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Cover Photograph: Bioacoustic recording location at the historic traprock quarry, Sleeping Giant State Park, Hamden, Connecticut. Photograph © C. Wisniewski.

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Bat Diversity, Assemblage, and Land Use in Connecticut

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Abstract - Human-induced landscape modifications have amplified the loss of biodiversity. Our goal was to survey bats across heterogeneous landscapes in Connecticut and examine how habitat features and scale influence community composition. This state is among areas most heavily impacted by white-nose syndrome, and the current status of bat biodiversity is largely unknown. We conducted acoustic surveys to examine how species richness, activity, and diversity varied across macrohabitats and a canonical correspondence analysis to assess the relation between community composition and land use at buffers with a radius of 200 and 500 m. We detected 8 of the 9 species historically reported in Connecticut. Species richness, activity, and diversity were greatest in macrohabitats dominated by natural water features and grasslands. Within the 200 m buffer area, species were grouped in forest, water-dominated, and cultivated landscapes; while within the 500 m buffer area, species were grouped away from development. Our results suggest that heterogeneous landscapes containing forest, water, and agricultural features are important for supporting communities at small spatial scales, and although development at any spatial scale hampers bat diversity, the negative effects are greatest within larger spatial scales.

Introduction

Anthropogenic activities, particularly intensified land use and urbanization, have altered landscapes and greatly reduced biodiversity. To mitigate the loss of species and identify how anthropogenic changes impact natural populations, understanding the natural history and biodiversity of a given area, monitoring population trends, and tracking changes in species assemblages alongside environmental shifts are essential. However, landscape changes affect species differently and, depending on scale, can influence community composition (Cordonnier et al. 2019). At large spatial scales, overall human impact and changes to the landscape may be concentrated. Thus, wildlife may easily avoid disturbed areas (Lowry et al. 2013). By default, at small spatial scales, risk of encountering landscape changes, anthropogenic structures, and experiencing interactions increases. Furthermore, the type of landscape change and other anthropogenic influences that exist in these areas also influence wildlife response (Tablado and Jenni 2017).

While understanding how wildlife communities respond to landscape changes is often difficult, the complexity increases for animals that are highly cryptic and mobile. Bats, compared to many other mammalian taxa, are understudied and under prioritized in terms of conservation efforts. Frick et al. (2020) showed that 80% of bat species assessed by the International Union for Conservation of Nature (IUCN) are either threatened, due to a range of anthropogenic and climate related factors, or are classified as data deficient, underscoring the need for expanded research initiatives to address data gaps and to inform and support conservation measures. This concern persists despite bats compelling species

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diversity (Burgin et al. 2018), broad global distribution (Procheş 2005), and the extensive range of ecosystem services they collectively provide in both natural and human-dominated landscapes (Kunz et al. 2011). Also, while habitat change and loss are the largest and most common threats to bats (Frick et al. 2020), the impacts of these changes are highly species specific. For example, some studies show high bat activity and thriving populations in urban areas (Skog 2021), whereas others show that bats avoid and/or are declining in developed landscapes (Moretto and Francis 2017, Russo and Ancillotto 2015). Furthermore, features within landscapes change how species use and move across space (Baguette et al. 2013) and, given that bats are highly mobile, their response to landscape and environmental changes varies with scale (Gallo et al. 2018, Kalda et al 2015, Treitler et al. 2016). In addition to various issues that threaten this group of animals (e.g., habitat change, lack of basic biological information, overexploitation, and persecution; Hammerson et al. 2017), many hibernating species in North America are having unparalleled declining numbers due to the disease white-nose syndrome (WNS; Cheng et al. 2021).

The state of Connecticut and its landscapes offer a unique platform for studying bats. With an area just under 13,000 sq. km, Connecticut differs from other New England and neighboring states by having a greater variety of climatic patterns within and across seasons (Kottek et al. 2006), dynamic topography, and heterogeneous landscapes. Connecticut has expanses of hardwood forests; surface waters; urban, suburban, and exurban developments; and patches of grassland and cultivation (Metzler and Tiner 1992). The state has a diversity of bats, including all 9 species native to New England: *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), *Lasiurus borealis* (Müller) (Eastern Red Bat), *L. cinereus* (Palisot de Beauvois) (Hoary Bat), *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), *Myotis leibii* (Audubon and Bachman) (Eastern Small-footed Bat), *M. lucifugus* (Le Conte) (Little Brown Bat), *M. septentrionalis* (Trouessart) (Northern Long-eared Bat), *M. sodalis* (Miller and Allen) (Indiana Bat) and *Perimyotis subflavus* (Cuvier) (Tricolored Bat). Six of these species are affected by WNS, which arrived in Connecticut in 2007 (*E. fuscus*, *M. leibii*, *M. lucifugus, M. septentrionalis, M. sodalis* and *P. subflavus*; WNSRT 2024). Presence of *Pseudogymnoascus destructans* (Blehert and Gargas) (Minnis and D.L. Lindner) has been detected on 2 other species (*L. borealis* and *L. noctivagans*), although WNS has not been confirmed. Four of the species are listed as endangered in Connecticut (*M. lucifugus*, *M. septentrionalis, M. sodalis* and *P. subflavus*). Because nearly 20% of this small state is developed (Arnold et al. 2020) and it is close to sites where bats have suffered some of the greatest declines in bat populations due to WNS (Frick et al. 2010), the bat diversity is notable.

Except for a few historical accounts of the natural history of Connecticut bats (Davis and Hitchcock 1965, Goodwin 1935, Griffin 1940, Linsley 1842) and 1 recent publication completed after our data were collected (Seewagen and Adams 2021), we are unaware of any published surveys of bat communities in this state. It is likely we have been missing important changes to the structure of bat communities in the era of WNS alongside changes in land use. As such, our first objective was to quantify bat diversity across largely understudied Connecticut landscapes. We predicted bat species richness, activity, and diversity would be greatest in macrohabitats that support foraging with open, natural spaces and available water. Our second objective was to examine how the distribution and assemblage of bats change with land use and landscape features at different spatial scales. We predicted development would shape bat communities within a larger spatial scale as they avoid human-made structures, whereas bat communities would be shaped more by natural land cover within smaller spatial scales.

Field-site Description

We conducted acoustic surveys in 11 locations (10 state parks and one golf course) spanning the state of Connecticut (Fig. 1). We selected locations that offered a mix of habitats, including natural unfragmented habitat with some natural and modified areas, open bodies of water and a mix of macrohabitats, and appropriate area (>0.6 km^2) for containing suitable bat habitats (Brooks 2009, 2011; Skalak et al. 2012).

