in the AMBU and PERO sites were connected by a thin but continuous corridor of forest cover along the Saline Branch (Figure 3.3), but we considered them separate as their core areas were separated by a distance of > 0.5 km. In addition, all street sites were kept separate from open park and forest sites regardless of distance due to stark differences in building density and impervious cover.

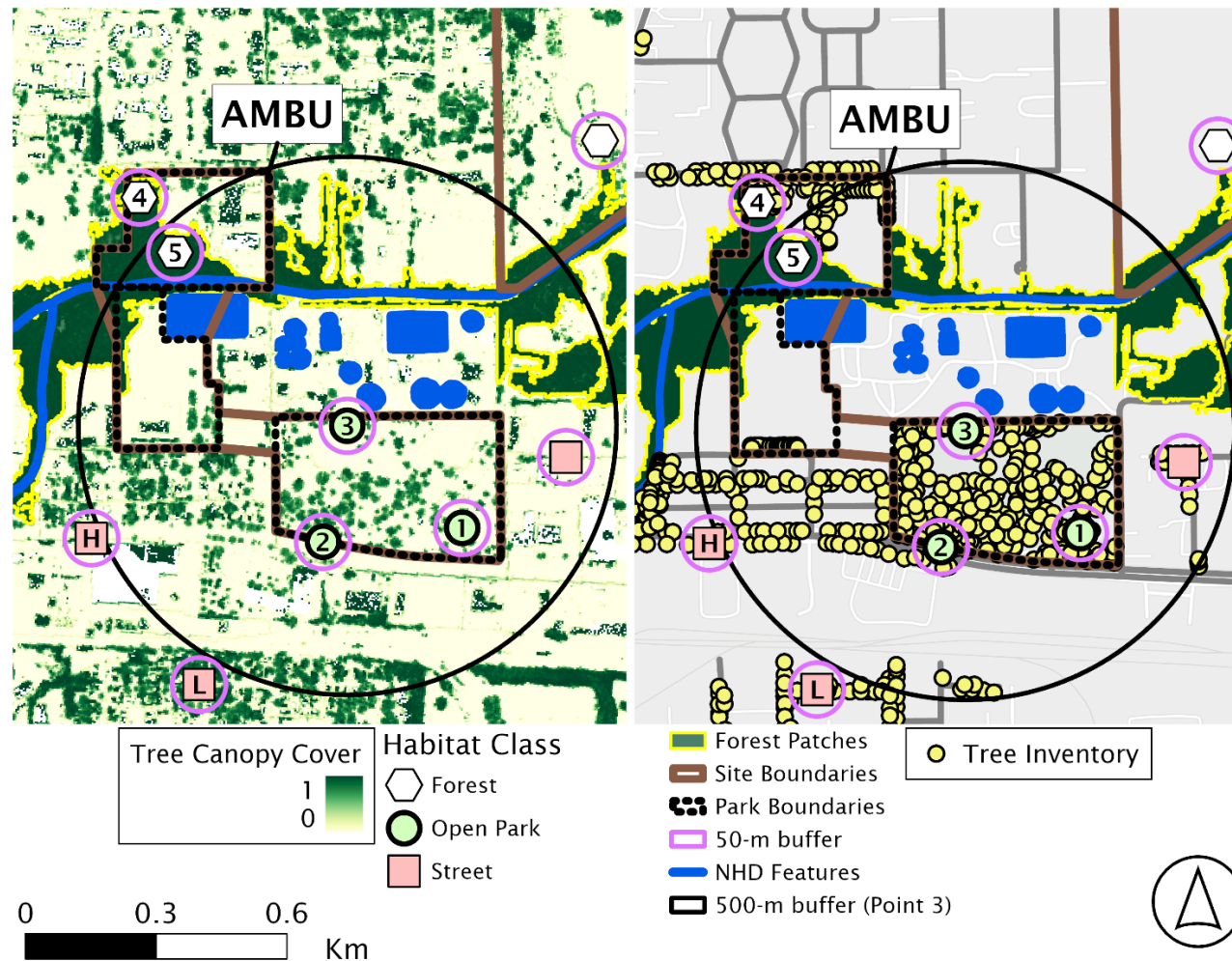


Figure 3.3: Maps of AMBUCS Park, Hickory Street Site, and Chief Shemauger Park in Urbana, IL. **Left**—due to their proximity, they have been combined into one site (“AMBU”) in the “large” size class and received three open park sample points at low (3), medium (1), and high (2) levels of tree canopy cover within a 50-m buffer. We also calculated environmental variables within a 500 m buffer around sample points (pictured for 3), but this did not factor into our survey design. As there was a small patch of woods in Chief Shemauger Park, two forest points were randomly placed (4 and 5). Also visible are two street points, each considered its own site, with one being placed in a low (L) and high (H) area of canopy cover. **Right**—map of the tree inventory data. There is near complete coverage in the open park habitat, while very little to none in the forest habitat. There is only data on public trees, meaning privately owned trees in backyards and commercial areas are not captured.

We removed all open park and forest sites <0.2 ha from consideration to differentiate habitats larger than the typical front or backyards common on urban streets. Depending on size and habitat composition (i.e., both open park and forest present), sites received 1–10 detector placements. We divided open park patches into four size classes to inform the sampling scheme (Table 3.2). We used 4 pre-existing tree inventories (City of Urbana, City of Champaign Public Works, Champaign Parks District, Welch, et al. 2022) for open parks to identify target trees for sample points. We merged all inventories into one dataset and filtered out all trees marked as removed or empty spaces. To sample a range of tree canopy densities within our bigger sites, we calculated the canopy cover within a 50-m buffer of every tree in the inventory, hereafter referenced as Cover (50 m), and placed detectors on suitable trees with the highest, lowest, and median Cover (50 m) values, depending on the site’s size class (Table 3.2). We chose 50 m for our buffer size as it is the approximate maximum detection range of the Chorus. We removed all trees within 50 m of forest patches from consideration so that the detectors on open park trees would not record calls coming from the forests.

Table 3.2: Park size strata involved in the survey scheme for placing sample points in parks. The number of all parks, parks that were sampled, and sample points per strata are listed. Open park area refers to the size of a site, excluding any forested areas. Target trees were identified from tree inventories in all open parks except for golf courses, which did not have associated tree inventories and had randomized placements.

Park size	No. of total parks	No. of sampled parks	No. of sample points/ park	Open park area (ha)	Target tree selection
Small	36	20	1	0.2–2.9	Random
Medium	15	15	2	2.9–7.7	Highest and lowest Cover (50 m) *
Large	13	13	3	7.7–50.6	Highest, median, and lowest Cover (50 m) *
Extra large	4	4	6	>50.6	Two highest, median, and lowest Cover (50 m) *

The forests in our study area have relatively homogeneous canopy densities and lack tree inventories, so we randomly generated 4 sample points within each forest patch (≥ 100 m apart) using the “Create Random Points” tool in ArcGIS Pro. We placed detectors on the nearest suitable tree to each random point. We targeted medium-sized trees and avoided areas with extensive understory clutter. For forest patches too small to accommodate 4 points spaced 100 m apart, we reduced the number of detector placements (Figure 3.3).

For street sample points, we placed detectors on 40 city-owned street trees along rights-of-way in Champaign and Urbana. We aimed to sample streets with high and low tree canopy densities, so we calculated the Cover (50 m) for every street tree and used the Jenks Natural Breaks method to classify every tree as being within high, medium, or low tree canopy cover. We merged the city boundaries of Champaign and Urbana, then broke the combined layer into a grid of 20 equal-sized areas and randomly selected one target tree, each within the high and low groups in each grid. If a grid lacked high- or low-density trees, we targeted the tree with the highest or lowest Cover (50 m) value from the medium group. We received permission from each city to place detectors on their rights-of-way and asked for permission from adjacent landowners. If unable to sample our target tree, we sampled the nearest available tree in the same cover class.

For our survey scheme, the number of sample points surveyed simultaneously depended on equipment and labor availability. To determine the survey order, we stratified sites by habitat and size, then randomly placed them into 9 groups (Table 3.3), ensuring that each group included small, medium, and large parks as well as open park, forest, and street points. Each group was sampled within the same week to control for temporal variation (Table 3.3). Each of the 9 groups was sampled 3–4 times from April to October in order, resulting in 4 total deployment cycles, though due to time constraints, street points were only sampled in two cycles. The 4th cycle was cut short due to cold weather, meaning Groups 7, 8, and 9 were only sampled 3 times.

Table 3.3: The survey scheme grouped by habitat class, with the number of points sample points within a weekly deployment group, number of three-day deployment cycles across the survey period, number of total sample points, and total number of nights sampled by a detector listed.

Class	Sample Points per Deployment Group	No. of Deployment Cycles (range, mean)	Sample Points	Nightly Samples
Open park	9–15	3–4, 3.6	103	1095
Forest	2–7	3–4, 3.6	40	434
Street	4–6	2, 2	40	244

Capture Survey

We also mist netted for 5 nights in 2023 and 3 nights in 2024 at 3 different sites in forested tracts to confirm bat species presence by another method. We were particularly interested in finding northern long-eared bats, as we found acoustic evidence to suggest that this endangered species was present in the area. Due to its imperiled status, we aimed to identify roost trees for any captured northern long-eared bats. For northern long-eared bats ≥ 6 g, we used surgical glue (Torbot, Inc.) to attach a 0.28-g radio transmitter (LB-2X, Holohil, Inc.) to the back between the scapulae, and we tracked bats to daytime roosts. We performed our bat captures under federal and state permits and institutional animal care and use protocol (University of Illinois Urbana-Champaign #22159) and followed white-nose decontamination procedures (White-nose Syndrome Disease Management Working Group 2020 [for 2023 netting] & 2024 [for 2024 netting]). All mist netting nights were ≥ 4 hours in duration after sunset.

Predictor variables

Detection covariates

To account for the effects of temperature and rainfall on bat detection, we used the daily mean temperature (Temp.) and daily precipitation (Precip.) collected in Champaign (Illinois State Climatologist 2023). We also included the quadratic of ordinal date (Date) to account for seasonal differences in bat activity (Metcalf et al. 2023). As bats are often drawn to water for foraging and drinking (Lehrer et al. 2021), we calculated the distance to National Hydrological Dataset Plus (U.S. Environmental Protection Agency 2014) area features (e.g., streams, rivers, ponds, and lakes) using the “Near” tool in ArcGIS Pro (Water Dist.).

Hypothesis Covariates

We generated several variables to quantify the environment of Champaign-Urbana. The scale at which particular environmental covariates are important may differ by species (e.g., Gallo et al. 2017), so we examined all activity covariates within a 50-m (“local-scale”) and 500-m (“neighborhood-scale”) buffer (Table 3.4). Within each buffer, we calculated the mean of the tree canopy cover raster (Cover; 3.048-m resolution) to represent natural foraging and roosting habitat and variability in canopy cover. We also calculated the standard deviation of the mean canopy cover to represent horizontal heterogeneity (Heterogeneity). We used the `spatialize_lsm()` function in the `landscapemetrics` package (Hesselbarth et al. 2019) in R (R Core Team 2023) to generate a raster of the patch-level area metrics (Area) using the unfiltered tree canopy cover binary raster (McGarigal et al. 2023). We calculated Cover, Heterogeneity, and Area using the “Zonal Statistics as Table” tool in ArcGIS Pro. To account for anthropogenic influence in an area, we used the “Summarize Within” tool to determine the proportion of National Landcover Database (NLCD) High and Medium Intensity Development (Dewitz 2023) within our buffers (Development). We used the “Near” tool to calculate the distance to the nearest road feature (U.S. Census Bureau 2023b) and used this distance metric instead of Development in analyses for species that were only recorded in forests, as there was little variation in Development land cover in these environments.

Each tree inventory included information about tree location and species. We used these inventories to calculate metrics of the public tree diversity for a subset of our sites, which included all street and all open park sample points except for golf courses but excluded all forest points. We calculated richness, Shannon Diversity, and Simpson Diversity at the family level, as there was some level of uncertainty at the species and genus level due to hybridization and occasional input errors in the inventories. We made calculations only at the 50-m scale, as for most points, the public tree data within 500 m did not accurately represent true tree diversity due to the larger proportions of privately owned land included at that scale. We used the “Spatial Join” tool in ArcGIS Pro to determine the abundance of every tree family within 50 m of each sample point, which gave us the total tree abundance (Abundance) and the abundance of all trees in the family Fagaceae (Fagaceae) as it contains oaks (genus *Quercus*) and these are known to support high lepidopteran diversity (Tallamy and Shropshire 2009) and provide cavities for roosting (Laux et al. 2022). We used the “diversity()” function in the `vegan` package in R to

calculate the family-level Shannon Diversity Index (Shannon), Simpson Diversity Index (Simpson), and richness (Richness).

We calculated Pearson's correlation coefficient for all pairs of predictor variables to determine whether any were highly correlated, defined as $r \geq 0.6$. For any correlated pairs, we retained the variable we believed to be more ecologically relevant. Heterogeneity (500 m) was excluded from our analysis because it was strongly correlated ($r = 0.86$) with Cover (500 m). Cover (50 m) and Heterogeneity (50 m) were not correlated across all points and were both included in the analysis, but they were correlated within habitat class (forest $r = -0.70$, open park $r = 0.77$, streets = 0.72). Area (50 m) and Area (500 m) were strongly correlated ($r = 0.94$); we retained Area (500 m) because patch area values are derived from contiguous cells of canopy cover, which were sometimes much greater than the area of our 50-m buffer. Within the tree inventory subset of our sample points, Shannon diversity was highly correlated with Simpson's diversity ($r = 0.95$) and family richness ($r = 0.90$), and Simpson's diversity was also highly correlated with richness ($r = 0.74$). The only diversity metric we retained for analysis was Shannon diversity.

Table 3.4: Name, abbreviation, and definitions of all fixed effect predictor variables used in models to predict bat activity and presence.

Name	Abbreviation	Definition
Tree Canopy Cover (50 m)	Cover (50 m)	The mean value of the LiDAR-derived percent tree canopy cover (see Methods text for calculation) within a 50-m buffer.
Tree Canopy Cover (500 m)	Cover (500 m)	The mean value of the LiDAR-derived percent tree canopy cover (see Methods text for calculation) within a 500-m buffer.
Patch Area (50 m) *	Area (50 m)	Mean patch-level area (McGarigal et al. 2023) generated from a 70% binary threshold of the LiDAR-derived tree canopy cover raster (see Methods text for calculation) within a 50-m buffer.
Patch Area (500 m)	Area (500 m)	Mean patch-level area (McGarigal et al. 2023) generated from a 70% binary threshold of the LiDAR-derived tree canopy cover raster (see Methods text for calculation) within a 500-m buffer.
Horizontal Heterogeneity (50 m)	Heterogeneity (50 m)	The standard deviation of the mean of the LiDAR-derived percent tree canopy cover (see Methods text) within a 50-m buffer.
Horizontal Heterogeneity (500 m) *	Heterogeneity (500 m)	The standard deviation of the mean of the LiDAR-derived percent tree canopy cover (see Methods text) within a 500-m buffer.
Abundance	Abundance	Number of trees from the merged dataset of publicly available tree inventories within a 50 m buffer.
Shannon Diversity	Shannon	Shannon diversity index (family level) from the dataset of available tree inventories within a 50 m buffer.
Simpson Diversity*	Simpson	Simpson diversity index (family level) from the dataset of available tree inventories within a 50 m buffer.
Family Richness*	Richness	Number of tree families represented from the dataset of available tree inventories within a 50 m buffer.
Fagaceae Abundance	Fagaceae	Abundance of trees in <i>Fagaceae</i> from the dataset of publicly available tree inventories within a 50 m buffer.
Distance to Water [^]	Water Dist.	Distance to National Hydrological Dataset Plus (NHD Plus; U.S. Environmental Protective Agency 2014) water features
High/ Med. Developed Cover (50 m)	Development (50 m)	Proportion of High and Medium Intensity Developed cover from the National Landcover Database (NLCD; Dewitz 2023) within a 50 m buffer.
High/ Med. Developed Cover (500 m)	Development (500 m)	Proportion of High and Medium Intensity Developed cover from the National Landcover Database (NLCD; Dewitz 2023) within a 500 m buffer.
Distance to Road [#]	Road Dist.	Distance to nearest road feature (U.S. Census Bureau 2023b) in meters, calculated only for points in sites with forest
Habitat Class	Habitat Class	Categorical variable, either “open park,” “forest,” or “street”. See methods text for class definitions.
Precipitation [^]	Precip.	24-hour precipitation reading in mm (Illinois State Climatologist 2023).
Temperature [^]	Temp.	Mean daily temperature converted to °C for survey night (Illinois State Climatologist 2023).
Day of Year [^]	Date	Ordinal date of the year for a survey night.
* Variables were not considered for analysis because they are highly correlated with other variables.		
[^] Variables considered detection covariates; all others are hypothesis covariates.		
[#] Variables only used in northern long-ear bat presence modeling		

Response variables

We considered each individual file recorded by the Chorus as a single call sequence or “call”. Calls had a duration of 2–15 seconds, with differing numbers of individual echolocation pulses. The Chorus was triggered by sounds 10–250 kHz and continued to record until it failed to detect sounds in this range or until the recording reached 15 seconds. We processed all acoustic data through the Kaleidoscope Pro AutoID software (version 5.6.6, Wildlife Acoustics, Inc) using the Bats of North America 5.4.0 classifier to identify calls to 9 bat species with known ranges in the area (Table 3.1). We define “bat activity” as the number of calls recorded across a night at one sample point. We used the idsummary.csv output to determine the number of calls identified to each species for each nightly sample. To reduce the likelihood of false positive identifications, we did not include calls for a given species if the maximum likelihood estimator (MLE) value for its predicted presence was ≥ 0.05 ($< 95\%$ confidence) on a given night or if fewer than 3 calls were identified. For our complete-dataset activity analysis (Analysis A) and analysis of our subset of data, including points with complete tree inventories (Analysis B), we used the number of call sequences for big brown (EPFU) and eastern red (LABO) bats as separate response variables. We manually vetted every call marked by the AutoID software as a northern long-eared bat (MYSE), as we wanted to eliminate any chance of false-positive identifications due to its endangered status. Because of the low number of manually identified northern long-eared bat calls ($n = 126$), we modeled the likelihood of presence (Analysis C) rather than its activity, with all nights with a manually vetted call marked as MYSE = 1 and those without as MYSE = 0. We also manually vetted calls from all other species until we found at least 3 voucher calls across all sites and nights to confirm their general presence in the Champaign-Urbana area; however, we only used AutoID call counts as our response variables for big brown bats and eastern red bats.

Statistical Analyses

Activity Modeling

For our complete-dataset activity analysis (Analysis A), we used the glmmTMB() function in the glmmTMB package (Brooks et al. 2024) in R (R Core Team 2023) to test a candidate suite of generalized linear mixed models (Table 3.5), with each model testing a hypothesis regarding the additive and interactive effects of urban vegetation on big brown and eastern red bat activity. We included our detection covariates as fixed effects in every model due to the high likelihood of significance for predicting bat activity. Vegetation and development

variables were fixed effects when included in models. Deployment cycle (Deployment, $n = 589$), sample point (Point, $n = 183$), and site (Site, $n = 96$) were included as random effects in all models, which collapsed all the nightly samples (Night, $n = 1774$) from the same location into one statistical unit, giving a total sample size of 96. As our activity data were counts, we used a negative binomial distribution model, specified as “family = ‘*ngbinom2*’” in *glmmTMB*. We used the base R function *scale()* to rescale and center covariates. We then ranked our suite of models to assess which was the most plausible for explaining bat activity using Akaike's Information Criterion corrected for small sample size (AICc; Hurvich and Tsai 1989, Burnham and Anderson 2004). All models with $\Delta\text{AICc} < 2$ were considered competitive, and all parameters with 85% lower (LCL) and upper (UCL) confidence limits that did not overlap with zero were considered ecologically significant (Arnold 2010). For the subset of data from points with complete tree inventories ($n_{\text{Night}} = 1276$, $n_{\text{Deployment}} = 426$, $n_{\text{Point}} = 137$, $n_{\text{Site}} = 91$), we ran a separate analysis (Analysis B) examining the effect of tree diversity and tree and Fagaceae abundance on bat activity. We ranked a suite of models using the variables from the top-performing model in Analysis A as a base, with additional variables derived from the tree inventory data (Table 3.6) to determine whether these metrics improved model performance. We also ran a separate analysis (Analysis C) to predict northern long-eared bat presence, using the same hypothesis-based models as Analysis A but under a binomial distribution. The data used for this analysis was a subset that contained all the forested and open park points ($n = 59$), deployment cycles ($n = 209$), and sample nights ($n = 633$) within sites with patches of forest ($n = 11$), as northern long-eared bats are highly associated with forest and all 7 sites in which they were recorded contained forest patches.

Table 3.5: Generalized linear mixed models tested in the complete-dataset analysis to predict local big brown bat and eastern red bat activity (Analysis A) and northern long-eared bat presence (Analysis C), along with hypothesized effects on bat activity or presence and a list of the fixed effects included in the models. Models were fitted under a negative binomial distribution in Analysis A and a binomial distribution for Analysis C. Deployment cycle, sample point, and site were included as random effects in all models.

Model Name	Activity/Presence Hypothesis	Fixed Effect
<i>Null</i>	Activity is constant	Constant
<i>Detection</i>	Activity varies with distance to water, weather conditions, and day of year	Water Dist. + Temp. + Precip. + Date
<i>Canopy Cover</i>	Activity is higher with increasing canopy cover	Development (50 m) [^] + Development (500 m) [^] + Hab. Class + Cover (50 m) + Cover (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Patch Area</i>	Activity is higher with increasing patch area	Development (50 m) [^] + Development (500 m) [^] + Hab. Class + Area (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Horizontal Heterogeneity</i>	Activity is higher with increasing horizontal canopy heterogeneity	Development (50 m) [^] + Development (500 m) [^] + Hab. Class + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date
<i>Local Canopy Cover * Development</i>	Activity decreases with increasing local-scale development, but this effect is not seen in areas with high local-scale canopy cover	Development (50 m) [^] * Cover (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date
<i>Neighborhood Canopy Cover * Development</i>	Activity decreases with increasing neighborhood-scale development, but this effect is less with high neighborhood-scale canopy cover	Hab. Class + Development (500 m) [^] * Cover (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Local Canopy Cover * Habitat Class</i>	Activity increases with increasing local-scale tree cover, but this effect will depend whether you are on a street, park, or forest	Development (50 m) [^] + Hab. Class * Cover (50 m) + Water Dist. + Temp. + Precip. + Date
<i>Neighborhood Canopy Cover * Habitat Class</i>	Activity increases with increasing neighborhood-scale canopy cover, but this effect will depend on if you are on a street, park, or forest	Development (500 m) [^] + Hab. Class * Cover (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Horizontal Heterogeneity * Habitat Class</i>	Activity decreases with increasing local-scale development, but this effect is not seen in areas with high local-scale horizontal canopy heterogeneity	Development (50 m) [^] * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date
<i>Horizontal Heterogeneity * Development</i>	Activity increases with increasing local-scale horizontal canopy heterogeneity, but this effect will depend whether on a street, park, or forest	Development (50 m) [^] + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date
<i>Canopy Cover * Canopy Cover</i>	Activity increases with increasing local-scale canopy cover, but this effect will be greater with increasing tree cover at the neighborhood scale	Hab. Class + Development (50 m) [^] + Development (500 m) [^] + Cover (50 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Local Canopy Cover Double Interaction</i>	Activity decreases with increasing local-scale development, but this effect is not seen in areas with high local-scale canopy cover. The effect of canopy cover will also depend on if you are on a street, park, or forest	Development (50 m) [^] * Cover (50 m) + Cover (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date
<i>Neighborhood Canopy Cover Double Interaction</i>	Activity decreases with increasing neighborhood-scale development, but this effect is less with high neighborhood-scale canopy cover. The effect of canopy cover will also depend on if you are on a street, park, or forest	Development (500 m) [^] * Cover (500 m) + Cover (500 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date
<i>Local Global</i>	Activity will depend on the local variables of development, canopy cover, and horizontal canopy heterogeneity	Development (50 m) [^] + Hab. Class + Cover (50 m) + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date
<i>Neighborhood Global</i>	Activity will depend on the neighborhood scale variables of development, canopy cover, and patch area size	Development (500 m) [^] + Hab. Class + Cover (500 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date
<i>Total Global</i>	Activity will depend on development, canopy cover, patch area size, and horizontal canopy heterogeneity at multiple scales	Development (50 m) [^] + Development (500 m) [^] + Hab. Class + Cover (50 m) + Cover (500 m) + Heterogeneity (50 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date

[^]For MYSE presence modeling, Development (50 m) and Development (500 m) were replaced with Road Dist.

Table 3.6: Generalized linear mixed models tested in the tree inventory subset analysis to predict local big brown bat and eastern red bat activity (Analysis B), along with hypothesized effects on bat activity. The fixed effects included in these models were contingent on the top models generated from Analysis A to compare how the addition of tree inventory variables affected model performance. Models were fitted under a negative binomial distribution. Nightly sample, deployment cycle, sample point, and site were included as random effects in all models.

Model Name	Activity Hypothesis	Model
<i>Analysis A (Null)</i>	The top model from Analysis A	Analysis A Top Model
<i>Diversity</i>	Bat activity increases with increasing public tree diversity	Shannon + Analysis A Top Model
<i>Abundance</i>	Bat activity increases with increasing public tree abundance	Abundance + Analysis A Top Model
<i>Fagaceae</i>	Bat activity increases with increasing abundance of Fagaceae trees	Fagaceae + Analysis A Top Model
<i>Diversity + Abundance</i>	Bat activity increases with increasing diversity and abundance of public trees	Diversity + Abundance + Analysis A Top Model

Results

Summary statistics

Across our 1773 nightly samples, we recorded 189,078 bat call files, for an average of 106.6 calls per nightly sample. Kaleidoscope Pro AutoID marked calls from all 9 potential species; however, with manual vetting, we only confirmed voucher calls from 7 species (see Table 3.7). We also found calls that were characteristic of either the little brown bat or the Indiana bat, suggesting the presence of at least 8 total species in the area. However, these two species make calls that are hard to distinguish (Agranat 2013), and neither was captured during mist netting; therefore, we cannot discern the species. Most of the recorded calls were marked as big brown bats by the AutoID (71.7%), followed by eastern red bats (3.6%), silver-haired bats (1.6%), evening bats (1.4%), and hoary bats (1.2%), and we manually vetted calls from all these species. Of note, via manual vetting, we also confirmed calls from the northern long-eared bats and tricolored bats, two species of conservation concern.

Table 3.7: Number of call files identified to species using Kaleidoscope Pro AutoID, and the percentage of total calls per species. NOID refers to bat calls that the AutoID could not identify to species, while NOISE refers to files that the AutoID determined were not bat calls. Checks represent species that had ≥ 3 positively identified call files from manual vetting.

Bat Species	AutoID Calls	Percent of Total Calls	Manually Vetted Presence
Big brown ¹	134,165	71.7	✓
Eastern red ¹	6,647	3.6	✓
Hoary ²	2,267	1.2	✓
Silver-haired ¹	2,646	1.4	✓
Little brown ²	1,885	1.0	
Northern long-eared ¹	235	0.1	✓
Indiana ²	23	<0.1	
Evening ¹	2,464	1.3	✓
Tricolored	156	0.1	✓
NOID	38,590	20.6	
Total bat calls	189,078	100.0	
NOISE	167,759		
Total files	356,837		

¹Species captured during mist netting efforts or confirmed present from iNaturalist.

²MYSO and MYLU make very similar calls; unable to confirm via manual vetting.

Analysis A: Big Brown Bat

For big brown bats, the *Horizontal Heterogeneity * Development* and *Horizontal Heterogeneity * Habitat Class* models were both competitive (Table 3.8). Both models showed significantly less big brown bat activity with increasing fine-scale development (Table 3.9, Figure 3.4A and 3.4F) and a significant effect of habitat class. In the *Horizontal Heterogeneity * Development* model, street points had four times fewer calls per night (mean = 5.2, LCL = 2.9, UCL = 9.7) compared to forest points (mean = 20.9, LCL = 12.0, UCL = 36.3), while open park activity had intermediary activity (mean = 12.7, LCL = 9.2, UCL = 17.6; Figure 3.4B). In this model, activity also increased with increasing fine-scale horizontal canopy heterogeneity, and there was a significant interaction with development. Within the interaction, bat activity was generally lower in areas with high development, but this effect was not observed in areas with high canopy variation. (Figure 3.4A). In the *Horizontal Heterogeneity * Habitat Class* model, there was a significant interaction between habitat class and horizontal canopy heterogeneity, with only open park points showing significantly higher big brown bat activity as local heterogeneity increased (Figure 3.4E). In both models, increasing temperature positively predicted activity, while increasing quadratic ordinal date negatively predicted activity (Figure 3.4C–D, 3.4G–H).

Table 3.8: AICc rankings, number of parameters (K), and weights (w_i) for 15 hypothesis-based generalized linear mixed models and the null model predicting nightly big brown bat activity across 96 sites in Champaign and Urbana, Illinois, in the complete-dataset analysis (Analysis A). The Horizontal Heterogeneity * Development and Horizontal Heterogeneity * Habitat Class, in **bold**, were the only competitive models. For all models, deployment cycle, sample point, and site were included as random effects.

Model Name	Fixed Effects	K	ΔAIC_c	w_i
Horizontal Heterogeneity * Development	Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	0.00	0.41
Horizontal Heterogeneity * Habitat Class	Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	15	0.40	0.33
Horizontal Heterogeneity	Development (50 m) + Development (500 m) + Hab. Class + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	14	2.49	0.12
Local Global	Development (50 m) + Hab. Class + Cover (50 m) + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	14	2.57	0.11
Total Global	Development (50 m) + Development (500 m) + Hab. Class + Cover (50 m) + Cover (500 m) + Heterogeneity (50 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date	17	6.10	0.02
Local Canopy Cover Double Interaction	Development (50 m) * Cover (50 m) + Cover (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	16	8.96	<0.01
Local Canopy Cover * Habitat Class	Development (50 m) + Hab. Class * Cover (50 m) + Water Dist. + Temp. + Precip. + Date	15	10.45	<0.01
Local Canopy Cover * Development	Development (50 m) * Cover (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	13.23	<0.01
Canopy Cover * Canopy Cover	Hab. Class + Development (500 m) + Cover (50 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	16	20.99	<0.01
Canopy Cover	Development (50 m) + Development (500 m) + Hab. Class + Cover (50 m) + Cover (500 m) + Water Dist. + Temp. + Precip. + Date	15	21.08	<0.01
Patch Area	Development (50 m) _ Development (500 m) + Hab. Class + Area (500 m)	14	22.04	<0.01
Neighborhood Canopy Cover * Development	Hab. Class + Development (500 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	14	27.69	<0.01
Neighborhood Global	Development (500 m) + Hab. Class + Cover (500 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date	14	29.34	<0.01
Neighborhood Canopy Cover Double Interaction	Development (500 m) * Cover (500 m) + Cover (500 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	16	30.63	<0.01
Neighborhood Canopy Cover * Habitat Class	Development (500 m) + Hab. Class * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	15	38.84	<0.01
Detection (Null)	Water Dist. + Temp. + Precip. + Date	9	54.27	<0.01

*Table 3.9: Parameters, estimates, standard errors (SE), lower (LCL) and upper (UCL) 85% confidence limits for fixed effects included in the top generalized linear mixed models (Horizontal Heterogeneity * Development and Horizontal Heterogeneity * Habitat Class) predicting nightly big brown bat activity across 96 sites in Champaign and Urbana, Illinois in the complete-dataset analysis (Analysis A). Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. For random effects, variance and standard deviation (Std. Dev.) are listed.*

z		Horizontal Heterogeneity * Development Model				Horizontal Heterogeneity * Habitat Class Model			
Fixed Effects	Parameter	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
	Intercept	3.06	0.43	2.44	3.68	1.61	0.44	0.98	2.24
	Development (50 m)	-0.72	0.14	-0.92	-0.53	-0.68	0.14	-0.88	-0.47
	Heterogeneity (50 m)	0.71	0.14	0.51	0.92	0.19	0.28	-0.21	0.60
	Hab. Class Open Park	-0.50	0.39	-1.05	0.06	-0.39	0.39	-0.96	0.17
	Hab. Class Street	-1.37	0.60	-2.23	-0.52	-1.09	0.67	-2.05	-0.12
	Development (50 m) * Heterogeneity (50 m)	0.27	0.16	0.03	0.51				
	Heterogeneity (50 m) * Hab. Class Open Park					0.70	0.34	0.21	1.18
	Heterogeneity (50 m) * Hab. Class Street					0.35	0.54	-0.43	1.13
	Water Dist.	-0.02	0.15	-0.24	0.20	-0.01	0.15	-0.23	0.21
	Temp.	0.003	3.38×10^{-4}	0.002	0.003	0.003	3.38×10^{-4}	0.002	0.003
	Date	-3.31×10^{-5}	4.66×10^{-6}	-3.98×10^{-5}	-2.64×10^{-5}	-3.32×10^{-5}	4.66×10^{-6}	-3.99×10^{-5}	-2.65×10^{-5}
	Precip.	-0.02	0.03	-0.07	0.02	-0.03	0.03	-0.07	0.02
Random Effects	Parameter	Variance	Std. Dev.			Variance	Std. Dev.		
Site	Intercept	1.72	1.31			1.87	1.37		
Sample Point	Intercept	0.586	0.77			0.51	0.72		
Deployment cycle	Intercept	2.18	1.47			2.17	1.47		