With guidance from the Connecticut Department of Energy and Environmental Protection, we identified 4 unique macrohabitats shared by all 11 locations (*n* = 44 recording sites): forest, grassland, areas dominated by natural water features (henceforth "water"), and areas dominated by a mix of rocky outcrops and development (henceforth "structure"). Macrohabitats were >200 m apart from each other (Rodhouse et al. 2011, Skalak et al. 2012). Within each macrohabitat we chose specific recording locations based on accessibility and suitability for acoustic sampling, including minimal canopy cover and clutter within recording range of the detector (i.e., ~9 m) and ability to erect recording devices safely and securely. Field work was approved by the Southern Connecticut State University Institutional Animal Care and Use Committee (IACUC protocol #S17-02.20) and the Connecticut Department of Energy and Environmental Protection (CT DEEP permit #AU17f).

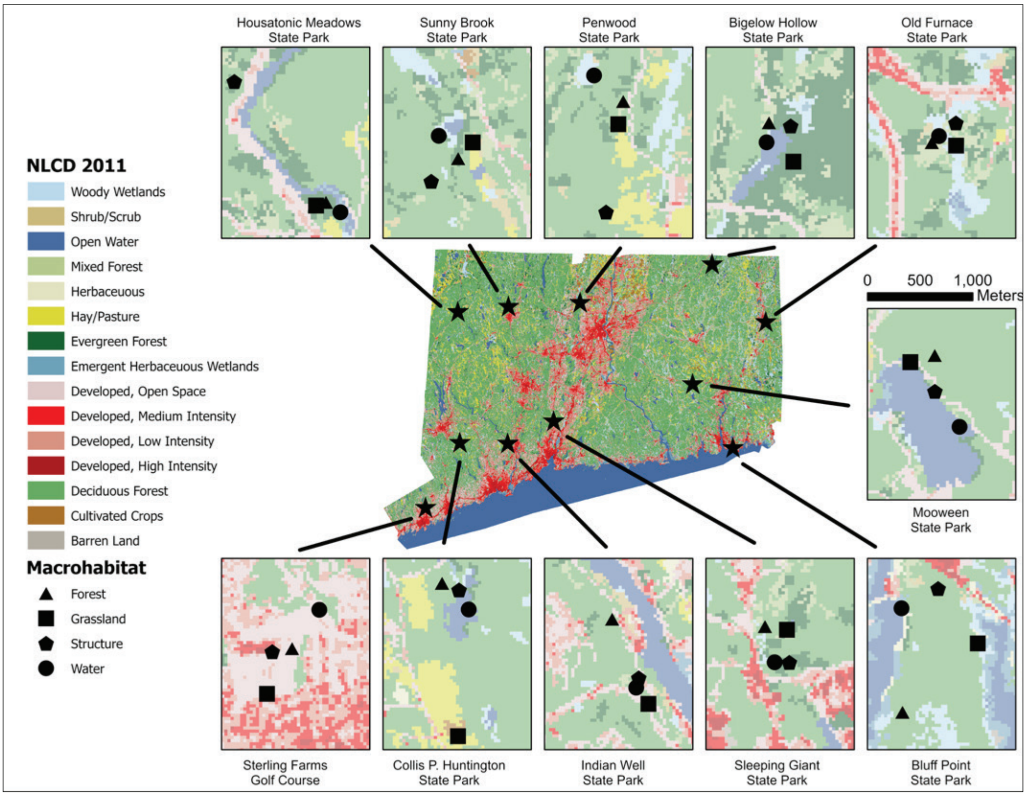

Figure 1. Acoustic sampling locations across protected areas in Connecticut in 2017. Within each of the 11 locations (stars), we identified 4 unique macrohabitats (*n* = 44 recording sites) in which we placed our stationary acoustic monitoring devices: Forest, Grassland, areas dominated by natural water features (Water), and areas dominated by a mix of rocky outcrops and development (Structure). Also shown are types of land cover provided by the National Land Cover Database (NLCD).

Methods

We used 1 SM3BAT and 1 SM4BAT full-spectrum bat detector (Wildlife Acoustics, Maynard, MA) to sample bats from 1 July through 31 October 2017. The time period was chosen to increase the probability of detecting fall migratory species. Each detector was programmed to turn on/off 30 min before/after sunset/sunrise. For each detector, we used the audio default amplification gain (12 dB) and set the sampling frequency to 256 kHz, which adjusted our sampling frequency range from 6 kHz to 128 kHz to capture low-through high-frequency species. We set the minimum call-recording duration to 1.5 ms with no maximum so that each call would be recorded in its entirety, as long as the animal was within the range of our detectors. We equipped each detector with an external ultrasonic microphone (SMM-U1; Wildlife Acoustics, Maynard, MA). Each microphone had an omnidirectional recording range, with a built-in high-pass filter (4-pole at 8 kHz) designed to reduce low frequency (<5 kHz) noise in recordings. We mounted detectors and microphones onto wooden poles 3 m above ground level. Working within our permit, time, and equipment constraints, we deployed detectors for 4 consecutive nights in each macrohabitat before moving them to a new recording site, following the rotation scheme recommended by Skalak et al. (2012). With exceptions for severe inclement weather and equipment maintenance, acoustic recording from 30 min before sunset to 30 min after sunrise was continuous.

We used SonoBat bioacoustics software (version 4.2.1, Northeast Suite; Sonobat, Arcata, CA) to scrub noise files and the Sonobatch feature to classify calls to species. We randomly selected calls from each species detected and examined call characteristics, including peak, minimum and maximum frequency, frequency modulation (i.e., frequency change within a single pulse), duration, and repetition rate, and we compared those to verified calls in the Sonobat reference library. The selected calls, along with files from *P. subflavus* and all *Myotis* species, were sent to experts from the Wildlife Division of the Connecticut Department of Energy and Environmental Protection to be vetted manually and help confirm presence/absence. Because *P. subflavus* and *Myotis* species show considerable overlap and can be difficult to classify (and are commonly misclassified), or are considered species of interest within the state, we enlisted outside help to provide second opinions. Our analyses are based on calls that were auto classified then confirmed by experts plus those that were also manually vetted by experts within the state of Connecticut.