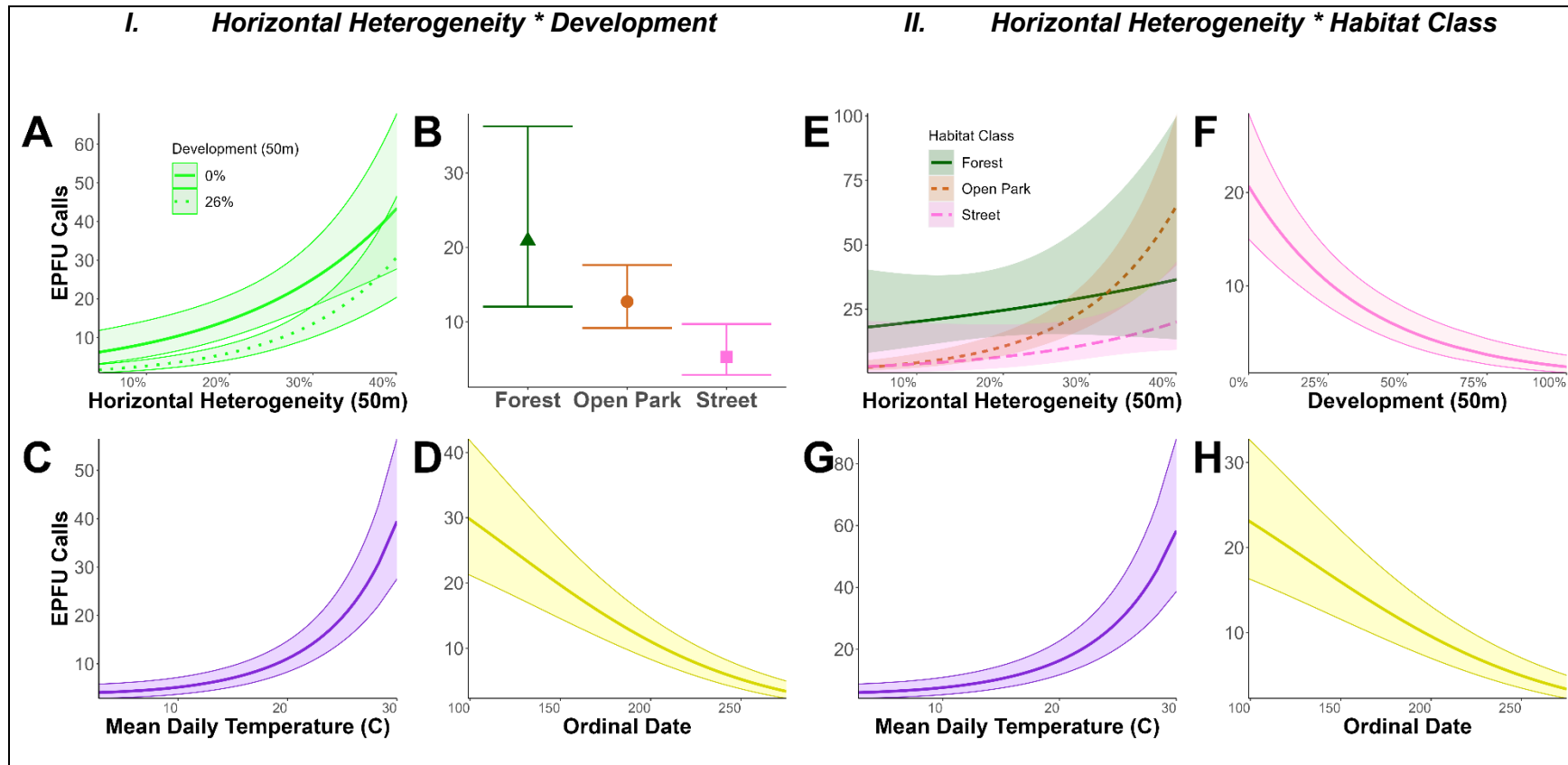


Figure 3.4: Predicted big brown bat activity (EPFU Calls) for ecologically significant variables for the two different competitive generalized linear mixed models (Horizontal Heterogeneity * Development and Horizontal Heterogeneity * Habitat Class) from Analysis A, **I.**—Horizontal Heterogeneity * Development. Variables, clockwise from top left: **A**—Development (50 m) * Heterogeneity (50 m), **B**—Hab. Class, **C**—Temp., **D**—Date. **II.**—Horizontal Heterogeneity * Habitat Class. Variables, clockwise from top left: **E**—Heterogeneity (50 m) * Hab. Class, **F**—Development (50 m), **G**—Temp., **H**—Date. All other variables in the model were held at their mean values when generating predictive plots.

Analysis A: Eastern Red Bat

For eastern red bats, only the *Horizontal Heterogeneity * Habitat Class* model was competitive (Table 3.10). Activity was greater with increasing local horizontal canopy heterogeneity and in the forest habitat class (Figure 3.5A, Table 3.11). There was a significant interaction between heterogeneity and habitat class, such that increasing heterogeneity had the greatest positive effect at forest points, a small positive effect at open park points, and no effect at street points (Figure 3.5B). Increasing development had a significant but weak negative effect on activity (Table 3.11, Figure 3.5C). Within the detection variables, increasing temperature positively predicted activity (Figure 3.5D), while the increasing quadratic of the ordinal date (Figure 3.5E) and daily precipitation decreased activity (Figure 3.5F).

Table 3.10: AICc rankings, number of parameters (K), and weights (w_i) for 15 hypothesis-based generalized linear mixed models and the null model predicting nightly eastern red bat activity across 96 sites in Champaign and Urbana, Illinois, in the complete-dataset analysis (Analysis A). The Horizontal Heterogeneity * Habitat Class, in **bold**, was the only competitive model. For all models, deployment cycle, sample point, and site were included as random effects.

Model Name	Fixed Effects	K	$\Delta AICc$	w_i
Horizontal Heterogeneity * Habitat Class	Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	15	0.00	0.73
Local Global	Development (50 m) + Hab. Class + Cover (50 m) + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	14	3.29	0.14
Local Canopy Cover * Habitat Class	Development (50 m) + Hab. Class * Cover (50 m) + Water Dist. + Temp. + Precip. + Date	15	5.16	0.06
Local Canopy Cover Double Interaction	Development (50 m) * Cover (50 m) + Cover (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	16	5.93	0.04
Total Global	Development (50 m) + Development (500 m) + Hab. Class + Cover (50 m) + Cover (500 m) + Heterogeneity (50 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date	17	6.76	0.02
Horizontal Heterogeneity * Development	Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	9.67	<0.01
Horizontal Heterogeneity	Development (50 m) + Development (500 m) + Hab. Class + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	14	12.29	<0.01
Detection	+ Water Dist. + Temp. + Precip. + Date	9	14.03	<0.01
Canopy Cover * Canopy Cover	Hab. Class + Development (500 m) + Cover (50 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	16	15.89	<0.01
Patch Area	Development (50 m) _ Development (500 m) + Hab. Class + Area (500 m) + Water Dist. + Temp. + Precip. + Date	14	17.23	<0.01
Local Canopy Cover * Development	Development (50 m) * Cover (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	17.37	<0.01
Neighborhood Global	Development (500 m) + Hab. Class + Cover (500 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date	14	18.36	<0.01
Neighborhood Canopy Cover * Habitat Class	Development (500 m) + Hab. Class * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	15	18.48	<0.01
Canopy Cover	Development (50 m) + Development (500 m) + Hab. Class + Cover (50 m) + Cover (500 m) + Water Dist. + Temp. + Precip. + Date	15	18.61	<0.01
Neighborhood Canopy Cover Double Interaction	Development (500 m) * Cover (500 m) + Cover (500 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	16	19.56	<0.01
Neighborhood Canopy Cover * Development	Hab. Class + Development (500 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	14	20.01	<0.01

Table 3.11: Parameters, estimates, standard errors (SE), lower (LCL) and upper (UCL) 85% confidence limits for fixed effects included in the top generalized linear mixed model (Heterogeneity * Habitat Class) predicting nightly eastern red bat activity across 96 sites in Champaign and Urbana, Illinois in the complete-dataset analysis (Analysis A). Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. For random effects, variance and standard deviation (Std. Dev.) are listed.

Fixed Effects		Parameter	Estimate	SE	LCI	UCL
	Intercept		-1.50	0.64	-2.42	-0.57
	Development (50 m)		-1.12	0.77	-2.22	-0.02
	Heterogeneity (50 m)		1.72	0.41	1.14	2.31
	Hab. Class Open Park		-0.76	0.53	-1.52	0.01
	Hab. Class Street		-0.36	0.85	-1.58	0.86
	Heterogeneity (50 m) * Hab. Class Open Park		-1.31	0.46	-1.98	-0.64
	Heterogeneity (50 m) * Hab. Class Street		-2.80	0.76	-3.90	-1.71
	Water Dist.		0.22	0.17	-0.03	0.46
	Temp.		0.004	7.25×10^{-4}	0.003	0.005
	Date		-2.43×10^{-5}	9.25×10^{-6}	-3.76×10^{-5}	-1.10×10^{-5}
	Precip.		-0.22	0.09	-0.35	-0.10
Random Effects		Parameter	Variance	Std. Dev.		
Site	Intercept		0.73	1.31		
Sample Point	Intercept		0.54	0.77		
Deployment cycle	Intercept		5.19	1.47		

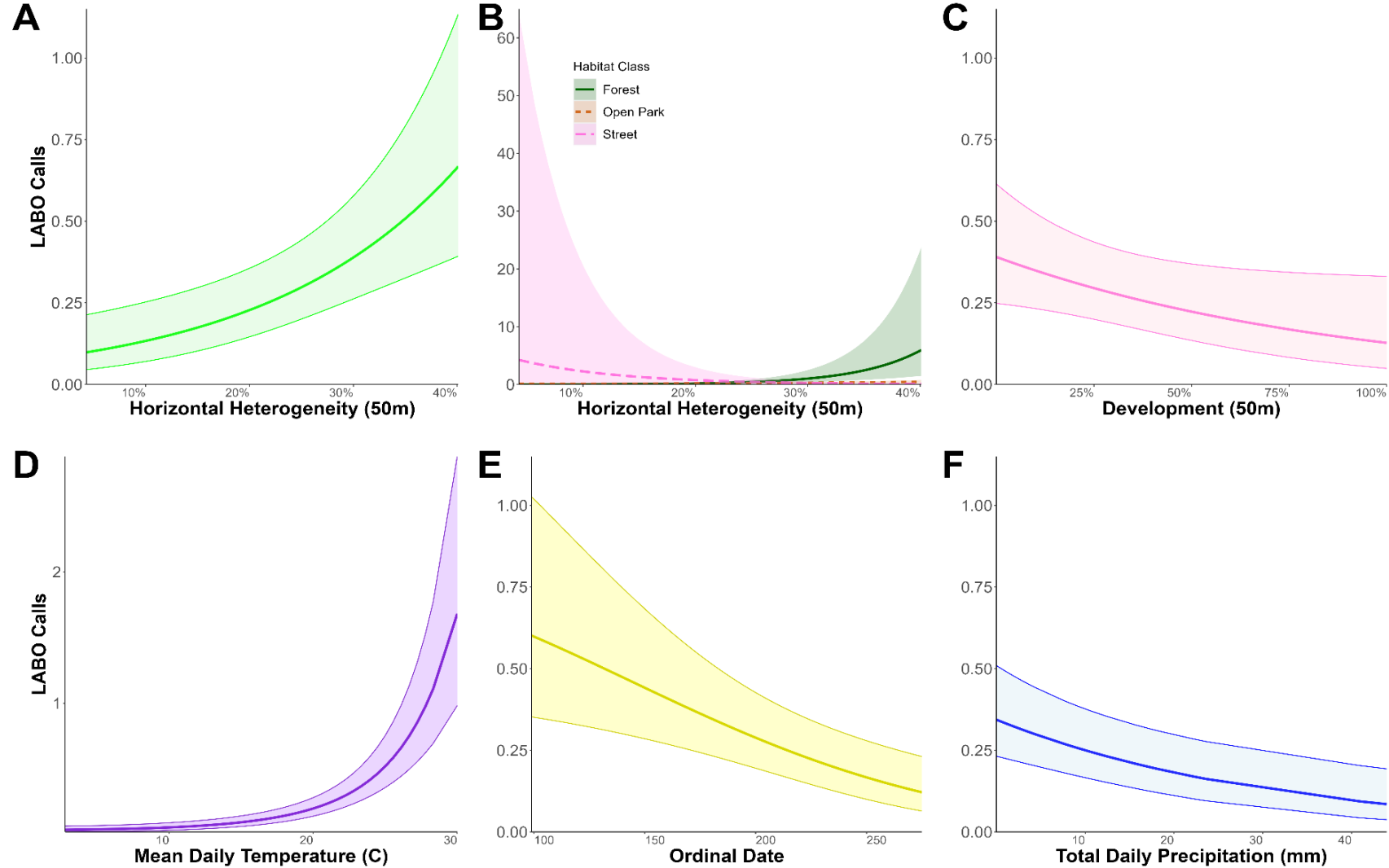


Figure 3.5: Predicted eastern red bat activity (LABO Calls) for ecologically significant variables for the top model from Analysis A, Horizontal Heterogeneity * Habitat Class. Variables, clockwise from top left: **A**–Heterogeneity (50 m), **B**– Heterogeneity (50 m) * Hab. Class, **C**–Development (50 m), **D**–Temp. **E**– Date, **F**–Precip. All other variables in the model were held at their mean values when generating predictive plots.

Analysis B

For big brown bats, there was considerable model uncertainty; adding diversity measures generated additional plausible models, but none of these outcompeted the base *Horizontal Heterogeneity * Development* or *Horizontal Heterogeneity * Habitat Class* models (Table 3.12). Therefore, no relationships are plotted. For eastern red bats, the *Diversity* model was the only competitive model and outperformed the base *Horizontal Heterogeneity * Habitat Class* model (Table 3.13). Increasing Shannon Diversity for the inventoried trees resulted in less eastern red bat activity (Table 3.14, Figure 3.6A). All other parameters shared with the original *Horizontal Heterogeneity * Habitat Class* remained ecologically significant in the *Diversity* model, and there was an additional positive effect of increasing distance to water features (Figure 3.6B).

Table 3.12: AICc rankings, number of parameters (K), and weights (w_i) for 10 generalized linear mixed models predicting nightly big brown bat activity across 91 sites in Champaign and Urbana, Illinois, in the tree-inventory-dataset analysis (Analysis B). The 9 models in **bold** were competitive models. For all models, deployment cycle, sample point, and site were included as random effects.

Model Name	Fixed Effects	K	$\Delta AICc$	w_i
<i>Horizontal Heterogeneity * Habitat Class (Null)</i>	Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	13	0.00	0.17
<i>Horizontal Heterogeneity * Development (Null)</i>	Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	13	0.20	0.15
<i>Diversity + Abundance + Horizontal Heterogeneity * Habitat Class</i>	Shannon + Abundance + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	15	0.79	0.11
<i>Abundance + Horizontal Heterogeneity * Habitat Class</i>	Abundance + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	0.84	0.11
<i>Diversity + Horizontal Heterogeneity * Habitat Class</i>	Shannon + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	1.13	0.10
<i>Abundance + Horizontal Heterogeneity * Development</i>	Abundance + Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	1.14	0.10
<i>Diversity + Horizontal Heterogeneity * Development</i>	Shannon + Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	1.81	0.07
<i>Fagaceae + Horizontal Heterogeneity * Habitat Class</i>	Fagaceae + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	1.95	0.06
<i>Diversity + Abundance + Horizontal Heterogeneity * Development</i>	Shannon + Abundance + Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	15	1.98	0.06
<i>Fagaceae + Horizontal Heterogeneity * Development</i>	Fagaceae + Development (50 m) * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	14	2.09	0.06

Table 3.13: AICc rankings, number of parameters (K), and weights (w_i) for 5 generalized linear mixed models predicting nightly eastern red bat activity across 91 sites in Champaign and Urbana, Illinois, in the tree-inventory-dataset analysis (Analysis B). The Diversity model, in **bold**, was the only competitive model. For all models, the deployment cycle, sample point, and site were included as random effects.

Model Name	Fixed Effects	K	ΔAIC_c	w_i
Diversity	Shannon + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	0.00	0.69
Diversity + Abundance	Shannon + Abundance + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	15	2.05	0.25
Horizontal Heterogeneity * Habitat Class (Null)	Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	13	6.17	0.03
Abundance	Abundance + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	7.28	0.02
Fagaceae	Fagaceae + Development (50 m) + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	14	7.97	0.01

Table 3.14: Parameters, estimates, standard errors (SE), lower (LCL) and upper (UCL) 85% confidence limits for fixed effects included in the top generalized linear mixed model (Heterogeneity * Habitat Class) predicting nightly eastern red bat activity across 91 sites in Champaign and Urbana, Illinois in the tree-inventory-dataset analysis (Analysis B). Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. For random effects, variance and standard deviation (Std. Dev.) are listed.

Fixed Effects		Parameter	Estimate	SE	LCI	UCL
	Intercept		0.82	0.65	-0.11	1.75
	Development (50 m)		-1.27	0.70	-2.28	-0.26
	Heterogeneity (50 m)		0.36	0.17	0.11	0.61
	Hab. Class Street		-0.50	0.56	-1.31	0.30
	Heterogeneity (50 m) * Hab. Class Street		-0.96	0.54	-1.73	-0.18
	Shannon		-1.03	0.36	-1.54	-0.51
	Water Dist.		0.35	0.18	0.08	0.61
	Temp.		0.76	0.15	0.55	0.97
	Date		-0.48	0.17	-0.73	-0.23
	Precip.		-0.30	0.11	-0.45	-0.14
Random Effects		Parameter	Variance	Std. Dev.		
Site	Intercept		1.32	0.85		
Sample Point	Intercept		0.57	0.001		
Deployment cycle	Intercept		2.46	2.14		

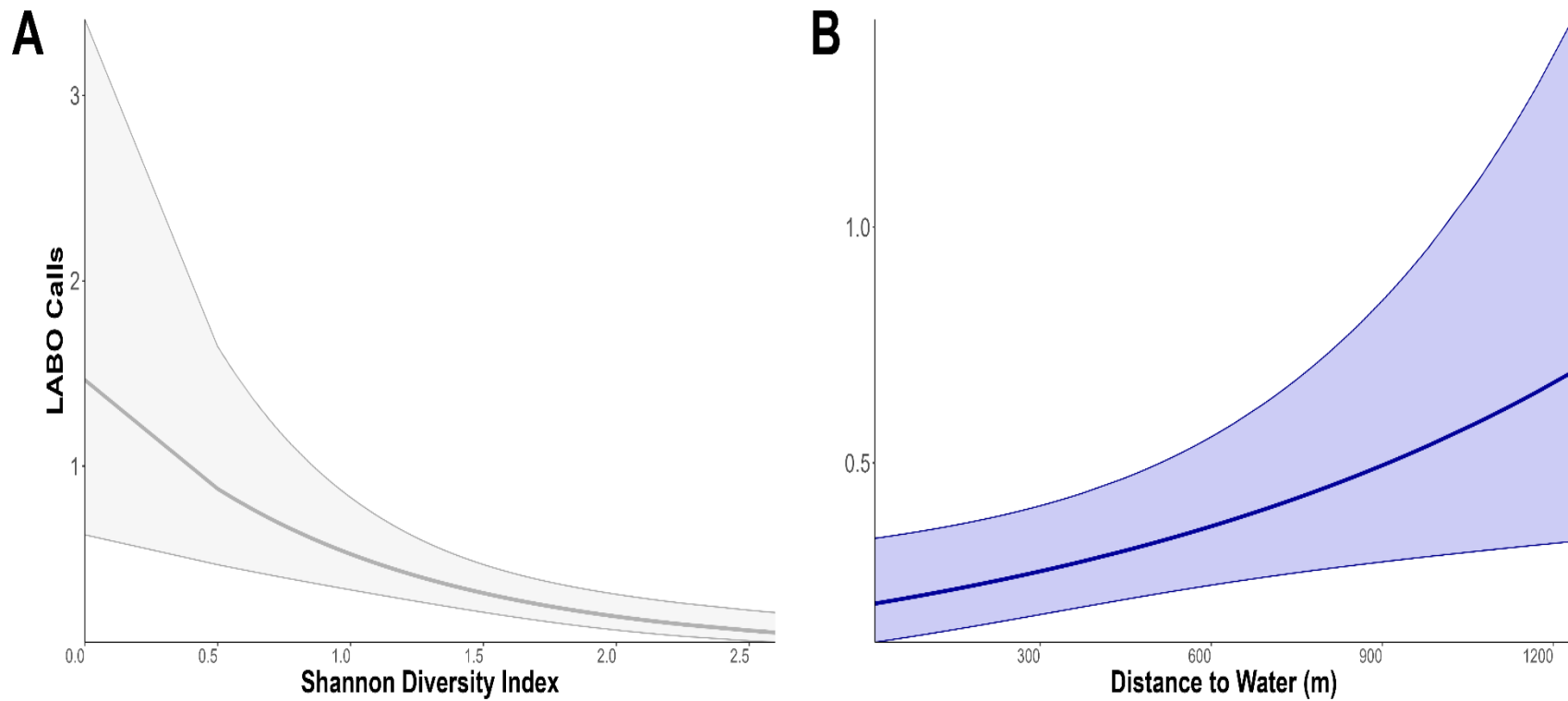


Figure 3.6: Predicted eastern red bat activity (LABO Calls) for ecologically significant variables highlighted in the top generalized linear mixed model from Analysis B, the Diversity model. Variables: **A**– Shannon and **B**– Water Dist. All other variables in the model were held at their mean values when generating predictive plots.

Northern long-eared Bat Acoustics, Capture Surveys, and Analysis C

During our acoustic survey, we only recorded northern long-eared bats in forests, with the exception of one sample point in nearby open park habitat (Figure 3.7, Table 3.15). We recorded 95 out of 126 manually vetted northern long-eared bat calls (75.4%) at Busey Woods, which is adjacent to a highly urbanized environment with a large medical campus, county fairground, outdoor aquatics center, in addition to a golf course, cemetery, and public park. All of the points with confirmed recordings were in sites that either bordered or were in the vicinity of the Saline Branch, and we had no positive identifications in our southern forest sites. Northern long-eared bats were first recorded near the beginning of our survey on 13 April 2023 and continued to be recorded throughout the summer, with the last vetted recording on 23 August 2023.

During mist netting surveys (Table 3.16), we confirmed the presence of northern long-eared bats (2 adult males, 1 adult female), and also captured big brown bats (12 adult females, 1 juvenile female, 21 adult males, 6 juvenile males), eastern red bats (3 juvenile females, 1 adult male, 3 juvenile females), and evening bats (2 adult females). No captured northern long-eared bats were actively reproductive. One adult northern long-eared bat male had considerable damage to one wing (Figure 3.8). We learned of two other records — two juvenile male northern long-eared bats from Urbana were tested for rabies by the Illinois Department of Public Health (IDPH) in 2012 and 2022 (Table 3.17), though both tested negative (J. Mengelkoch, Mammologist at the Illinois Natural History Survey, personal correspondence). Our results demonstrate the persistence of this species, post-WNS, over the past 3 years; it is unknown whether they were present between 2012–2022 or if they were extirpated and then recolonized the area. We placed transmitters on both northern long-eared bats captured in 2024 and successfully tracked the male to one day-roost, after which the transmitter fell off. The male day roost tree was located ~750 m from the point of capture in a public open park habitat < 50 m from a public roadway. The transmitter on the female fell off before any day roosts could be identified and was recovered two days later.

Table 3.15: Northern long-eared (MYSE) presence and call number by site, total site, and forest area in hectares calculated using ArcGIS Pro with a North American Albers Equal Area Conic Projection, number of sample points at each site and within forest patches. Only sites with sampled forest patches are listed. Totals are marked in **bold**.

Site	Forest Patch Name	Site Area (ha)	Forest habitat area (ha)	Number of Sample Points		Sample Points with MYSE Presence	Vetted MYSE Calls
				Total	Forest		
AMBU	Chief Shemauger Park ¹	20.4	3.5 ¹	5	2	0	0
ARBO	UIUC Arboretum	55.5	5.6	6	3	0	0
BRWO	Brownfield Woods	27.0	27.0	4	4	1	1
CRLA	Busey Woods	113.4	21.7	10	4	5	102 ²
HOWO	Holcomb Woods	84.1	84.1	5	5	2	2
MEBR	Illini Experimental Forest	62.2	9.7	9	3	0	0
PERO	Judge Webber Park ¹	34.1	12.6 ¹	6	3	2	3
PHTR	Phillips Tract	53.9	53.9	4	4	1	11
PRAI	Weaver Park	38.9	1.4	4	2	0	0
RAWO	Raintree Woods	10.7	10.7	2	2	1	1
TREL	Trelease Woods	25.3	25.3	4	4	2	6
All other sample sites		428.0		124	0	0	0
Sample site total		936	275	183	40	14	126
Unsampled sites		148	120				
All sites total		1084	395				

¹Chief Shemauger Park and Judge Webber Park Forest tracts are within the same contiguous patch, along with 29.4 ha of privately owned forest (for a total contiguous patch of 45.5 ha) but are considered separate sites due to distance.

²Seven MYSE calls at the CRLA site were recorded in open park habitat rather than forest

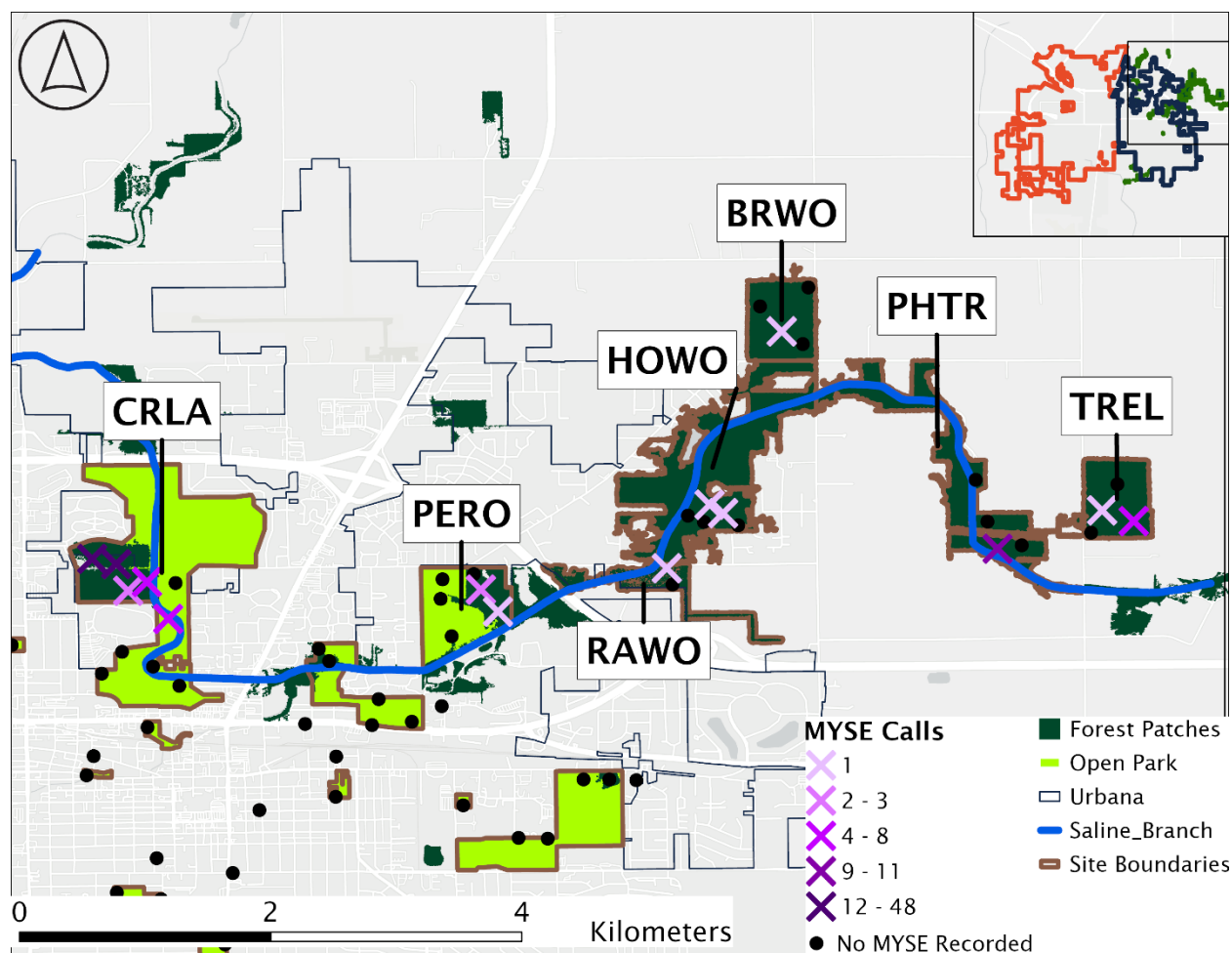


Figure 3.7: Map of all sample points with confirmed northern long-eared (MYSE) presence, along with how many calls were recorded at each point. All confirmed calls were in forests in northeast Urbana. White labels refer to site codes: CRLA– Crystal Lake Park + Busey Woods, PERO– Perkins Road Site (no detections) + Judge Webber Park, RAWO– Raintree Woods, HOWO– Holcomb Woods, BRWO– Brownfield Woods, PHTR– Phillips Tract, TREL– Trelease Woods.

Table 3.16: Captured capture counts of big brown (EPFU), eastern red (LABO), evening (NYHU), and northern long-eared bats (MYSE) from 8 mist netting nights by year, date, forest site in Urbana, IL.

Year	Date	Forest Site	EPFU	LABO	NYHU	MYSE
2023	8/2	Brownfield Woods	6	0	0	0
	8/8	Busey Woods	6	1	0	0
	8/24		4	5	0	0
	8/15	Judge Webber Park	0	1	0	1
	9/5		0	0	0	0
2024	4/29	Busey Woods	10	0	2	2
	5/7		11	0	0	0
	5/23	Judge Webber Park	2	0	0	0
Total			39	7	2	3



Figure 3.8: Adult male northern long-eared bat captured 15 August 2023, with significant previously acquired wing damage of unknown origin.

Table 3.17: Year, date, location, and demographics of five confirmed northern long-eared bat occurrences in Urbana, IL, from 2023 and 2024 capture surveys and Illinois Department of Public Health (IDPH) rabies testing since 2012.

Year	Date	Location	Source	Female		Male	
				Adult	Juvenile	Adult	Juvenile
2012	7/10	Unknown	ILDPH				1
2022	7/11	Unknown	ILDPH				1
2023	8/15	Judge Webber Park	Capture Survey			1	
2024	4/29	Busey Woods	Capture Survey	1		1	
Total				1	0	2	2

For our northern long-eared bat acoustic presence analysis (Analysis C), only the *Neighbor Canopy Cover Double Interaction* model was competitive (Table 3.18). For this model, increasing distance to the nearest road positively predicted presence, and there was a significant interaction with neighborhood-scale canopy cover (Table 3.19, Figure 3.9). At points that are close to roads, presence was predicted to be higher in areas with higher neighborhood-scale tree canopy cover. However, at points far from roads, presence was predicted to be higher in areas with lower canopy cover. Increasing temperature positively predicted northern long-eared bat presence in this model but was the only important detection variable.

Table 3.18: AICc rankings, number of parameters (K), and weights (w_i) for 15 hypothesis-based generalized linear mixed models and the null model predicting nightly northern long-eared bat presence across 11 sites in Urbana, Illinois (Analysis C). The Neighborhood Canopy Cover Double Interaction model in **bold**, was the only competitive model. For all models, the deployment cycle, sample point, and site were included as random effects.

Model Name	Model	K	$\Delta AICc$	w_i
Neighborhood Canopy Cover Double Interaction	Road Dist. * Cover (500 m)+ Cover (500 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	13	0.00	0.62
Neighborhood Canopy Cover * Habitat Class	Road Dist. + Hab. Class * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	12	2.05	0.22
Horizontal Heterogeneity * Habitat Class	Road Dist. + Heterogeneity (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	12	5.86	0.03
Canopy Cover * Canopy Cover	Road Dist. + Hab. Class + Cover (50 m) * Cover (500 m) + Water Dist. + Temp. + Precip. + Date	13	5.93	0.03
Detection (Null)	Water Dist. + Temp. + Precip. + Date	8	7.62	0.01
Canopy Cover	Road Dist. + Hab. Class + Cover (50 m) + Cover (500 m) + Water Dist. + Temp. + Precip. + Date	12	7.86	0.01
Horizontal Heterogeneity	Road Dist. + Hab. Class + Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	11	7.99	0.01
Total Global	Road Dist. + Hab. Class + Cover (50 m) + Cover (500 m) + Heterogeneity (50 m) + Area (500 m) + Water Dist. + Temp. + Precip. + Date	14	8.04	0.01
Horizontal Heterogeneity * Development	Road Dist. * Heterogeneity (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	12	8.46	<0.01
Neighborhood Canopy Cover * Development	Road Dist. * Cover (500 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	12	8.80	<0.01
Local Global	Road Dist. + Hab. Class + Cover (50 m)+ Heterogeneity (50 m) + Water Dist. + Temp. + Precip. + Date	12	8.90	<0.01
Neighborhood Global	Road Dist. + Hab. Class + Cover (500 m)+ Area (500 m) + Water Dist. + Temp. + Precip. + Date	12	9.03	<0.01
Local Canopy Cover * Development	Road Dist. * Cover (50 m) + Hab. Class + Water Dist. + Temp. + Precip. + Date	12	9.84	<0.01
Local Canopy Cover * Habitat Class	Road Dist. + Hab. Class * Cover (50 m) + Water Dist. + Temp. + Precip. + Date	12	9.88	<0.01
Patch Area	Road Dist. + Hab. Class + Area (500 m) + Water Dist. + Temp. + Precip. + Date	11	11.36	<0.01
Local Canopy Cover Double Interaction	Road Dist. * Cover (50 m)+ Cover (50 m) * Hab. Class + Water Dist. + Temp. + Precip. + Date	13	11.77	<0.01

Table 3.19: Parameters, estimates, standard errors (SE), lower (LCL), and upper (UCL) 85% confidence limits for fixed effects included in the top generalized linear mixed model (Neighborhood Canopy Cover Double Interaction) predicting nightly northern long-eared bat presence in 11 sites in Urbana, Illinois (Analysis C). Variables marked in **bold** have 85% confidence intervals that do not overlap with zero and are considered ecologically significant. For random effects, variance and standard deviation (Std. Dev.) are listed.

Fixed Effects	Parameter	Estimate	SE	LCL	UCL
	Intercept	-8.51	3.20	-13.12	-3.90
	Road Dist.	6.03	2.54	2.38	9.68
	Cover (500 m)	10.21	7.67	-0.84	21.25
	Hab. Class Open Park	-4,227.39	194,273.26	-283,889.87	275,435.09
	Cover (500 m) * Hab. Class Open Park	10,675.02	490,470.27	-695,372.37	716,722.41
	Cover (500 m) * Road Dist.	-14.12	6.64	-23.68	-4.56
	Water Dist.	0.82	0.66	-0.12	1.77
	Temp.	0.45	0.30	0.01	0.89
	Date.	-0.16	0.28	-0.56	0.25
	Precip.	-0.14	0.57	-0.96	0.67
Random Effects	Parameter	Variance	Std. Dev.		
Site	Intercept	4.55	2.13		
Sample Point	Intercept	1.15 x 10 ³⁴	3.39 x 10 ⁻¹³		
Deployment cycle	Intercept	1.07	1.03		

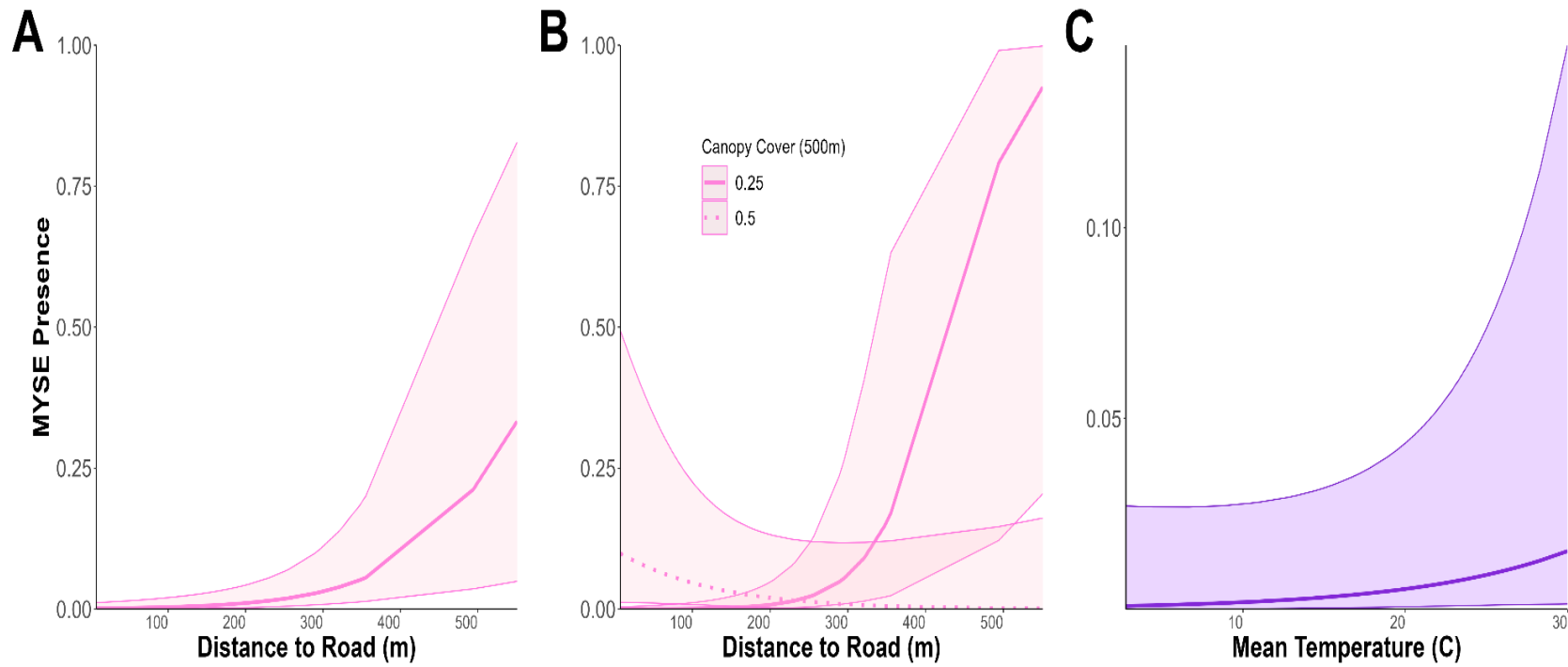


Figure 3.9: Predicted northern long-eared bat presence (MYSE Presence) for the top Neighborhood Canopy Cover Double Interaction model generalized linear mixed model from Analysis C. Variables, from left: **A**– Road Dist., **B**– Road Dist. * Canopy Cover (500 m), **C**- Temp. All other variables in the model were held at their mean values when generating predictive plots.