For each of the 4 macrohabitats we defined richness as the number of species detected. Activity was calculated as the number of call files per hour of recording time, which included any call files recorded 30 min before/after sunset/sunrise, to standardize for temporal variation across the survey period. We calculated Simpson’s Diversity Index using R package “vegan” (Oksanen et al. 2018). Each of these 3 variables was analyzed in separate linear mixed-effects models in R package “lme4” (Bates et al. 2015), with macrohabitat as the main effect and location as the random effect. To evaluate assumptions for each model, we plotted residuals against fitted values and main effects to inspect heteroscedasticity and non-linearity, respectively. We used Q-Q plots to evaluate normality of residuals. Initial inspection of model fits indicated that residuals presented some degree of skew from normal for all 3 response variables. We, therefore, transformed response variables for analysis, using the natural log of the raw value +1 (Ives 2015), although linear models are generally robust to such deviations from model assumptions (Schielzeth et al. 2020). Within each model, we used the R function “glht” from the “multcomp” package (Hothorn et al. 2008) to conduct Tukey contrasts between macrohabitat features, with alpha adjusted by a Bonferroni-Holm correction.

We downloaded layers from National Land Cover Database (https://apps.nationalmap.gov/viewer/; Jin et al. 2013), created point layers of the sampling locations using GPS coordinates recorded at each site, and created 200 and 500 m buffers around each point. Because bats, in general, are highly mobile and the home ranges of different species vary by a factor of 60 (Peixoto et al. 2018), we consider the 200 and 500 m buffers as relevant small scales for examination of interspecific differences in habitat use. Furthermore, the 200 m buffer reflects the local macrohabitat and the 500 m buffer reflects the broader local range of bat movement. For each macrohabitat, we extracted the Land Use and Land Cover (LULC) layers (listed in Fig. 1) and calculated the percentages of land-cover type within each buffer distance. The LULCs categorize physical characteristics of landscape surfaces and include both natural and human-modified features. We calculated the percentages of land-cover type within each buffer by macrohabitat. We also included presence of any bridge type within a 2 km radius because shorter distances matching the LULC scales contained very few bridges, and some species (*E. fuscus, P. subflavus, M. lucifugus,* and *M. sodalis*) use bridges as roosts (Keeley and Tuttle 1999). Furthermore, many species disperse this distance from daytime roosts to foraging sites (Duchamp et al. 2004, Rainho and Palmeirim 2011). We acquired bridge locations from the National Bridge Inventory (Federal Highway Administration 2016). The number of bridges within 2 km of each of the 11 study locations was determined through a buffer and spatial join of the study locations with the bridge layer within GIS (ArcMap, version 10.7, ESRI, Redlands, CA).

We used the R package "vegan" (Oksanen et al. 2018) to conduct constrained ordination to examine the relation between species distribution and LULC at each spatial scale. Specifically, for each recording location, we used the proportion of each type of LULC present within 200 and 500 m as ordination constraints. The number of bridges within 2 km was also included in each analysis. In all models, the species matrix included total number of calls per species at each recording location and was scaled to unit variance. The environmental matrix included all LULC variables at the corresponding scale along with number of bridges. We applied an angular transformation to LULC variables because they were based on proportions.

Before model selection, we evaluated the relative performance of 2 common ordination techniques at each buffer scale: redundancy analysis (RDA) and canonical correspondence analysis (CCA). For each technique, we compared the proportion of variance explained by the first 2 ordination axes in each full model (i.e., containing all LULC and bridges) for the 2 different spatial scales. In both cases, the constrained eigenvalues from CCA models explained more variation (82–83%) than those from RDA models (66–73%); therefore, we chose CCA as the ordination technique for our analyses. For each of the 2 full models analyzed by CCA, we used backward model selection (function "ordistep") with 10,000 permutations, to select the suite of LULC variables for inference. Constrained ordination techniques do not produce AIC values, and the permutation approach to model selection has a random component (Oksanen et al. 2018). Thus, for inference, we chose the first reduced model where all selected variables had $P < 0.10$ at each spatial scale.

Results

With nearly 2000 h of recording and 10,100 bat calls, we identified 65% of calls representing 8 species historically present in Connecticut. The remaining files contained insect or other environmental interference, producing a file of poor quality that could not be confidently classified through Sonobatch. A batch scrubber in Sonobat helped to isolate and remove files of poor quality. On average, *E. fuscus* accounted for 73% (and as high as 90%) of confirmed calls in each macrohabitat. *Myotis lucifugus* contributed 10%, *P. subflavus, L. borealis, L. noctivagans*, and *L. cinereus* each accounted for 3%, and *M. leibii* and *M. sodalis* produced < 2% of confirmed calls in each habitat type (Table 1). We did not detect *M. septentrionalis*.

Richness ranged from 1 to 7 species per macrohabitat, with an average of 4.1 species detected per sampling location (Fig. 2). In separate linear mixed models (Table 2), macrohabitat explained variation in log-transformed species richness ($F_{3, 30} = 11.86$; $P < 0.001$), activity ($F_{3, 40} = 7.63$; $P < 0.001$), and diversity ($F_{3, 30} = 5.18$; $P = 0.005$). Estimates for each of these variables within each macrohabitat are shown in Figure 2, with Tukey contrasts indicated. Water and grassland macrohabitats supported the highest richness, with 3.04 species versus 2.35 in forest and structure. The greatest richness in a single location was at Collis P. Huntington Park (Fig. 1), with 7 species. Water and grasslands also supported the highest activity (Fig. 2) with a back-transformed average value of 0.27 calls/h, compared to 0.20 calls/h in structure and forests. The greatest diversity was found in water macrohabitats (Fig. 2) with a back-transformed estimated diversity value of 0.58 in these sites, versus an average of 0.36 in other macrohabitats.

Within a 200 m radius, the top performing model included 5 LULC variables: herbaceous, forest, cultivated, wetlands, and water ($F_{5, 32} = 1.075$; $P = 0.013$; Table 3). We used this reduced model for inference and found it explains species distribution in relation to the environment matrix ($F_{5, 34} = 3.27$; $P = 0.008$; Fig. 3a). Constrained inertia (0.737), which represents the amount of variance in species data explained by the environmental variables, accounted for 34% of total inertia (2.179). The eigenvalues for CCA axis 1 (0.354) and 2

Table 1. Number of calls recorded per species, location, and macrohabitat between July and October 2017. Calls were filtered by the "corrected count" feature in Sonobat. Species include: Myle = *Myotis leibii,* Myse = *Myotis septentrionalis,* Pesu = *Perimyotis subflavus,* Myso = *Myotis sodalis,* Mylu = *Myotis lucifugus,* Labo = *Lasiurus borealis,* Epfu = *Eptesicus fuscus,* Lano = *Lasionycteris noctivagans,* and Laci = *Lasiurus cinereus.*