Discussion

Our results demonstrate that LiDAR-derived data can be used to measure fine-scale environmental variables with ecological significance to urban bats. This work supports the findings of Moretto et al. (2019) and Mimet et al. (2020), which found bats respond positively to fine-scale vegetation metrics; in contrast to these studies, we found horizontal canopy heterogeneity, not cover, to be most informative. Because bats respond to fine-scale environments, this suggests that land-use changes across an area of < 1 ha could impact their foraging behavior. In urban environments, where large-scale management actions may be difficult due to competing human interests, small-scale habitat restoration projects within greenspaces could still provide benefits to city-dwelling bats. Parker et al. (2019) found that the construction of two wetlands at sites with areas of < 0.08 ha increased bat activity, showing the potential benefits of fine-scale conservation efforts. Our analyses show that urban forestry has the potential to play a role in supporting bats and that LiDAR data is a useful tool for investigating this possibility. While seldom utilized within urban bat research, publicly accessible LiDAR data offers opportunities for researchers to generate high-quality, fine-scale vegetation data with relatively low effort compared to field measurements. LiDAR-derived vegetation metrics can be used to predict fine-scale urban bat activity and should be considered a useful tool when quantifying the environmental mosaic of a city from the perspective of bats.

Big brown bats responded positively to horizontal canopy heterogeneity within 50 m in open park habitat, suggesting that this environment can support bat foraging under the right conditions. Big brown bats are thought to be fast-flying, open-space foragers (Menzel et al. 2005), but in urban areas, they respond negatively to open habitat (Dixon 2011, Gallo et al. 2017) and positively to tree cover within 100 m (Gallo et al. 2017). Within turf-dominated parks, horizontal canopy heterogeneity and cover were positively correlated, so fine-scale increases in tree density that introduce greater heterogeneity in more open environments should result in higher big brown activity. Meanwhile, eastern red bats responded positively to horizontal canopy heterogeneity in forests; this is in line with their association with forests in urban environments (Walters et al. 2007). Increasing the heterogeneity in the canopy structure of urban forests is likely to result in greater activity by eastern red bats. Both eastern red bats and big brown bats are more active in forest gaps (Brooks et al. 2017, Loeb and O’Keefe 2011) and edge habitat

(Morris et al. 2010), which are sources of horizontal canopy heterogeneity in tree-dominated landscapes. Our results corroborate work showing positive responses to gaps and edges, though this has rarely been documented within urban landscapes.

Several ecological mechanisms could explain why bats may have higher activity with increasing canopy heterogeneity. Villarroya-Villalba et al. (2021) found higher insect diversity and abundance in Zurich, Switzerland, with increasing vertical vegetation heterogeneity at the 100-m scale (2021); if this relationship holds true for horizontal heterogeneity at a 50-m scale, increasing prey access may be one mechanism to explain bat response to canopy heterogeneity. Divoll et al. (2021) found that Indiana and northern-long eared bats were attracted to openings created by small regenerative cuts in south-central Indiana and hypothesized that this was driven by greater insect diversity along forest edges. Beyond prey access, areas with high horizontal canopy heterogeneity may provide bats with other benefits from both cluttered and open structural environments. Tree canopy cover also buffers bats from light pollution (Straka et al. 2019) and offers roosting opportunities for some species (Threlfall et al. 2013), while open spaces can provide easier foraging for fast-flying bats with high aspect ratios and wing loadings due to fewer obstructions (Loeb and O’Keefe 2011). Parsing out the precise mechanism driving the increase in bat activity with increasing horizontal heterogeneity would be difficult but could be an interesting avenue for future research.

While we showed that urban bats exhibit ecological responses to LiDAR-derived horizontal canopy heterogeneity, we also found that this effect varied within forest, open park, and street environments. Other studies have also found broadly defined forest and open park categories as informative for predicting bat activity (e.g., Avila-Flores and Fenton 2005), and our research highlights that general habitat classifications can work in concert with fine-scale vegetation metrics to describe bat ecology. Cities are often a complex mosaic of environments that provide varying degrees of habitat for bats. It appears that bats respond to tree structure differently depending on which environment they are in, and conservation actions for urban bats should be context-dependent, rather than a “one-size fits all” approach. For example, we showed that introducing horizontal canopy heterogeneity in cities could promote bat activity; in open parks, this would involve planting more trees in open green spaces like turf-dominated parks (Frey-Ehrenhold et al. 2013). However, in forests, heterogeneity would be achieved by thinning some patches of cluttered forest stands (Divoll et al. 2021). Our results also differed by species,

so urban land managers should have clear goals in mind, such as which species are targets, when planning conservation efforts.

Alternatively, our results could also be explained by other mechanisms that we did not account for in our study design. There are several other LiDAR-derived metrics that we did not calculate but could provide greater insight into urban bat ecology than our measure of horizontal canopy heterogeneity. Perhaps specific forest edge (Blanchard et al. 2022) and forest gap (Chung et al. 2022) predictor variables derived from LiDAR data could give us a better understanding of why bats respond positively to higher horizontal heterogeneity. Vertical tree structure influences bat ecology (Froidevaux et al. 2016), but we did not examine the effects of tree height or vertical canopy heterogeneity in our analysis. By grouping all vegetation-class points in our metrics of tree canopy cover and horizontal heterogeneity, we reduced the number of variables included in our models but may have lost ecologically relevant information. Bat studies using LiDAR data should consider utilizing vertical and horizontal predictors of tree structure, which are both likely to influence 3-D foraging movements.

It is possible that the measured increase in bat activity with horizontal canopy heterogeneity is more related to differing detection rates as a result of clutter. Higher clutter reduces the quality and maximum range at which acoustic calls can be detected (Patriquin et al. 2003), and midstory clutter especially reduces detection rates for high-frequency bats (O’Keefe et al. 2014). Additionally, removing forest canopy through tree harvest increases the detection of low frequency and eastern red bats (O’Keefe et al. 2013), suggesting that areas of high horizontal canopy heterogeneity in forests (i.e., gaps and edges) have a higher probability of detection. Thus, it is possible we detected bats less readily in forests. Future research should seek to disentangle the true responses of bats to canopy heterogeneity from differences in acoustic detection rate.

We recorded lower eastern red and big brown activity on streets, mirroring previous work showing urban-associated bats are less active on streets (Oprea et al. 2009) and in residential environments (Avila-Flores and Fenton 2005). Roads have several negative ecological effects on bats, such as car-collision-induced mortality (Bennett and Zurcher 2013), barrier effects preventing movement (Kerth and Melber 2009), and behavioral changes (Bennett et al. 2013) any of which may be mechanisms driving our results. However, it is difficult to disentangle whether bats truly made fewer calls at our street points or whether detection rates were lower due

to interference from road noise. Big brown bats and eastern red bats were also less active in areas with higher local development, suggesting that urbanization reduces foraging habitat (Coleman and Barclay 2013, Threlfall et al. 2012b). For the big brown bat, which tends to roost in buildings, this indicates that the surroundings selected for artificial roosts and foraging may be quite different. Further research is needed to understand the dynamic between these two key aspects of urban ecology surrounding the energetic tradeoffs associated with commuting during foraging.

Future urban bat research should focus on whether changes in urban forestry management can improve the conservation standing of city-dwelling species. Research to this point has projected that increasing discontinuous woodland habitat (Gili et al. 2020) and increasing private and public green space (Mimet et al. 2020) positively impacts bats, but there have been few direct recommendations in the literature for actions that urban land managers can take to support bats. Conducting manipulative experiments could reveal whether there are positive causal effects of management actions on bat activity and diversity, such as increasing canopy heterogeneity through tree thinning, interspersed planting, or wholesale reforestation in urban public parks. However, as trees take many years to grow, experiments testing bats' responses to tree plantings would need to be conducted over long time scales (Vega-Hidalgo et al. 2021). Other aspects of urban forestry may be conducive to experiments on shorter timeframes than the effectiveness of urban forestry management on bat response. De Oyarzabal Barba (2023) found that increasing the straightness of tree lines increased bat activity and recommended pruning canopies into more linear shapes. Experimental tree felling in rural forests increased bat activity (Wright et al. 2023), but the impact may be negative for city-dwelling bats, depending on context. In other taxa, tree removal in urban parks reduces possum (*Phalangeriformes*) and nectarivorous bird abundance (Ordóñez et al. 2023). An experiment measuring bats' response to the pruning or removal of trees is more feasible in a timeframe of a few years rather than a potential decades-long study of reforestation (Ordóñez et al. 2023). Retaining large, old trees, both living and dead (i.e., snags), would offer more natural roosting opportunities for bat species (Threlfall and Jung 2023) and would support deadwood-eating beetles, which bats may eat (Sandström et al. 2019). However, these trees have perceived risks to public safety and are often removed by municipalities from urban landscapes (Threlfall and Jung 2023). Future research should test whether retaining trees that would typically be removed, in conjunction with safety measures like crown thinning and

protective barriers, results in greater bat occupancy. For all of these proposed future directions, city forestry, and parks departments would be crucial partners due to their landholdings and active role in managing urban trees, and identifying concrete steps for these agencies to take to improve bat habitat is the next step needed to make cities more bat-friendly.

Tree inventory data was not a strong predictor of big brown bat activity, but we did find decreasing eastern red bat activity with increasing Shannon diversity at a family level. The negative impact of tree diversity on eastern red bats was surprising; there have been few attempts to quantify the effect of tree diversity on bat response, though one study found increasing bat activity with increasing tree species evenness (Ampoorter et al. 2019) and higher tree diversity in temperate forests results in increased bird diversity and abundance (Poulsen 2002). Increasing tree diversity may be driven by the presence of non-native, exotic species that do not serve valuable ecological functions for bats. In Melbourne, Australia, increasing proportions of native vegetation positively affect bat occupancy and activity (Threlfall et al. 2016 and 2017). *Plecotus* bats are more active near native oaks in the city of Karlsruhe, Germany, compared to non-native oaks (Laux et al. 2022), further suggesting some bats may be negatively affected by exotic species in urban areas. Eastern red bats preferentially roost in native sweetgum and oak trees in urban environments (Mager and Nelson 2001) and increasing tree family diversity could be associated with decreases in the availability of their preferred roosts. If areas with high family-level Shannon diversity do have higher proportions of non-native vegetation, then our results would suggest that cities should plant more native trees to support eastern red bats.

However, we caution that there could be several alternative explanations beyond native tree status for why we saw declining red bat activity with increasing family-level tree diversity. It is possible that there was an interaction between tree diversity and habitat, as we did not test for it. The parks we sampled had complete tree inventories, but our measurement for the diversity of trees around street points was likely skewed by not including trees in nearby yards. Privately owned residential trees in Salt Lake City, Utah, were more diverse than public street trees (Avolio et al. 2018), but it is unknown whether this is the case in Champaign-Urbana. Overall, further investigation is needed into the impact of native and non-native urban tree diversity on bat ecology. Studies using street tree inventories should supplement data from private yards, potentially through the use of community science (Johnson et al. 2018), to get a more complete picture of urban tree diversity.

The bat assemblage in Champaign-Urbana is dominated by the big brown bat, but this twin city also hosts many other species, including the endangered northern long-eared bat. It is unsurprising that the big brown bat is dominant in Champaign-Urbana, as this is true for many cities throughout the Midwest (Dixon 2011, Kurta and Teramino 1992, Gehrt and Chelsvig 2004, Gallo et al. 2017). However, we were surprised to discover the presence of the northern long-eared bat due to its severe population declines of 97–100% in WNS-affected areas (U.S. Fish and Wildlife Service 2023a) and preferences for regions with a high proportion of forest (Pauli et al. 2015); Champaign-Urbana has little forest and high urban density. The closest known winter hibernaculum for northern long-eared bats is 80 km away along the Wabash River in Indiana (Whitaker and Rissler 1992), but it is also possible bats from our study area are overwintering in an undiscovered location.

While the northern long-eared bats are not typically considered urban-associated, and thus their presence in Champaign-Urbana was unexpected, they have been captured in or near urban areas across their range, such as Washington, D.C (Deeley et al. 2021); Fort Wayne, Indiana (Burrell and Bergeson 2022); Long Island, New York (Hoff et al. 2024b); and Toronto, Ontario (Thorne et al. 2021). Thorne et al. (2019) concluded that the northern long-eared bat is not a synurban species, as tracked individuals did not leave forested habitat to forage within the urban matrix of Toronto; rather, they suggested that this species can be found in urban areas only if there is sufficient forested habitat. Hoff et al. (2024a) found similar results, as development negatively influenced northern long-eared occupancy in Long Island despite coastal populations being observed roosting in anthropogenic structures. Our results are in line with these conclusions, as 13 out of 14 sample points with northern long-eared calls were in forested habitat. However, for non-coastal northern long-eared bat populations, the smallest forest patch area with confirmed captures was the 245-ha Fox Island County Park, Allen County, Indiana (Burrell and Bergeson 2022), which is nearly ten times larger than our forest with the highest activity, the 21.7-ha Busey Woods. In the northeastern Atlantic Coastal Plain, northern long-eared bats were recorded in forest fragments < 0.5 ha, complementing our finding that the species can exist in small urban forest fragments. We recommend that urban land managers consider all forest patches as potential northern long-eared habitat within its range. While Busey Woods is nestled within urban development and relatively small, we speculate that the Saline Branch provides a crucial role in connecting it to the other remnant forest patches in northeast

Urbana, as this riparian corridor has nearly continuous canopy cover. Riparian areas promote the movement of many wildlife taxa, including birds, through urban areas (Dallimer et al. 2012). Urbanization along waterways can reduce bat activity (Lintott et al. 2015, McGowan 2023) and may impede movement. Further research should investigate the role of streams and rivers in providing habitat connectivity for northern long-eared bats in urban areas and across its distribution. We recommend that steps be taken to ensure the continued preservation of tree cover along the Saline Branch to prevent further fragmentation between the various forest fragments, particularly Busey Woods, in the region.

In addition, future studies should examine how the health and fitness of northern long-eared bats may be impacted by residing in or near cities and how this may have implications for the conservation of this imperiled species. Northern long-eared are actively reproducing within urban areas (Deeley et al. 2021, Burrell and Bergeson 2022, Thorne et al. 2021), but whether these urban populations are sustainable is not known despite the species having persisted for several years post-WNS in all urban studies. Coleman and Barclay (2011a) found that its congener, the little brown bat, had reduced body condition and reproductive success in urban Calgary, Alberta, Canada, compared to rural areas. However, little brown bats are known to use artificial roosts readily (Coleman and Barclay 2011a), and no comparable studies have been done on primarily tree-roosting urban species in general or on northern long-eared bats specifically. Two of our captured bats appeared to be in good health. Still, one captured male had significant wing damage, and two juveniles were submitted for rabies testing, as documented by the Illinois Department of Public Health. The cause of the wing injury and the reason the juveniles were submitted is unknown, as is whether these anecdotal reports of potentially poor health reflect a broader negative trend caused by urbanization. Research relating to the fitness and health of urban northern long-eared bats relative to rural populations will be necessary to determine whether city-adjacent forests are potential ecological traps (Russo and Ancillotto 2015), refugia (Valentine et al. 2014) or neutral habitat for the northern long-eared bat. Regardless, steps should be undertaken to limit deforestation and other potential threats caused by human disturbances in sites with northern long-eared bats to promote the conservation of the species.

In regard to northern long-eared bat occupancy, our modeling suggested that there may be an interaction between distance to road and canopy cover within 500 m, where northern long-eared presence is higher in lower canopy cover and far from roads, though the current evidence

is weak. Northern long-eared have negative (Thalke et al. 2018, Kentucky), positive (Hyzy et al. 2020, Michigan), and non-linear responses (Pauli et al. 2015, Indiana) to increasing distance to roads in different regions, so their association with roads remains unclear and may depend on larger landscape-scale factors. Future research on this population of northern long-eared bats should collect more data on roosting and foraging locations and measure more specific covariates like canopy height, understory and midstory cover, and insect community composition to quantify their ecology better.