Macrohabitat	Location	Myle	Myse	Pesu	Myso	Mylu	Labo	Epfu	Lano	Laci	Totals
Forest	Bigelow Hollow	-	-	-	33	79	-	2	1	-	115
	Indian Well	-	-	-	-	-	-	532	-	-	532
	Collis P. Huntington	-	-	-	-	-	2	6	-	-	8
	Mooween	-	-	-	-	-	-	-	-	-	0
	Housatonic Meadows	-	-	-	3	-	-	1	-	-	4
	Old Furnace	-	-	-	-	-	-	4	1	-	5
	Bluff Point	-	-	-	-	-	-	-	-	1	1
	Penwood	-	-	-	-	-	-	14	2	-	16
	Sterling Farms	-	-	-	-	-	-	-	-	1	1
	Sunnybrook	-	-	-	-	-	-	-	-	-	0
	Sleeping Giant	-	-	1	-	-	-	10	-	-	11

Table 1 Cont. Number of calls recorded per species, location, and macrohabitat between July and October 2017. Calls were filtered by the "corrected count" feature in Sonobat. Species include: Myle = *Myotis leibii,* Myse = *Myotis septentrionalis,* Pesu = *Perimyotis subflavus,* Myso = *Myotis sodalis,* Mylu = *Myotis lucifugus,* Labo = *Lasiurus borealis,* Epfu = *Eptesicus fuscus,* Lano = *Lasionycteris noctivagans,* and Laci = *Lasiurus cinereus.*

Grassland	Housatonic Meadows	-	-	1	-	-	4	48	-	-	53
	Collis P. Huntington	-	-	-	-	-	37	237	-	-	274
	Bluff Point	-	-	-	-	-	1	8	9	-	18
	Sterling Farms	-	-	-	-	-	-	66	3	-	69
	Mooween	-	-	1	-	-	7	299	-	-	307
	Penwood	-	-	-	-	-	-	64	-	4	68
	Sleeping Giant	2	-	-	-	-	1	341	19	-	363
	Sunnybrook	-	-	-	-	-	7	785	-	-	792
	Indian Well	-	-	-	-	-	-	12	-	-	12
	Bigelow Hollow	-	-	-	-	-	1	14	19	-	34
	Old Furnace	-	-	2	-	-	8	322	-	35	367
Structure	Sterling Farms	-	-	2	-	-	-	-	41	-	43
	Bigelow Hollow	-	-	-	-	-	-	1	1	-	2
	Sleeping Giant	-	-	-	-	-	1	24	-	-	25
	Old Furnace	-	-	-	-	-	1	2	-	1	4
	Collis P. Huntington	21	-	-	-	-	-	1	1	-	23
	Indian Well	-	-	-	-	-	-	232	-	-	232
	Housatonic Meadows	-	-	-	-	1	-	8	-	-	9
	Mooween	-	-	-	-	-	-	-	-	-	0
	Bluff Point	-	-	-	-	-	-	-	-	-	0
	Penwood	-	-	-	-	-	-	-	-	-	0
	Sunnybrook	-	-	-	-	-	-	-	-	-	0
Water	Indian Well	-	-	-	-	-	-	65	-	-	65
	Old Furnace	-	-	1	1	-	3	7	-	13	25
	Penwood	4	-	-	-	-	1	143	14	16	178
	Sunnybrook	-	-	-	-	-	2	586	39	64	691
	Housatonic Meadows	-	-	230	-	-	128	148	8	-	514
	Collis P. Huntington	79	-	-	7	198	14	397	30	72	797
	Mooween	-	-	-	-	-	-	1	-	-	1
	Bluff Point	-	-	-	-	-	1	9	18	2	30
	Bigelow Hollow	-	-	-	-	441	-	40	6	4	491
	Sterling Farms	-	-	-	-	-	1	39	7	-	47
	Sleeping Giant	2	-	3	-	-	9	402	4	-	420
Totals		108	0	241	44	719	229	4870	223	213	6647

(0.294) accounted for 48% and 40% of the constrained inertia. Thus, the first 2 CCA axes together explained 88% of the variance in the species data that can be attributed to the environmental variables.

Within a 500 m radius, stepwise model selection supported retention of all LULC variables and the number of bridges (selection model: $F_{8,29} = 1.075$, $P < 0.001$; Table 3). The final CCA model explained a significant portion of species distribution in relation to the environmental matrix ($F_{8,29} = 3.53$, $P = 0.002$; Fig. 3b), and was used for inference. Constrained inertia (0.993) accounted for 46% of total inertia (2.179). The first 2 constrained eigenvalues accounted for 56% and 32% of the constrained inertia. Thus, the first 2 CCA axes explained 88% of the variance in species occurrence data associated with the environmental variables.

Discussion

Ours is the first study in decades to document bat dynamics in Connecticut, and the first ever in this area to use a multifactorial and multiscale approach. This work sheds a long-overdue light on bat communities in Connecticut and serves as a baseline upon which future studies may build. We detected *E. fuscus*, *L. borealis*, *L. cinereus*, *L. noctivagans, M. leibii*, *M. lucifugus*, *M. sodalis*, and *P. subflavus*—8 of the 9 species historically known to inhabit Connecticut. Documenting such high species richness for the region is notable, given the bleak predictions for WNS (Frick et al. 2010), suggesting some individuals of

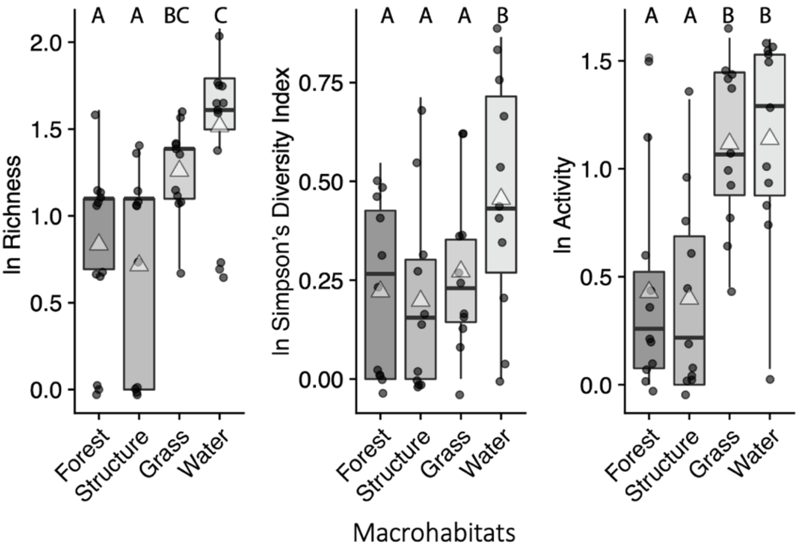

Figure 2. Species richness, diversity, and activity across 4 types of macrohabitat. Richness represents the total number of species. Diversity was calculated using Simpson's Diversity Index. Activity corresponds to the number of calls per hour of darkness, defined as 30 min before sunset and 30 min after sunrise. All values were log-transformed as ln(value + 1). Boxplots are overlaid. Means are indicated by triangles. Letters placed above the *x*-axis show the results of Tukey contrasts applied between macrohabitat types.

Table 2. Main effects from linear mixed models of bat species A) richness, B) diversity, and C) activity at 11 locations in Connecticut. Estimates are based on Type III sums of squares and inference is based on Satterthwaite's degrees of freedom. In each model, the response variable was transformed with the natural log.

A)	**log(Richness + 1)**			**B**)	**log(Diversity + 1)**			**C**)	**log(Activity + 1)**		
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	0.83	0.55–1.12	<0.001	(Intercept)	0.22	0.07–0.37	0.005	(Intercept)	0.19	0.07–0.31	0.003
Habitat [Structure]	-0.12	0.43–0.19	0.436	Habitat [Structure]	-0.02	0.17–0.12	0.747	Habitat [Structure]	-0.01	0.18–0.16	0.877
Habitat [Grass]	0.42	0.12–0.73	0.008	Habitat [Grass]	0.05	0.10–0.20	0.488	Habitat [Grass]	0.3	0.13–0.47	0.001
Habitat [Water]	0.68	0.37–0.99	<0.001	Habitat [Water]	0.23	0.09–0.38	0.003	Habitat [Water]	0.31	0.14–0.48	0.001
Observations	44			Observations	44			Observations	44		
Marginal R^2 / Conditional R^2	0.330 / 0.601			Marginal R^2 / Conditional R^2	0.148 / 0.589			Marginal R^2 / Conditional R^2	0.386 / 0.398		

species affected by WNS are persisting. One location (Collis P. Huntington Park; Fig. 1) was particularly species-rich, with 7 of the 8 detected species; only *L. borealis* was not recorded here. We speculate this is due to the availability of suitable roosting and foraging habitat for these 7 species in a compact location.

While we did not detect *M. septentrionalis*, we cannot conclude that the species is absent. We may have had temporal effects, such as time of year or too few sampling nights. The number of sampling nights necessary to detect individual, rare, or challenging-to-detect species varies greatly (Deeley et al. 2021a) and may exceed 45 sampling nights (Skalak et al. 2012). Alternatively, we may have recorded *M. septentrionalis* but not identified it due to poor-quality recordings or was simply not captured within our sampling area. Given that this species is endangered in the United States (U.S. Fish and Wildlife Service 2023) and listed as near threatened by the IUCN (2018), the absence of *M. septentrionalis* in our study adds to the concern for this species.

Eptesicus fuscus was the most commonly recorded species across all macrohabitats and sampling locations (Table 1). It is a generalist that uses various habitats for foraging and roosting (Brigham 1991, Willis et al. 2003, Willis and Brigham 2004), and its abundance in our study can be explained also by their resistance to WNS (Frank et al. 2014, Hoyt et al. 2015, Lemieux-Labonté et al. 2020, Moore et al. 2017). We also recognize that the profusion of calls from *E. fuscus* may be biased because this species broadcasts more frequently (Moss et al. 2011, Wheeler et al. 2016) and emits higher-energy calls than do other species in this area (Hulgard et al. 2015).

Table 3. Canonical correspondence analyses model selection results at each scale.

		200 m Buffer	
Variable	*df*	*F*	*P*
Forest	1	2.25	0.074
Water	1	3.27	0.031
Wetlands	1	3.85	0.015
Herbaceous	1	3.88	0.014
Cultivated	1	4.67	0.001

		500 m Buffer	
Variable	*df*	*F*	*P*
Bridges	1	2.15	0.099
Developed	1	2.63	0.066
Water	1	3.52	0.012
Wetlands	1	3.19	0.011
Shrubland	1	6.13	0.004
Forest	1	5.13	0.003
Herbaceous	1	5.62	0.002
Cultivated	1	7.94	0.001