In conclusion, urban areas like Champaign-Urbana may be dominated by synurban species but can still host endangered species, underscoring the need for more studies investigating the fitness of urban bats and whether conservation actions are needed. LiDAR-derived habitat variables can be used to predict bat responses, and the positive effect of horizontal canopy heterogeneity on big brown bats may be an urban manifestation of previously demonstrated positive gap and edge effects or reflect differences in detection probabilities. We found weak evidence of a negative impact of family-level tree diversity on eastern red activity, suggesting that there should be further investigation into how urban tree communities impact bat populations

CHAPTER 4: SUMMARY

We sought to address two knowledge gaps in urban bat ecology. We aimed to 1) understand how bats respond to their environment across differing cities exhibiting stark differences in vegetation and land use regimes and 2) elucidate how bats respond to LiDAR-derived tree metrics at a fine scale across an urban mosaic. Overall, we found that the intensity of the urban forest gradient significantly impacts bat occupancy and activity and at varying scales and with different metrics. At the landscape scale, we found that high tree canopy cover negatively affects bat occupancy for some groups but has positive effects at a local scale. In the big brown + silver-haired bat group, the magnitude of the response of bats to local tree canopy cover varied depending on city-wide canopy cover. These results demonstrate the importance of considering between-city differences when studying urban bats and the utility of using a multi-city approach. At a fine scale, we found that LiDAR-derived horizontal canopy heterogeneity positively predicted big brown and eastern red bat activity but that this effect depended on local habitat context. These results suggest that small-scale management actions altering the urban tree canopy would likely affect bat foraging behavior and highlight the potential for LiDAR-derived data to generate informative predictor variables in urban bat studies.

We also examined how bat species richness might vary across cities and aimed to discover whether species of conservation concern were present in the small cities of the Midwestern United States. We were unable to generate informative models predicting differences in bat species richness across different cities, likely due to the relatively short sampling timeframe. However, we discovered that some cities had high bat diversity and were host to rare and imperiled bat species, including the tricolored bat and, notably, the northern long-eared bat. We recorded northern long-eared bat calls in several forests in northeastern Urbana, Illinois. We also captured three individuals, providing further evidence that these species can persist in urban forests, even in forest fragments < 25 ha. We found evidence to suggest that proximity to roads may have a negative impact on the presence of northern long-eared bats in areas with less tree canopy cover; conversely, the only confirmed roost location we found for the species was that of a male roosting close to a road. Northern long-eared bats were only present in forests near the Saline Branch Drainage Ditch in Urbana, IL, and this riparian corridor may provide crucial habitat connectivity between forest patches.

We have identified several future directions for the study of urban bats. We recommend further implementation of multi-city urban bat monitoring efforts to glean between-city differences in ecological patterns. Such efforts should be spatially distributed and aim to sample across entire nights and multiple seasons. We further propose that there is a need for manipulative experiments that test bats' response to aspects of urban forestry management, such as tree trimming, tree removal, and tree planting. In the context of our results, these actions would impact the degree of horizontal canopy heterogeneity in urban areas, which we predict would increase bat activity. Lastly, we urge that additional research on the population of northern long-eared bats in Urbana, IL, is needed. Due to its endangered status, understanding how the health and fitness of this species may be impacted by living in an urban environment could provide insights into how to manage habitat for its conservation. We recommend that steps should be taken to preserve the tree cover along the Saline Branch Drainage Ditch to promote connectivity between forest fragments. In summary, our research indicates that the urban tree gradient provides a critical role in supporting bat activity and occupancy in small Midwestern cities, underscoring the value of preserving urban tree canopies to advance bat conservation efforts.

LITERATURE CITED

- Adams, M. D., B. S. Law, and K. O. French. 2009. Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. *Forest Ecology and Management* 258:2090–2100.
- Agosta, S. J. 2002. Habitat use, diet and roost selection by the big brown bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species. *Mammal Review* 32:179–198.
- Aguiar, L. M. S., I. D. Bueno-Rocha, G. Oliveira, E. S. Pires, S. Vasconcelos, G. L. Nunes, M. R. Frizzas, and P. H. B. Togni. 2021. Going out for dinner—The consumption of agriculture pests by bats in urban areas. *PLOS ONE* 16:e0258066.
- Ampoorter, E., L. Barbaro, H. Jactel, L. Baeten, J. Boberg, M. Carnol, B. Castagneyrol, Y. Charbonnier, S. M. Dawud, M. Deconchat, P. D. Smedt, H. D. Wandeler, V. Guyot, S. Hättenschwiler, F.-X. Joly, J. Koricheva, H. Milligan, B. Muys, D. Nguyen, S. Ratcliffe, K. Raulund-Rasmussen, M. Scherer-Lorenzen, F. van der Plas, J. V. Keer, K. Verheyen, L. Vesterdal, and E. Allan. 2020. Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. *Oikos* 129:133–146.
- Andersson Skog, N. 2021. Bats in Urban Sweden: A multiple regression analysis of bats' relationship to urbanization.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Aronson, M. F. J., F. A. La Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, N. S. G. Williams, S. Cilliers, B. Clarkson, C. Dobbs, R. Dolan, M. Hedblom, S. Klotz, J. L. Kooijmans, I. Kühn, I. MacGregor-Fors, M. McDonnell, U. Mörtberg, P. Pyšek, S. Siebert, J. Sushinsky, P. Werner, and M. Winter. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281:20133330.
- Avila-Flores, R., and M. B. Fenton. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy* 86:1193–1204.

- Avolio, M. L., D. E. Pataki, T. L. E. Trammell, and J. Endter-Wada. 2018. Biodiverse cities: The nursery industry, homeowners, and neighborhood differences drive urban tree composition. *Ecological Monographs* 88:259–276.
- Bailey, A. M., H. K. Ober, B. E. Reichert, and R. A. McCleery. 2019. Canopy cover shapes bat diversity across an urban and agricultural landscape mosaic. *Environmental Conservation* 46:193–200.
- Barclay, R. M. R., J. H. Fullard, and D. S. Jacobs. 1999. Variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*): Influence of body size, habitat structure, and geographic location 77.
- Barclay, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behavioral Ecology and Sociobiology* 24:31–37.
- Beilke, E. A., R. V. Blakey, and J. M. O’Keefe. 2021. Bats partition activity in space and time in a large, heterogeneous landscape. *Ecology and Evolution* 11:6513–6526.
- Bennett, V. J., and E. J. Agpalo. 2022. Citizen science helps uncover the secrets to a bat-friendly swimming pool in an urban environment. *Frontiers in Ecology and Evolution* 10.
- Bennett, V. J., D. W. Sparks, and P. A. Zollner. 2013. Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology* 28:979–991.
- Bennett, V. J., and A. A. Zurcher. 2013. When corridors collide: Road-related disturbance in commuting bats. *The Journal of Wildlife Management* 77:93–101.
- Bienz, C. 2016. Surface texture discrimination by bats: Implications for reducing bat mortality at wind turbines. M.S., Texas Christian University, United States -- Texas.
- Blanchard, G., N. Barbier, G. Vieilledent, T. Ibanez, V. Hequet, S. McCoy, and P. Birnbaum. 2023. UAV-Lidar reveals that canopy structure mediates the influence of edge effects on forest diversity, function and microclimate. *Journal of Ecology* 111:1411–1427.
- Bonaccorso, F. J., C. M. Todd, A. C. Miles, and P. M. Gorresen. 2015. Foraging range movements of the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 96:64–71.
- Brasileiro, L. A. M., R. B. Machado, and L. M. S. Aguiar. 2022. Ecosystems services provided by bats are at risk in Brazil. *Frontiers in Ecology and Evolution* 10.
- Brigham, R. 2007. Bats in forests: What we know and what we need to learn. *Bats in Forests: Conservation and Management*:1–16.

- Brigham, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology* 69:117–121.
- Brooks, M., B. Bolker, K. Kristensen, M. Maechler, A. Magnusson, M. McGillicuddy, H. Skaug, A. Nielsen, C. Berg, K. van Benthem, N. Sadat, D. Lüdtke, R. Lenth, J. O’Brien, C. J. Geyer, M. Jagan, B. Wiernik, and D. B. Stouffer. 2024, March 20. glmmTMB: Generalized linear mixed models using template model builder.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel Inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.
- Burrell, G. E., and S. M. Bergeson. 2022. Roosting behavior of northern long-eared bats (*Myotis septentrionalis*) in an urban-adjacent forest fragment. *Forests* 13:1972.
- Callaghan, C. T., R. E. Major, J. H. Wilshire, J. M. Martin, R. T. Kingsford, and W. K. Cornwell. 2019. Generalists are the most urban-tolerant of birds: A phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos* 128:845–858.
- Caryl, F. M., A. K. Hahs, L. F. Lumsden, R. Van der Ree, C. Wilson, and B. A. Wintle. 2014. Continuous predictors of species distributions support categorically stronger inference than ordinal and nominal classes: an example with urban bats. *Landscape Ecology* 29:1237–1248.
- Caryl, F. M., L. F. Lumsden, R. van der Ree, and B. A. Wintle. 2016. Functional responses of insectivorous bats to increasing housing density support ‘land-sparing’ rather than ‘land-sharing’ urban growth strategies. *Journal of Applied Ecology* 53:191–201.
- Champaign County GIS Consortium. (n.d.). GIS Data and Services.
<https://www.ccgisc.org/DataAndServices.aspx>.
- Champaign Park District. (n.d.). Public Tree Map.
<https://cparkdistirct.maps.arcgis.com/apps/View/index.html?appid=88afa8b642a1464585eaad55a999dd5a>.

- Chung, C.-H., J. Wang, S.-L. Deng, and C. Huang. 2022. Analysis of canopy gaps of coastal broadleaf forest plantations in northeast Taiwan using UAV LIDAR and the Weibull distribution. *Remote Sensing* 14:667.
- City of Champaign Public Works Department. (n.d.). City Trees Map.
<https://cityofchampaign.maps.arcgis.com/apps/webappviewer/index.html?id=7e979451571143abbf5bafb6eeb9b01b>.
- City of Urbana. (n.d.). TreeKeeper 8 System for City of Urbana, IL.
<https://urbanail.treekeepersoftware.com/index.cfm?deviceWidth=1920>.
- Clement, M. J., T. J. Rodhouse, P. C. Ormsbee, J. M. Szewczak, and J. D. Nichols. 2014. Accounting for false-positive acoustic detections of bats using occupancy models. *Journal of Applied Ecology* 51:1460–1467.
- Coleman, J. L., and R. M. R. Barclay. 2011a. Influence of urbanization on demography of little brown bats (*Myotis lucifugus*) in the Prairies of North America. *PLOS ONE* 6:e20483.
- Coleman, J. L., and R. M. R. Barclay. 2011b. Urbanization and the abundance and diversity of Prairie bats. *Urban Ecosystems* 15:87–102.
- Coleman, J. L., and R. M. R. Barclay. 2013. Prey availability and foraging activity of grassland bats in relation to urbanization. *Journal of Mammalogy* 94:1111–1122.
- Collins, M. K., S. B. Magle, and T. Gallo. 2021. Global trends in urban wildlife ecology and conservation. *Biological Conservation* 261:109236.
- Croci, S., A. Butet, and P. Clergeau. 2008. Does urbanization filter birds on the basis of their biological traits. *The Condor* 110:223–240.
- Crome, F. H. J., and G. C. Richards. 1988. Bats and gaps: Microchiropteran community structure in a Queensland rain forest. *Ecology* 69:1960–1969.
- Dallimer, M., J. R. Rouquette, A. M. J. Skinner, P. R. Armsworth, L. M. Maltby, P. H. Warren, and K. J. Gaston. 2012. Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. *Diversity and Distributions* 18:742–753.
- Deeley, S., J. B. Johnson, W. M. Ford, and J. E. Gates. 2021. White-nose syndrome-related changes to Mid-Atlantic bat communities across an urban-to-rural gradient. *BMC Zoology* 6:12.
- Dewitz, J. 2023. National Land Cover Database (NLCD) 2021 Products. U.S. Geological Survey.

- Divoll, T. J., S. P. Aldrich, G. S. Haulton, and J. M. O’Keefe. 2022. Endangered *Myotis* bats forage in regeneration openings in a managed forest. *Forest Ecology and Management* 503:119757.
- Dixon, M. D. 2011. Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosystems* 15:683–695.
- Ducatez, S., F. Sayol, D. Sol, and L. Lefebvre. 2018. Are urban vertebrates city specialists, artificial habitat exploiters, or environmental generalists? *Integrative and Comparative Biology* 58:929–938.
- Duchamp, J. E., and R. K. Swihart. 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology* 23:849–860.
- Earth Observation Group. 2023, June. VIIRS Nighttime Light.
<https://eogdata.mines.edu/products/vnl/>.
- Erasmy, M. 2021. Bat activity and diversity in a temperate old-growth forest - Influence of horizontal and vertical structural heterogeneity on the bat assemblage of the Belovezhskaya Pushcha, Belarus. Doctoral Thesis.
- Esri Inc. 2021. Estimating forest canopy density and height—ArcMap | Documentation.
<https://desktop.arcgis.com/en/arcmap/latest/manage-data/las-dataset/lidar-solutions-estimating-forest-density-and-height.htm>.
- Esri Inc. 2023. ArcGIS Pro. Esri Inc.
- Everette, A. L., T. J. O’Shea, L. E. Ellison, L. A. Stone, and J. L. McCance. 2001. Bat use of a high-plains urban wildlife refuge. *Wildlife Society Bulletin (1973-2006)* 29:967–973.
- Fenoglio, M. S., A. Calviño, E. González, A. Salvo, and M. Videla. 2021. Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecological Entomology* 46:757–771.
- Ferenc, M., O. Sedláček, R. Fuchs, M. Dinetti, M. Fraissinet, and D. Storch. 2014. Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Global Ecology and Biogeography* 23:479–489.
- Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. M. Kay, H. A. Sander, B. MacDougall, C. M. Salsbury, T. J. Ryan, J. L. Angstmann, J. Amy Belaire, B. Dugelby, C. J. Schell, T. Stankowich, M. Amaya, D. Drake, S. H. Hursh, A. A. Ahlers, J. Williamson, L. M. Hartley, A. J. Zellmer, K. Simon, and S. B. Magle. 2021. Landscape-scale differences

- among cities alter common species' responses to urbanization. *Ecological Applications* 31:e02253.
- Fisher, A., M. Day, T. Gill, A. Roff, T. Danaher, and N. Flood. 2016. Large-area, high-resolution tree cover mapping with multi-temporal SPOT5 imagery, New South Wales, Australia. *Remote Sensing* 8:515.
- Frank, C. L., A. Michalski, A. A. McDonough, M. Rahimian, R. J. Rudd, and C. Herzog. 2014. The resistance of a North American bat species (*Eptesicus fuscus*) to White-nose syndrome (WNS). *PLOS ONE* 9:e113958.
- Fraser, E. E. 2018. Manual analysis of recorded bat echolocation calls: Summary, synthesis, and proposal for increased standardization in training practices. *CJZ Virtual Special Issues* 01:505–512.
- Frey-Ehrenbold, A., F. Bontadina, R. Arlettaz, and M. K. Obrist. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology* 50:252–261.
- Frick, W. F., S. J. Puechmaille, and C. K. R. Willis. 2016. White-nose syndrome in bats. Pages 245–262 *in* C. C. Voigt and T. Kingston, editors. *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham.
- Froidevaux, J. S. P., F. Zellweger, K. Bollmann, G. Jones, and M. K. Obrist. 2016. From field surveys to LiDAR: Shining a light on how bats respond to forest structure. *Remote Sensing of Environment* 175:242–250.
- Fuentes-Montemayor, E., D. Goulson, L. Cavin, J. M. Wallace, and K. J. Park. 2013. Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment* 172:6–15.
- Gallo, T., E. W. Lehrer, M. Fidino, R. J. Kilgour, P. J. Wolff, and S. B. Magle. 2017. Need for multiscale planning for conservation of urban bats. *Conservation Biology* 32:638–647.
- GBIF.org. 2024. Occurrence Download. The Global Biodiversity Information Facility.
- Geggie, J. F., and M. B. Fenton. 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology* 63:263–266.
- Gehrt, S. D., and J. E. Chelsvig. 2003. Bat Activity in an Urban Landscape: Patterns at the landscape and microhabitat scale. *Ecological Applications* 13:939–950.

- Gehrt, S. D., and J. E. Chelsvig. 2004. Species-specific patterns of bat activity in an urban landscape. *Ecological Applications* 14:625–635.
- Gili, F., S. E. Newson, S. Gillings, D. E. Chamberlain, and J. A. Border. 2020. Bats in urbanising landscapes: Habitat selection and recommendations for a sustainable future. *Biological Conservation* 241:108343.
- Goodwin, K. R., and E. H. Gillam. 2021. Testing accuracy and agreement among multiple versions of automated bat call classification software. *Wildlife Society Bulletin* 45:690–705.
- Gorman, K. M., E. L. Barr, L. Ries, T. Nocera, and W. M. Ford. 2021. Bat activity patterns relative to temporal and weather effects in a temperate coastal environment. *Global Ecology and Conservation* 30:e01769.
- Haight, J. D., S. J. Hall, M. Fidino, S. A. Adalsteinsson, A. A. Ahlers, J. Angstmann, W. J. B. Anthonysamy, E. Biro, M. K. Collins, B. Dugelby, T. Gallo, A. M. Green, L. Hartley, M. J. Jordan, C. A. M. Kay, E. W. Lehrer, R. A. Long, B. MacDougall, S. B. Magle, D. E. Minier, C. Mowry, M. Murray, K. Nininger, M. E. Pendergast, K. R. Remine, T. Ryan, C. Salsbury, H. A. Sander, C. J. Schell, Ç. H. Şekercioğlu, C. J. Shier, K. C. Simon, C. C. St. Clair, T. Stankowich, C. J. Stevenson, L. Wayne, D. Will, J. Williamson, L. Wilson, A. J. Zellmer, and J. S. Lewis. 2023. Urbanization, climate and species traits shape mammal communities from local to continental scales. *Nature Ecology & Evolution* 7:1654–1666.
- Hale, J. D., A. J. Fairbrass, T. J. Matthews, G. Davies, and J. P. Sadler. 2015. The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Global Change Biology* 21:2467–2478.
- Hall, E. M., and V. J. Bennett. 2021. Seasonal variation in home range size of evening bats (*Nycticeius humeralis*) in an urban environment. *Journal of Mammalogy* 102:1497–1506.
- Harvey, M. J., J. S. Altenbach, and T. L. Best. 2011. *Bats of the United States and Canada*. JHU Press.
- Henderson, L. E., L. J. Farrow, and H. G. Broders. 2008. Intra-specific effects of forest loss on the distribution of the forest-dependent northern long-eared bat (*Myotis septentrionalis*). *Biological Conservation* 141:1819–1828.