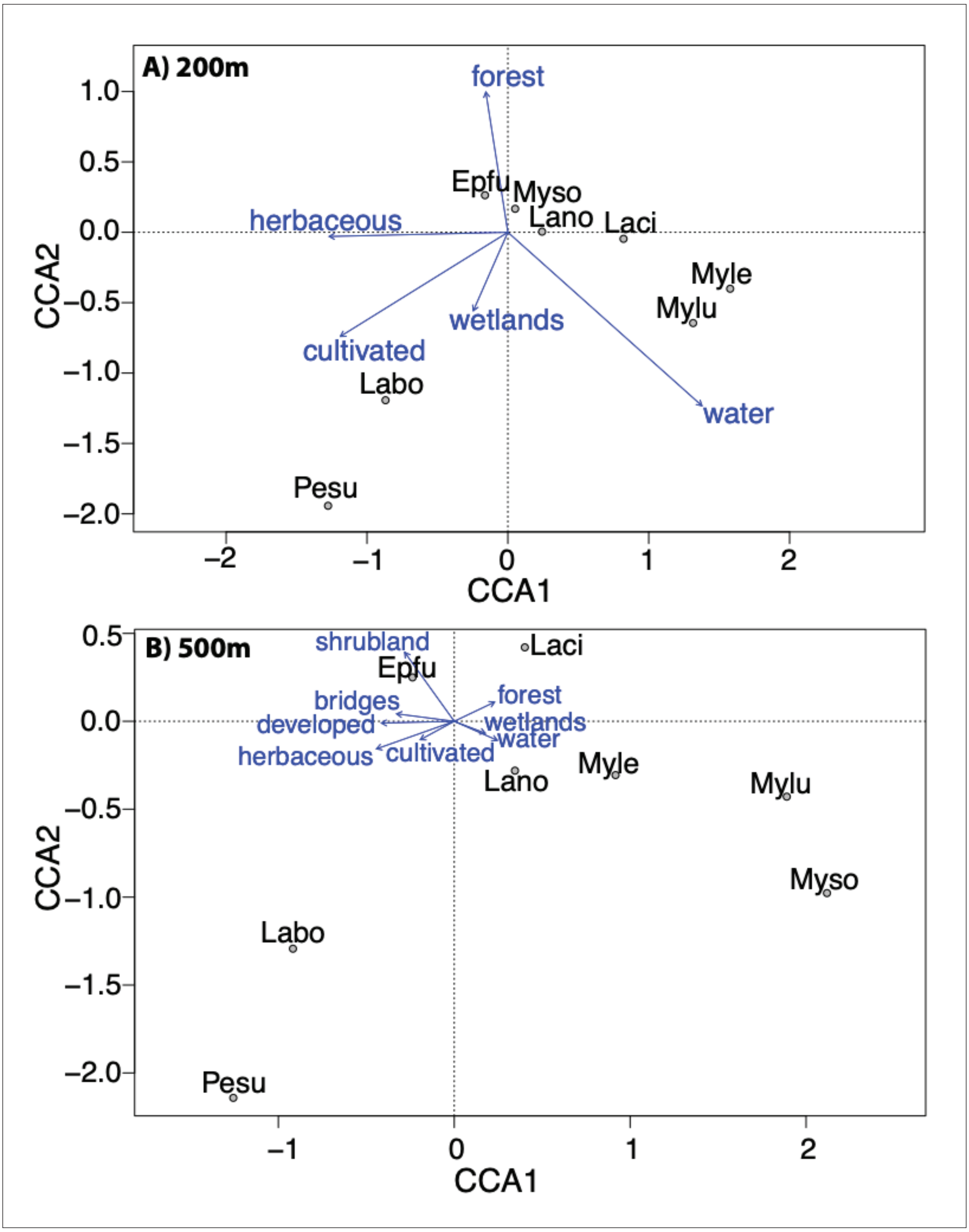

Figure 3. Ordination plots from canonical correspondence (CCA) analyses of species in relation to the constrained ordination space of land use land cover (LULC) features present in each of the 2 spatial scales: 200 m (A) and 500 m (B). Position of arrows indicates the contribution of each LULC variable to each CCA axis, with the strength of correlation indicated by arrow length. Species positions represent the centroid of their distribution across sampling sites in the ordination space, and their relation to LULC variables is indicated by arrows. The 8 species we detected include: Myle = *Myotis leibii,* Pesu = *Perimyotis subflavus,* Myso = *Myotis sodalis,* Mylu = *Myotis lucifugus,* Labo = *Lasiurus borealis,* Epfu = *Eptesicus fuscus,* Lano = *Lasionycteris noctivagans,* and Laci = *Lasiurus cinereus.*

Species richness, activity, and diversity were all greatest in water macrohabitats, and grasslands supported higher bat species richness and activity than did forest or structure macrohabitats (Table 2). The water and grassland macrohabitats that we sampled have features that enhance foraging (e.g., water and more open spaces) and thus attract bats (Bruckner 2016). While our forest and structure macrohabitats did not support the same level of richness, activity, or diversity, we were able to record species that were undetected in other locations and species that are listed under various endangered species protections.

While overall activity was highest for *E. fuscus,* in water macrohabitats *M. lucifugus* was also prevalent (Table 1), agreeing with previous work (Kalcounis and Brigham 1995). Although we did not explore species abundance, we suspect low relative activity from *M. lucifugus* may indicate populations declining due to WNS-related mortality (Frick et al. 2010). While once as common as *E. fuscus* in some areas, populations of *M. lucifugus* have been decimated by WNS across their range where WNS is present (Davis and Hitchcock 1965; Hoyt et al. 2020, 2021; Kramer et al. 2019). They are now listed as endangered by the IUCN (2021) and are currently being considered for listing by the U.S. Fish and Wildlife Service (2024). Other acoustic studies from neighboring Massachusetts and New York also found substantial decreases (>70%) in *Myotis* activity in summer post-WNS (Brooks 2011, Dzal et al. 2011). Our detections of *M. lucifugus* indicate that the species is not regionally extirpated. Our research supports other studies showing that summer abundance and community composition may be driven by species less affected by WNS, such as *E. fuscus* (Deeley et al. 2021b, Simonis et al. 2023). Furthermore, persisting species may be occupying habitats or adapting to fill ecological niches once held by formerly prevalent species (Morningstar et al. 2019).

In grassland macrohabitats, we recorded the greatest number of calls from *E. fuscus* and, to a lesser extent, *L. noctivagans.* However, we note that the calls of *E. fuscus* and *L. noctivagans* are similar in structure, making it difficult to differentiate potentially skewing results. *E. fuscus* prefers foraging in open habitats (Coleman and Barclay 2013, Patriquin and Barclay 2003), and it is quite possible we primarily recorded this species there, due to this factor.

In forest macrohabitats *M. lucifugus* and *M. sodalis* were most commonly detected. *Myotis* species are small-bodied with wings well adapted for navigating through cluttered forests (Brooks 2009, Fenton and Barclay 1980, Sleep and Brigham 2003) and often roost and forage in forested habitat (Brack et al. 2002, Fenton and Barclay 1980, Kalcounis and Brigham 1995).

In structured macrohabitats *L. noctivagans* and *M. leibii* were the dominant species. While *L. noctivagans* roosts primarily in tree crevices during summer (Barclay et al. 1988, Betts 1998, Bohn 2017), they also roost in various human-made structures while migrating and in the winter (Kurta et al. 2018, McGuire et al. 2012). Similarly, *M. leibii* uses rocky outcrops and anthropogenic structures for roosting (Johnson et al. 2011, Johnson and Gates 2008, Moosman et al. 2015). While our study area falls within the historic range of *M. leibii* (Best and Jennings 1997), they have not been documented in Connecticut for several decades, so it was a welcome discovery to have detected this species. *M. leibii* was detected in both water and structured macrohabitats in 3 separate locations (Sleeping Giant, Collis P. Huntington, and Penwood; Fig. 1). The detection of *M. leibii* and *M. sodalis* is noteworthy because of the rarity of these species and their WNS susceptibility. Files attributed to either *M. leibii* or *M. sodalis* received increased scrutiny in this study due to their conservation status and overlap in call characteristics; however, we recommend that the presence of these species be verified with capture records.

Canonical correspondence analysis

We assessed the relation between community composition and land use at 200 and 500 m around each of our 11 recording locations, and found that detections were related to environmental variables in similar ways. Regardless of scale, species grouped strongly on the ordination plot in association with forests, water, and cultivated areas. However, at 200 m the preferred model included all natural LULC layers but excluded human-made structures. Yet at 500 m, the preferred model also included all natural LULC variables but included human-made structures. This suggests that, at smaller spatial scales, community composition is most strongly influenced by natural land cover. Natural land cover caters to species-specific needs for roosting (Kalcounis and Brigham 1998, Willis and Brigham 2005) and foraging (Denzinger and Schnitzler 2013), and it shapes flight and echolocation performance (Denzinger and Schnitzler 2013). At larger spatial scales, though, bat communities appear more strongly influenced by development; at 500 m, bats grouped away from structure, bridges, and grassland. While grasslands supported high species richness and activity, bats apparently group away from this land cover, should it border development within larger spatial scales. Similarly, other studies have shown that in intensely modified areas there is a decrease in overall species richness alongside an increase in the number of individuals of opportunistic species (Avila-Flores and Fenton 2005, Krauel and LeBuhn 2016). For example, *E. fuscus* has been reported as the most abundant species in urbanized areas (Arnett et al. 2008, Gehrt and Chelsvig 2008). Our findings agree with previous studies demonstrating that bats' use of open space is a function of scale-dependent elements within the landscape (Avila-Flores and Fenton 2005). Within smaller areas bats may be less sensitive to some development, yet at larger scales, developed land has a negative effect on bat community diversity. Still, relationships between species and environmental variables should be treated with caution because a substantial amount of variability was unaccounted for in our models, as indicated by the proportion of inertia they explained. While environmental variables apparently influence the occurrence of bat detections and differ across spatial scales, other unmeasured variables (such as food resources, disease, predation, and/or stochasticity in movement and detection) are likely important.

At the 200 m scale, CCA axis 1 was dominated by a strong negative correlation with herbaceous cover and a positive but weaker correlation with water. Most species' scores were located at the positive end of this axis away from heavily herbaceous habitats and in habitats with open water. This could be due to roost selection of these species (primarily trees and structures) often located closer to water resources. CCA axis 2 was related to the presence of water (wetlands and water cover types).

At the 500 m scale CCA axis 1 showed a strong, negative correlation with developed landscape attributes (structure macrohabitat, including bridges and development, followed by cultivated fields and herbaceous cover) and a positive correlation with water and wetlands followed by forest cover. Most species were on the positive side of this axis, indicating their association with water and forest. CCA axis 2 was most closely associated with shrubland, which showed positive, but not particularly strong, correlation. A positive correlation is not surprising, given our general knowledge of how various species can utilize "narrow" foraging spaces, whereas foraging bats exploit insect prey that is positioned near background objects, such as vegetation (Denzinger and Schnitzler 2013).

The strongest associations between species and environmental variables appear to be water with *M. lucifugus* and *M. leibii* at 200 and 500 m, as well as water with *L. noctivagans* and *M. sodalis* at 500 m, which is not surprising because water acts as a primary gathering spot for foraging (Greif and Siemers 2010, Mackey and Barclay 1989). Interestingly, we did not find a strong association between *M. sodalis* with water at the 200 m scale, but this may be because we recorded too few calls (n = 44) from this endangered species to reveal a pattern. Both *P. subflavus* and *L. borealis* associated away from water, regardless of scale. While *L. borealis* sometimes congregates near water (Walters et al. 2007), our lack of detections in that habitat might be explained by seasonal changes and migration patterns of the species (e.g., they may have already vacated and/or not yet arrived, in given recording locations; Kunz 1971, Walters et al. 2006). It is notable that we found *P. subflavus* associated away from water, given that previous work shows roost locations and activity in this species are higher around water bodies (Cable and Willcox 2024). It may be that access to water is selected for at smaller scales and other factors, such as access to foraging habitat, are selected for at larger spatial scales.

Our work improves our understanding of bat dynamics across a largely understudied area and suggests how communities of bats are shaped by land use. We show greater species richness, activity, and diversity in macrohabitats that are dominated by natural water features and grasslands. Forested landscapes are an important and common focus for habitat restoration and preservation, and they have long been known to provide suitable habitat and allow species to persist in larger regions that have suffered declines in biodiversity (Estrada et al. 1993, Sedgeley and O'Donnell 1999). It appears that water macrohabitats, grasslands, and cultivated areas also promote diverse bat assemblies. We also show that natural landscape features on a small scale strongly predicted species distribution; however, as the lens widens to include larger spaces, the presence of development negatively disrupted species richness, diversity, and activity. We may see that within these modified landscapes, generalist species (e.g., *E. fuscus*) occupy and replace others (e.g., WNS-affected *M. sodalis, M. lucifugus,* and *M. septentrionalis*), as has been described in Jachowski et al. (2014). Regardless, these surviving bat communities in Connecticut are especially important because they offer insight into potential mechanisms of disease persistence (Dobony and Johnson 2018, Gignoux-Wolfsohn et al. 2021), adaptive evolution (Auteri and Knowles 2020, Forsythe et al. 2018, Frank et al. 2014, Wilcox et al. 2014), and behavioral plasticity (Johnson and Johnson 2024, Lilley et al. 2016) in the wake of WNS. Also, our work reveals even more of the nuances of how bats respond to changing landscapes. With this, we can better inform survey and conservation efforts allowing for more precise investigation on the interaction of bats with natural and modified lands.

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Literature Cited

Arnett, E.B., W.K. Brown, W.P. Erickson, J.K. Fiedler, B.L. Hamilton, T.H. Henry, A. Jain, G.D. Johnson, J. Kerns, R.R. Koford, C.P. Nicholson, T.J. O'Connell, M.D. Piorkowski, and R.D. Tankersley. 2008. Patterns of bat fatalities at wind energy facilities in North America. Journal of Wildlife Management 72:61–78.

Arnold, C., E. Wilson, J. Hurd, and D. Civco. 2020. 30 years of land cover change in Connecticut, USA: A case study of long-term research, dissemination of results, and their use in land use planning and natural resource conservation. Land 9(8):255.

Auteri, G.G., and L.L. Knowles. 2020. Decimated Little Brown Bats show potential for adaptive change. Scientific Reports 10:3023.

Avila-Flores, R., and M. Brock Fenton. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. Journal of Mammalogy 86:1193–1204.

Baguette, M., S. Blanchet, D. Legrand, V.M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity, and ecological networks. Biological Reviews 88:310–326.

Barclay, R.M.R., P.A. Faure, and D.R. Farr. 1988. Roosting behavior and roost selection by migrating Silver-haired Bats (*Lasionycteris noctivagans*). Journal of Mammalogy 69:821–825.

Bates, D., M. Mächler, B.M. Bolker, and S.C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1–48.

Best, T.L., and J.B. Jennings. 1997. *Myotis leibii*. Mammalian Species 547:1–6.

Betts, B.J. 1998. Roosts used by maternity colonies of Silver-haired Bats in northeastern Oregon. Journal of Mammalogy 79:643–650.

Bohn, S.J. 2017. Tall timber: Roost tree selection of reproductive female Silver-haired Bats (*Lasionycteris noctivagans*). Masters Thesis. University of Regina, Regina, SK. 25 pp.