- Hernández-Brito, D., M. Carrete, C. Ibáñez, J. Juste, and J. L. Tella. 2018. Nest-site competition and killing by invasive parakeets cause the decline of a threatened bat population. *Royal Society Open Science* 5:172477.
- Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography* 42:1648–1657.
- Hoff, S., B. Mosher, M. Watson, L. Johnson, E. Olson, D. O’Dell, C. Pendergast, D. Bogan, C. Herzog, and W. Turner. 2024a. Widespread occupancy of the endangered northern myotis on northeastern Atlantic Coastal Plain islands. *Endangered Species Research* 54:141–153.
- Hoff, S., C. Pendergast, L. Johnson, E. Olson, D. O’Dell, Z. R. Dowling, K. M. Gorman, C. Herzog, and W. C. Turner. 2024b. Seasonal roost characteristics and fall behavior of coastal populations of northern myotis (*Myotis septentrionalis*). *Journal of Mammalogy* 105:277–288.
- Hoggatt, M. L., C. A. Starbuck, and J. M. O’Keefe. 2024. Acoustic monitoring yields informative bat population density estimates. *Ecology and Evolution* 14:e11051.
- Hogue, A. S., and A. T. McGowan. 2018. Comparison of driving transect methods for acoustic monitoring of bats. *Page Bats*. IntechOpen.
- Housman, I., S. Bender, K. Schleeweis, J. Heyer, B. Ruefenacht, and K. Megown. 2023. National Land Cover Database Tree Canopy Cover methods. Forest Service, U.S. Department of Agriculture.
- Hoyt, J. R., A. M. Kilpatrick, and K. E. Langwig. 2021. Ecology and impacts of white-nose syndrome on bats. *Nature Reviews Microbiology* 19:196–210.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Hyzy, B. A., R. E. Russell, A. Silvis, W. M. Ford, J. Riddle, and K. Russell. 2020. Occupancy and detectability of northern long-eared bats in the Lake States region. *Wildlife Society Bulletin* 44:732–740.
- Illinois Geospatial Data Clearinghouse. 2019. Illinois Height Modernization (ILHMP): LiDAR Data | City of Champaign-Urbana Special Collection.
<http://clearinghouse.isgs.illinois.edu/data/elevation/illinois-height-modernization-ilhmp>.

Illinois State Climatologist. 2023, October. Champaign-Urbana Data.

<https://stateclimatologist.web.illinois.edu/data/champaign-urbana/>.

- Johnson, J. B., W. M. Ford, J. W. Edwards, and M. A. Menzel. 2010. Bat community structure within riparian areas of northwestern Georgia, USA. *Folia Zoologica* 59:192–202.
- Johnson, J. B., J. E. Gates, and W. M. Ford. 2008. Distribution and activity of bats at local and landscape scales within a rural–urban gradient. *Urban Ecosystems* 11:227–242.
- Johnson, M. L., L. K. Campbell, E. S. Svendsen, and P. Silva. 2018. Why count trees? Volunteer motivations and experiences with tree monitoring in New York City.
- Jung, K., and E. K. V. Kalko. 2010. Where forest meets urbanization: Foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy* 91:144–153.
- Jung, K., and C. G. Threlfall. 2016. Urbanisation and its effects on bats—A global meta-analysis. Pages 13–33 in C. C. Voigt and T. Kingston, editors. *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham.
- Jung, K., and C. G. Threlfall. 2018. Trait-dependent tolerance of bats to urbanization: A global meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 285:20181222.
- Kendal, D., M. Egerer, J. A. Byrne, P. J. Jones, P. Marsh, C. G. Threlfall, G. Allegretto, H. Kaplan, H. K. D. Nguyen, S. Pearson, A. Wright, and E. J. Flies. 2020. City-size bias in knowledge on the effects of urban nature on people and biodiversity. *Environmental Research Letters* 15:124035.
- Kerth, G., and M. Melber. 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation* 142:270–279.
- Kong, F., H. Yin, P. James, L. R. Hutyra, and H. S. He. 2014. Effects of spatial pattern of greenspace on urban cooling in a large metropolitan area of eastern China. *Landscape and Urban Planning* 128:35–47.
- Kopits, E., V. McConnell, and D. Miles. 2009. Lot size, zoning, and household preferences: Impediments to smart growth? SSRN Electronic Journal.
- Krauel, J. J., and G. LeBuhn. 2016. Patterns of bat distribution and foraging activity in a highly urbanized temperate environment. *PLOS ONE* 11:e0168927.
- Kubista, C. E., and A. Bruckner. 2015. Importance of urban trees and buildings as daytime roosts for bats. *Biologia* 70:1545–1552.

- Kurta, A., and J. A. Teramino. 1992. Bat community structure in an urban park. *Ecography* 15:257–261.
- Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. Page 25. AFSC Processed Rep., Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA.
- Laforge, A., J. Pauwels, B. Faure, Y. Bas, C. Kerbiriou, J. Fonderflick, and A. Besnard. 2019. Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecology* 34:793–809.
- Langwig, K. E., J. R. Hoyt, K. L. Parise, J. Kath, D. Kirk, W. F. Frick, J. T. Foster, and A. M. Kilpatrick. 2015. Invasion dynamics of white-nose syndrome fungus, Midwestern United States, 2012–2014. *Emerging Infectious Diseases* 21:1023–1026.
- Lausen, C. L., and R. M. R. Barclay. 2006. Benefits of living in a building: Big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *Journal of Mammalogy* 87:362–370.
- Lausen, C. L., G. A. Falxa, D. I. Solick, A. L. McEwan, M. D. Baker, E. de Freitas, and M. Sarell. 2023. Singing silver-haired bats (*Lasionycteris noctivagans*). *Wildlife Society Bulletin* 47:e1500.
- Laux, M., H. Lv, M. H. Entling, J. Schirmel, A. Narang, M. Köhler, and S. Saha. 2022. Native pedunculate oaks support more biodiversity than non-native oaks, but non-native oaks are healthier than native oaks: A study on street and park trees of a city. *Science of The Total Environment* 853:158603.
- Lehrer, E. W., T. Gallo, M. Fidino, R. J. Kilgour, P. J. Wolff, and S. B. Magle. 2021. Urban bat occupancy is highly influenced by noise and the location of water: Considerations for nature-based urban planning. *Landscape and Urban Planning* 210:104063.
- Li, H., C. Cui, Y. Feng, G. Gaje, E. Guzman, T. Heckman, A. Mellis, L. Moore, N. Romo Bechara, S. Sanchez, S. Whittington, J. G. Wolf, R. Garshong, K. Morales, R. Petric, L. A. Zarecky, and M. D. Schug. 2020. The weekend effect on urban bat activity suggests fine scale human-induced bat movements. *Animals* 10:1636.
- Li, H., and K. T. Wilkins. 2014. Patch or mosaic: Bat activity responds to fine-scale urban heterogeneity in a medium-sized city in the United States. *Urban Ecosystems* 17:1013–1031.

- Li, H., and K. T. Wilkins. 2022. Predator-prey relationship between urban bats and insects impacted by both artificial light at night and spatial clutter. *Biology* 11:829.
- Lintott, P. R., K. Barlow, N. Bunnefeld, P. Briggs, C. Gajas Roig, and K. J. Park. 2016. Differential responses of cryptic bat species to the urban landscape. *Ecology and Evolution* 6:2044–2052.
- Lintott, P. R., N. Bunnefeld, and K. J. Park. 2015. Opportunities for improving the foraging potential of urban waterways for bats. *Biological Conservation* 191:224–233.
- Loeb, S. C. 2015. A plan for the North American Bat Monitoring Program (NABat). Gen. Tech. Rep. SRS-208. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 208:1–100.
- Loeb, S. C., and J. M. O’Keefe. 2011. Bats and gaps: The role of early successional patches in the roosting and foraging ecology of bats. Pages 167–189 in C. Greenberg, B. Collins, and F. Thompson III, editors. *Sustaining Young Forest Communities: Ecology and Management of early successional habitats in the central hardwood region, USA*. Springer Netherlands, Dordrecht.
- Loeb, S. C., C. J. Post, and S. T. Hall. 2009. Relationship between urbanization and bat community structure in national parks of the southeastern U.S. *Urban Ecosyst*, Vol. 12: 197–214 12:197–214.
- Luck, G. W., L. Smallbone, C. Threlfall, and B. Law. 2013. Patterns in bat functional guilds across multiple urban centres in south-eastern Australia. *Landscape Ecology* 28:455–469.
- Lumsden, L. F., and A. F. Bennett. 2005. Scattered trees in rural landscapes: Foraging habitat for insectivorous bats in south-eastern Australia. *Biological Conservation* 122:205–222.
- Ma, B., R. J. Hauer, J. Östberg, A. K. Koeser, H. Wei, and C. Xu. 2021. A global basis of urban tree inventories: What comes first, the inventory or the program. *Urban Forestry & Urban Greening* 60:127087.
- Mager, K. J., and T. A. Nelson. 2001. Roost-site selection by eastern red bats (*Lasiurus borealis*). *The American Midland Naturalist* 145:120–126.
- Magle, S. B., M. Fidino, E. W. Lehrer, T. Gallo, M. P. Mulligan, M. J. Ríos, A. A. Ahlers, J. Angstmann, A. Belaire, B. Dugelby, A. Gramza, L. Hartley, B. MacDougall, T. Ryan, C. Salsbury, H. Sander, C. Schell, K. Simon, S. St Onge, and D. Drake. 2019. Advancing

- urban wildlife research through a multi-city collaboration. *Frontiers in Ecology and the Environment* 17:232–239.
- Magle, S. B., M. Fidino, H. A. Sander, A. T. Rohnke, K. L. Larson, T. Gallo, C. A. M. Kay, E. W. Lehrer, M. H. Murray, S. A. Adalsteinsson, A. A. Ahlers, W. J. B. Anthonysamy, A. R. Gramza, A. M. Green, M. J. Jordan, J. S. Lewis, R. A. Long, B. MacDougall, M. E. Pendergast, K. Remine, K. C. Simon, C. C. St. Clair, C. J. Shier, T. Stankowich, C. J. Stevenson, A. J. Zellmer, and C. J. Schell. 2021. Wealth and urbanization shape medium and large terrestrial mammal communities. *Global Change Biology* 27:5446–5459.
- Markovchick-Nicholls, L., H. M. Regan, D. H. Deutschman, A. Widyanata, B. Martin, L. Noreke, and T. Ann Hunt. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology* 22:99–109.
- Marsden, G. E., D. Vosloo, and M. C. Schoeman. 2023. Urban tolerance is phylogenetically constrained and mediated by pre-adaptations in African bats. *Ecology and Evolution* 13:e9840.
- Marsh, D. M., T. Finnegan, I. Kinney, S. Smith, and C. R. Stern. 2023. Changes in reptile and amphibian communities across urbanization gradients in eastern North America. *Global Ecology and Conservation* 48:e02734.
- McCracken, G. F., R. F. Bernard, M. Gamba-Rios, R. Wolfe, J. J. Krauel, D. N. Jones, A. L. Russell, and V. A. Brown. 2018. Rapid range expansion of the Brazilian free-tailed bat in the southeastern United States, 2008–2016. *Journal of Mammalogy* 99:312–320.
- McGarigal, K., S. Cushman, and E. Ene. 2023. FRAGSTATS v4: Spatial pattern analysis program for categorical maps.
- McGowan, K. A. 2023. Evaluating bat response to human-altered landscape in a Midwestern river corridor: An abundance modeling analysis using bioacoustics. PhD Thesis, Ball State University.
- Melaun, C., A. Werblow, M. W. Busch, A. Liston, and S. Klimpel. 2014. Bats as Potential Reservoir Hosts for Vector-Borne Diseases. Pages 25–61 *in* S. Klimpel and H. Mehlhorn, editors. *Bats (Chiroptera) as vectors of diseases and parasites: Facts and myths*. Springer, Berlin, Heidelberg.

- Menzel, J. M., M. A. Menzel Jr., J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the Coastal Plain of South Carolina. *The Journal of Wildlife Management* 69:235–245.
- Menzel, M. A., T. C. Carter, L. R. Jablonowski, B. L. Mitchell, J. M. Menzel, and B. R. Chapman. 2001. Home range size and habitat use of big brown bats (*Eptesicus fuscus*) in a maternity colony located on a rural-urban interface in the Southeast. *Journal of the Elisha Mitchell Scientific Society* 117:36–45.
- Metcalfe, A. N., C. A. Fritzinger, T. J. Weller, M. J. Dodrill, J. D. Muehlbauer, C. B. Yackulic, P. B. Holton, C. M. Szydlo, L. E. Durning, J. B. Sankey, and T. A. Kennedy. 2023. Insectivorous bat foraging tracks the availability of aquatic flies (Diptera). *The Journal of Wildlife Management* 87:e22414.
- Meyer, C. F. J., M. J. Struebig, and M. R. Willig. 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. Pages 63–103 *in* C. C. Voigt and T. Kingston, editors. *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, Cham.
- Mimet, A., C. Kerbiriou, L. Simon, J.-F. Julien, and R. Raymond. 2020. Contribution of private gardens to habitat availability, connectivity and conservation of the common pipistrelle in Paris. *Landscape and Urban Planning* 193:103671.
- Moretto, L., L. Fahrig, A. C. Smith, and C. M. Francis. 2019. A small-scale response of urban bat activity to tree cover. *Urban Ecosystems* 22:795–805.
- Moretto, L., and C. M. Francis. 2017. What factors limit bat abundance and diversity in temperate, North American urban environments? *Journal of Urban Ecology* 3:jux016.
- Morris, A. D., D. A. Miller, and M. C. Kalcounis-Rueppell. 2010. Use of forest edges by bats in a managed pine forest landscape. *The Journal of Wildlife Management* 74:26–34.
- Murray, M. H., C. A. Sánchez, D. J. Becker, K. A. Byers, K. E. Worsley-Tonks, and M. E. Craft. 2019. City sicker? A meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment* 17:575–583.
- Nichols, J. D., L. L. Bailey, A. F. O’Connell Jr., N. W. Talancy, E. H. Campbell Grant, A. T. Gilbert, E. M. Annand, T. P. Husband, and J. E. Hines. 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology* 45:1321–1329.

- Nowak, D. J., and E. J. Greenfield. 2020. The increase of impervious cover and decrease of tree cover within urban areas globally (2012–2017). *Urban Forestry & Urban Greening* 49:126638.
- Neubaum, D. J., K. R. Wilson, and T. J. O'shea. 2007. Urban maternity-roost selection by big brown bats in Colorado. *The Journal of Wildlife Management* 71:728–736.
- Nystrom, G. S., and V. J. Bennett. 2019. The importance of residential swimming pools as an urban water source for bats. *Journal of Mammalogy* 100:394–400.
- O'Keefe, J. M., S. C. Loeb, P. D. Gerard, and J. D. Lanham. 2013. Effects of riparian buffer width on activity and detection of common bats in the southern Appalachian Mountains. *Wildlife Society Bulletin* 37:319–326.
- O'Keefe, J. M., S. C. Loeb, H. S. Hill, and J. Drew Lanham. 2014. Quantifying clutter: A comparison of four methods and their relationship to bat detection. *Forest Ecology and Management* 322:1–9.
- Olimpi, E. M., and S. M. Philpott. 2018. Agroecological farming practices promote bats. *Agriculture, Ecosystems & Environment* 265:282–291.
- Oprea, M., P. Mendes, T. B. Vieira, and A. D. Ditchfield. 2009. Do wooded streets provide connectivity for bats in an urban landscape? *Biodiversity and Conservation* 18:2361–2371.
- Ordóñez, C., C. G. Threlfall, D. Kendal, J. Baumann, C. Sonkkila, D. F. Hochuli, R. van der Ree, R. A. Fuller, M. Davern, K. Herzog, A. English, and S. J. Livesley. 2023. Quantifying the importance of urban trees to people and nature through tree removal experiments. *People and Nature* 5:1316–1335.
- de Oyarzabal Barba, M. 2023. Improving urban flyways for bats: The importance of the tree canopy structure - ProQuest. <https://www.proquest.com/docview/2903097151?pq-origsite=gscholar&fromopenview=true&sourcetype=Dissertations%20&%20Theses>.
- Park, K. J. 2015. Mitigating the impacts of agriculture on biodiversity: Bats and their potential role as bioindicators. *Mammalian Biology* 80:191–204.
- Parker, K. A., B. T. Springall, R. A. Garshong, A. N. Malachi, L. E. Dorn, A. Costa-Terryll, R. A. Mathis, A. N. Lewis, C. L. MacCheyne, T. T. Davis, A. D. Rice, N. Y. Varh, H. Li, M. D. Schug, and M. C. Kalcounis-Rueppell. 2019. Rapid increases in bat activity and diversity after wetland construction in an urban ecosystem. *Wetlands* 39:717–727.

- Parkins, K. L. 2015. Bats in New York City: An acoustic survey and the role of green roofs. M.S., Fordham University, United States -- New York.
- Parkins, K. L., and J. A. Clark. 2015. Green roofs provide habitat for urban bats. *Global Ecology and Conservation* 4:349–357.
- Partridge, D. R., K. L. Parkins, S. B. Elbin, and J. A. Clark. 2020. Bat activity correlates with moth abundance on an urban green roof. *Northeastern Naturalist* 27:77–89.
- Patriquin, K. J., L. K. Hogberg, B. J. Chruszcz, and R. M. R. Barclay. 2003. The influence of habitat structure on the ability to detect ultrasound using bat detectors. *Wildlife Society Bulletin (1973-2006)* 31:475–481.
- Pavlacky Jr., D. C. 2022. larksparrow: Lark Sparrow in RMark: R Code for MARK Analysis. <https://rdrr.io/cran/RMark/man/larksparrow.html>.
- Pavlacky Jr., D. C., J. A. Blakesley, G. C. White, D. J. Hanni, and P. M. Lukacs. 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *The Journal of Wildlife Management* 76:154–162.
- Pauli, B. P., H. A. Badin, G. S. Haulton, P. A. Zollner, and T. C. Carter. 2015. Landscape features associated with the roosting habitat of Indiana bats and northern long-eared bats. *Landscape Ecology* 30:2015–2029.
- Perry, R. W., and R. E. Thill. 2007. Roost characteristics of hoary bats in Arkansas. *The American Midland Naturalist* 158:132–138.
- Peurach, S. C. 2003. High-altitude collision between an airplane and a hoary bat, *Lasiurus cinereus*.
- Pollock, H. S., C. J. van Riper, D. J. Goodson, S. B. Lerman, and M. E. Hauber. 2024. The public–private divide and seasonal variation shape bird diversity in greenspaces of two neighboring midwestern USA cities. *Landscape and Urban Planning* 247:105060.
- Polyakov, A. Y., T. J. Weller, and W. D. Tietje. 2019. Remnant trees increase bat activity and facilitate the use of vineyards by edge-space bats. *Agriculture, Ecosystems & Environment* 281:56–63.
- Poulsen, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. *Biodiversity & Conservation* 11:1551–1566.
- R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Rega-Brodsky, C. C., M. F. J. Aronson, M. R. Piana, E.-S. Carpenter, A. K. Hahs, A. Herrera-Montes, S. Knapp, D. J. Kotze, C. A. Lepczyk, M. Moretti, A. B. Salisbury, N. S. G. Williams, K. Jung, M. Katti, I. MacGregor-Fors, J. S. MacIvor, F. A. La Sorte, V. Sheel, C. G. Threfall, and C. H. Nilon. 2022. Urban biodiversity: State of the science and future directions. *Urban Ecosystems* 25:1083–1096.
- Riley, S. P. D., J. L. Brown, J. A. Sikich, C. M. Schoonmaker, and E. E. Boydston. 2014. Wildlife friendly roads: The impacts of roads on wildlife in urban areas and potential remedies. Pages 323–360 *in* R. A. McCleery, C. E. Moorman, and M. N. Peterson, editors. *Urban Wildlife conservation: Theory and Practice*. Springer US, Boston, MA.
- Ritzel, K., and T. Gallo. 2020. Behavior change in urban mammals: A systematic review. *Frontiers in Ecology and Evolution* 8.
- Rodhouse, T. J., S. Rose, T. Hawkins, and R. M. Rodriguez. 2021. Audible bats provide opportunities for citizen scientists. *Conservation Science and Practice* 3:e435.
- Romano, W. B., J. R. Skalski, R. L. Townsend, K. W. Kinzie, K. D. Coppinger, and M. F. Miller. 2019. Evaluation of an acoustic deterrent to reduce bat mortalities at an Illinois wind farm. *Wildlife Society Bulletin* 43:608–618.
- Russo, D., and L. Ancillotto. 2015. Sensitivity of bats to urbanization: A review. *Mammalian Biology* 80:205–212.
- Russo, D., J. L. Coleman, L. Ancillotto, and C. Korine. 2022. Ecosystem services by bats in urban areas. Pages 167–180 *in* L. Moretto, J. L. Coleman, C. M. Davy, M. B. Fenton, C. Korine, and K. J. Patriquin, editors. *Urban Bats: Biology, Ecology, and Human Dimensions*. Springer International Publishing, Cham.
- Russo-Petrack, K., and K. V. Root. 2023. Factors impacting bat activity and species richness in protected parks in the oak openings region of Northwest Ohio. *Environmental Management* 72:1086–1098.
- Sæbø, A., R. Popek, B. Nawrot, H. M. Hanslin, H. Gawronska, and S. W. Gawronski. 2012. Plant species differences in particulate matter accumulation on leaf surfaces. *Science of The Total Environment* 427–428:347–354.
- Sandström, J., C. Bernes, K. Junninen, A. Löhmus, E. Macdonald, J. Müller, and B. G. Jonsson. 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. *Journal of Applied Ecology* 56:1770–1781.

- Schell, C. J., K. Dyson, T. L. Fuentes, S. Des Roches, N. C. Harris, D. S. Miller, C. A. Woelfle-Erskine, and M. R. Lambert. 2020. The ecological and evolutionary consequences of systemic racism in urban environments. *Science* 369:eaay4497.
- Siemers, B. M., and H.-U. Schnitzler. 2004. Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* 429:657–661.
- Simkin, R. D., K. C. Seto, R. I. McDonald, and W. Jetz. 2022. Biodiversity impacts and conservation implications of urban land expansion projected to 2050. *Proceedings of the National Academy of Sciences* 119:e2117297119.
- Skalak, S. L., R. E. Sherwin, and R. M. Brigham. 2012. Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution* 3:490–502.
- Sol, D., C. González-Lagos, D. Moreira, J. Maspons, and O. Lapiedra. 2014. Urbanisation tolerance and the loss of avian diversity. *Ecology Letters* 17:942–950.
- Sorace, A., and M. Gustin. 2009. Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning* 90:111–118.
- Straka, T. M., M. Wolf, P. Gras, S. Buchholz, and C. C. Voigt. 2019. Tree cover mediates the effect of artificial light on urban bats. *Frontiers in Ecology and Evolution* 7.
- Suarez-Rubio, M., C. Ille, and A. Bruckner. 2018. Insectivorous bats respond to vegetation complexity in urban green spaces. *Ecology and Evolution* 8:3240–3253.
- Tallamy, D. W., and K. J. Shropshire. 2009. Ranking Lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941–947.
- Tella, J. L., D. Hernández-Brito, G. Blanco, and F. Hiraldo. 2020. Urban sprawl, food subsidies and power lines: An ecological trap for large frugivorous bats in Sri Lanka? *Diversity* 12:94.
- Tena, E., G. Fandos, Ó. de Paz, R. de la Peña, and J. L. Tellería. 2020. Size does matter: Passive sampling in urban parks of a regional bat assemblage. *Urban Ecosystems* 23:227–234.
- Thalke, M. M., M. J. Lacki, and J. Yang. 2018. Landscape-scale distribution of tree roosts of the northern long-eared bat in Mammoth Cave National Park, USA. *Landscape Ecology* 33:1103–1115.

- Thorne, T. J., E. Matczak, M. Donnelly, M. C. Franke, and K. C. R. Kerr. 2021. Occurrence of a forest-dwelling bat, northern myotis (*Myotis septentrionalis*), within Canada's largest conurbation. *Journal of Urban Ecology* 7:juab029.
- Threlfall, C. G., and K. Jung. 2023. A cross-continental synthesis of urban insectivorous bat research and future directions. Page Routledge Handbook of Urban Biodiversity. Routledge.
- Threlfall, C. G., B. Law, and P. B. Banks. 2012a. Sensitivity of insectivorous bats to urbanization: Implications for suburban conservation planning. *Biological Conservation* 146:41–52.
- Threlfall, C. G., B. Law, and P. B. Banks. 2012b. Influence of landscape structure and human modifications on insect biomass and bat foraging activity in an urban landscape. *PLOS ONE* 7:e38800.
- Threlfall, C. G., B. Law, and P. B. Banks. 2013. Roost selection in suburban bushland by the urban sensitive bat *Nyctophilus gouldi*. *Journal of Mammalogy* 94:307–319.
- Threlfall, C. G., L. Mata, J. A. Mackie, A. K. Hahs, N. E. Stork, N. S. G. Williams, and S. J. Livesley. 2017. Increasing biodiversity in urban green spaces through simple vegetation interventions. *Journal of Applied Ecology* 54:1874–1883.
- Threlfall, C. G., N. S. G. Williams, A. K. Hahs, and S. J. Livesley. 2016. Approaches to urban vegetation management and the impacts on urban bird and bat assemblages. *Landscape and Urban Planning* 153:28–39.
- Threlfall, C., B. Law, T. Penman, and P. B. Banks. 2011. Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography* 34:814–826.
- U.S. Census Bureau. 2023a. Urban and rural. <https://www.census.gov/programs-surveys/geography/guidance/geo-areas/urban-rural.html>.
- U.S. Census Bureau. 2023b. MAF/TIGER feature class code definitions. <https://www.census.gov/library/reference/code-lists/mt-feature-class-codes.html>.
- U.S. Environmental Protection Agency, O. 2014, October 29. NHDPlus (National Hydrography Dataset Plus). Overviews and factsheets. <https://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus>.

- U.S. Fish and Wildlife Service. 2022, September 14. Endangered and Threatened Wildlife and Plants; Endangered Species Status for tricolored bat.
<https://www.federalregister.gov/documents/2022/09/14/2022-18852/endangered-and-threatened-wildlife-and-plants-endangered-species-status-for-tricolored-bat>.
- U.S. Fish and Wildlife Service. 2023a, January 26. Endangered and Threatened Wildlife and Plants; Endangered Species Status for northern long-eared bat; Delay of Effective Date.
<https://www.federalregister.gov/documents/2023/01/26/2023-01656/endangered-and-threatened-wildlife-and-plants-endangered-species-status-for-northern-long-eared-bat>.
- U.S. Fish and Wildlife Service. 2023b, May 23. Little brown bat (*Myotis lucifugus*) | U.S. Fish & Wildlife Service. <https://www.fws.gov/species/little-brown-bat-myotis-lucifugus>.
- Valentine, L. E., R. Fisher, B. A. Wilson, T. Sonneman, W. D. Stock, P. A. Fleming, and R. J. Hobbs. 2014. Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape. *Biological Conservation* 175:1–9.
- Vega-Hidalgo, Á., E. Flatt, A. Whitworth, and L. Symes. 2021. Acoustic assessment of experimental reforestation in a Costa Rican rainforest. *Ecological Indicators* 133:108413.
- Villarroya-Villalba, L., J. Casanelles-Abella, M. Moretti, P. Pinho, R. Samson, A. Van Mensel, F. Chiron, F. Zellweger, and M. K. Obrist. 2021. Response of bats and nocturnal insects to urban green areas in Europe. *Basic and Applied Ecology* 51:59–70.
- Vlaschenko, A., V. Hukov, O. Timofieieva, M. Moiseienko, A. Domanska, O. Zinenko, and A. Prylutska (Gukasova). 2023a. Leaping on urban islands: Further summer and winter range expansion of European bat species in Ukraine. *European Journal of Ecology* 9:70–85.
- Vlaschenko, A., V. Kovalov, V. Hukov, K. Kravchenko, and O. Rodenko. 2019. An example of ecological traps for bats in the urban environment. *European Journal of Wildlife Research* 65:20.
- Vlaschenko, A., O. Rodenko, V. Hukov, V. Kovalov, A. Prylutska, and K. Kravchenko. 2023b. Do bats avoid the urban core in the breeding season? A case study from temperate latitudes. *Diversity* 15:967.
- Walters, B. L., C. M. Ritzi, D. W. Sparks, and J. O. Whitaker. 2007. Foraging behavior of eastern red bats (*Lasiurus borealis*) at an urban-rural interface. *The American Midland Naturalist* 157:365–373.

- Wang, Q., J. Feng, H. Wu, and T. Jiang. 2023. Insectivorous bats provide more pest suppression services than disservices - A case study in China. *Biological Control* 188:105435.
- Wang, Z., Z. Wang, Z. Zou, X. Chen, H. Wu, W. Wang, H. Su, F. Li, W. Xu, Z. Liu, and J. Zhu. 2024. Severe global environmental issues caused by Canada's record-breaking wildfires in 2023. *Advances in Atmospheric Sciences* 41:565–571.
- Watkins, L. C. 1972. *Nycticeius humeralis*. *Mammalian species*:1–4.
- Weather Underground. (n.d.). Weather History & Data Archive.
<https://www.wunderground.com/history>.
- Welch, R., D. Reifsteck, S. Drews, M. White, M. Smith, and B. Lewis, 2022. Campus Tree Inventory (Completed) | iCAP Portal | University of Illinois.
<https://icap.sustainability.illinois.edu/project/campus-tree-inventory>.
- Williams, D. R., A. Balmford, and D. S. Wilcove. 2020. The past and future role of conservation science in saving biodiversity. *Conservation Letters* 13:e12720.
- Whitaker, J. O., and S. L. Gummer. 1992. Hibernation of the big brown bat, *Eptesicus fuscus*, in buildings. *Journal of Mammalogy* 73:312–316.
- Whitaker, J. O., and L. J. Rissler. 1992. Winter activity of bats at a mine entrance in Vermillion County, Indiana. *The American Midland Naturalist* 127:52–59.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- White-nose Syndrome Disease Management Working Group. 2020, October. National White-Nose Syndrome Decontamination Protocol 2020.
- White-nose Syndrome Disease Management Working Group. 2024, March. National White-Nose Syndrome Decontamination Protocol 2024.
- Wolf, J. M., J. M. Jeschke, C. C. Voigt, and Y. Itescu. 2022. Urban affinity and its associated traits: A global analysis of bats. *Global Change Biology* 28:5667–5682.
- Wolf, K. L., S. T. Lam, J. K. McKeen, G. R. A. Richardson, M. van den Bosch, and A. C. Bardekjian. 2020. Urban trees and human health: A scoping review. *International Journal of Environmental Research and Public Health* 17:4371.
- Wright, D. W., C. D. Rittenhouse, K. Moran, T. E. Worthley, and T. A. G. Rittenhouse. 2023. Responses of insectivorous bats to tree felling in forested wetlands. *Wildlife Society Bulletin* 47:e1431.

APPENDIX A: SUPPLEMENTAL TABLE

Supplemental Table A.1: Species classifiers, marked by four-digit species code, that were selected in Kaleidoscope Pro for each city's acoustic data in the Bats in Small Cities Project. A "P" signifies that a species is considered to be possibly present as it lies within the range of the species. Cities with the same list of potential species are considered a cohort. Species codes, from left: Townsend's big-eared bat (*Corynorhinus townsendii*, COTO), big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), southeastern myotis (*Myotis austroriparius*, MYAU), western small-footed myotis (*Myotis ciliolabrum*, MYCI), gray bat (*Myotis grisescens*, MYGR), small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), evening bat (*Nycticeius humeralis*, NYHU), tricolored bat (*Perimyotis subflavus*, PESU), Brazilian free-tailed bat (*Tadarida brasiliensis*, TABR).

City	Cohort	COTO	EPFU	LABO	LACI	LANO	MYAU	MYCI	MYGR	MYLE	MYLU	MYSE	MYSO	NYHU	PESU	TABR
Cape Girardeau	1	0	P	P	P	P	P	0	P	P	P	P	P	P	P	0
Carbondale	1	0	P	P	P	P	P	0	P	P	P	P	P	P	P	0
Evansville	1	0	P	P	P	P	P	0	P	P	P	P	P	P	P	0
Springfield, MO	2	P	P	P	P	P	0	0	P	P	P	P	P	P	P	0
Bloomington, IL	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Bloomington, IN	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Champaign	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Danville	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Decatur	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Lafayette	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Terre Haute	3	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Sioux City	4	0	P	P	P	P	0	P	0	0	P	P	0	0	P	0
Columbia	5	0	P	P	P	P	0	0	P	0	P	P	P	P	P	0
Jefferson City	5	0	P	P	P	P	0	0	P	0	P	P	P	P	P	0
St. Joseph, MO	5	0	P	P	P	P	0	0	P	0	P	P	P	P	P	0
Topeka	6	0	P	P	P	P	0	0	0	0	P	P	P	P	P	P
Lincoln	7	0	P	P	P	P	0	0	0	0	P	P	0	P	P	P
Ames	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Ann Arbor	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Cedar Rapids	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Davenport	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Des Moines	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0

Supplemental Table A.1 (Cont.)

City	Cohort	COTO	EPFU	LABO	LACI	LANO	MYAU	MYCI	MYGR	MYLE	MYLU	MYSE	MYSO	NYHU	PESU	TABR
Iowa City	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Kalamazoo	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Lansing	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Racine	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Rockford	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
South Bend	8	0	P	P	P	P	0	0	0	0	P	P	P	P	P	0
Canton	9	0	P	P	P	P	0	0	0	P	P	P	P	P	P	0
Springfield, OH	9	0	P	P	P	P	0	0	0	P	P	P	P	P	P	0
Toledo	9	0	P	P	P	P	0	0	0	P	P	P	P	P	P	0
Eau Claire	10	0	P	P	P	P	0	0	0	0	P	P	0	0	P	0
Mankato	10	0	P	P	P	P	0	0	0	0	P	P	0	0	P	0
Oshkosh	10	0	P	P	P	P	0	0	0	0	P	P	0	0	P	0
Rochester	10	0	P	P	P	P	0	0	0	0	P	P	0	0	P	0
West Bend	10	0	P	P	P	P	0	0	0	0	P	P	0	0	P	0