Brack, V., C.W. Stihler, R.J. Reynolds, C.M. Butchkoski, and C.S. Hobson. 2002. Effect of climate and elevation on distribution and abundance in the mideastern United States. Pp. 21–28, *In* A. Kurta and J. Kennedy (Eds.). The Indiana Bat: Biology and management of an endangered species. Bat Conservation International, Inc., Austin, TX. 253 pp.

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, R.T. 2009. Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. Biodiversity and Conservation 18:529–545.

Brooks, R.T. 2011. Declines in summer bat activity in central New England 4 years following the initial detection of white-nose syndrome. Biodiversity and Conservation 20:2537–2541.

Bruckner, A. 2016. Recording at water bodies increases the efficiency of a survey of temperate bats with stationary, automated detectors. Mammalia 80:645–653.

Burgin, C.J., J.P. Colella, P.L. Kahn, and N.S. Upham. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–14.

Cable, A.B., and Willcox, E.V. 2024. Summer habitat for the female Tricolored Bat (*Perimyotis subflavus*) in Tennessee, United States. Journal of Mammalogy 105(3):667–678.

Cheng, T.L., J.D. Reichard, J.T.H. Coleman, T.J. Weller, W.E. Thogmartin, B.E. Reichert, A.B. Bennett, H.G. Broders, J. Campbell, K. Etchison, D.J. Feller, R. Geboy, T. Hemberger, C. Herzog, A.C. Hicks, S. Houghton, J. Humber, J.A. Kath, R.A. King, S.C. Loeb, A. Massé, K.M. Morris, H. Niederriter, G. Nordquist, R.W. Perry, R.J. Reynolds, D.B. Sasse, M.R. Scafini, R.C. Stark, C.W. Stihler, S.C. Thomas, G.G. Turner, S. Webb, B.J. Westrich, and W.F. Frick. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35:1586–1597.

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.

Cordonnier, M., C. Gibert, A. Bellec, B. Kaufmann, and G. Escarguel. 2019. Multi-scale impacts of urbanization on species distribution within the genus *Tetramorium*. Landscape Ecology 34:1937–1948.

Davis, W.H., and H.B. Hitchcock. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. Journal of Mammalogy 46:296–313.

Deeley, S., J.B. Johnson, W.M. Ford, and J.E. Gates. 2021a. White-nose syndrome-related changes to Mid-Atlantic bat communities across an urban-to-rural gradient. BMC Zoology 6:12.

Deeley, S., N.J. Kalen, S.R. Freeze, E.L. Barr, and W.M. Ford 2021b. Post-white-nose syndrome passive acoustic sampling effort for determining bat species occupancy within the Mid-Atlantic region. Ecological Indicators 125:107489.

Denzinger, A., and H.-U. Schnitzler. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in Physiology 4(164):1–15.

Dobony, C.A., and J.B. Johnson. 2018. Observed resiliency of Little Brown Myotis to long-term white-nose syndrome exposure. Journal of Fish and Wildlife Management 9:168–179.

Duchamp, J.E., D.W. Sparks, and J.O. Whitaker, Jr. 2004. Foraging-habitat selection by bats at an urban–rural interface: Comparison between a successful and a less successful species. Canadian Journal of Zoology 82:1157–1164.

Dzal, Y., L.P. McGuire, N. Veselka, and M.B. Fenton. 2011. Going, going, gone: The impact of white-nose syndrome on the summer activity of the Little Brown Bat (*Myotis lucifugus*). Biology Letters 7:392–394.

Estrada, A., R. Coates-Estrada, and D. Meritt. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16:309–318.

Fenton, M.B., and R.M.R. Barclay. 1980. *Myotis lucifugus*. Mammalian Species 142:1–8.

Federal Highway Administration. 2016. National Bridge Inventory – National geospatial data asset (NGDA). Available online at https://www.fhwa.dot.gov/bridge/nbi/element2016.cfm. Accessed January 1, 2017.

Forsythe, A., V. Giglio, J. Asa, and J. Xu. 2018. Phenotypic divergence along geographic gradients reveals potential for rapid adaptation of the white-nose syndrome pathogen, *Pseudogymnoascus destructans*, in North America. Applied and Environmental Microbiology 84:e00863-18.

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(12): e113958.

Frick, W.F., T. Kingston, and J. Flanders. 2020. A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences 1469:5–25.

Frick, W.F., J.F. Pollock, A.C. Hicks, K.E. Langwig, D.S. Reynolds, G.G. Turner, C.M. Butchkoski, and T.H. Kunz. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682.

Gallo, T., E.W. Lehrer, M. Fidino, R.J. Kilgour, P.J. Wolff, and S.B. Magle. 2018. Need for multi-scale planning for conservation of urban bats. Conservation Biology 32:638–647.

Gehrt, S.D., and J.E. Chelsvig. 2008. Bat activity in an urban landscape: Patterns at the landscape and microhabitat scale. Pp. 437–453, *In* J. Marzluff, G. Bradley, C. Ryan, E. Shulenberger, W. Endlicher, M. Alberti, U. Simon, C. ZumBrunnen (Eds.). Urban Ecology: An International Perspective on the Interaction Between Humans and Nature. Springer, New York, NY. 808 pp.

Gignoux-Wolfsohn, S.A., M.L. Pinsky, K. Kerwin, C. Herzog, M. Hall, A.B. Bennett, N.H. Fefferman, and B. Maslo. 2021. Genomic signatures of selection in bats surviving white-nose syndrome. Molecular Ecology 30:5643–5657.

Goodwin, G.G. 1935. The Mammals of Connecticut. State of Connecticut Press, Hartford, CT. 221 pp.

Greif, S., and B.M. Siemers. 2010. Innate recognition of water bodies in echolocating bats. Nature Communications 1:107.

Griffin, D.R. 1940. Notes on the life histories of New England cave bats. Journal of Mammalogy 21:181–187.

Hammerson, G.A., M. Kling, M. Harkness, M. Ormes, and B.E. Young. 2017. Strong geographic and temporal patterns in conservation status of North American bats. Biological Conservation 212:144–152.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Hoyt, J.R., T.L. Cheng, K.E. Langwig, M.M. Hee, W.F. Frick, and A.M. Kilpatrick. 2015. Bacteria isolated from bats inhibit the growth of *Pseudogymnoascus destructans*, the causative agent of white-nose syndrome. PLoS ONE 10(4):e0121329.

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.

Hoyt, J.R., K.E. Langwig, K. Sun, K.L. Parise, A. Li, Y. Wang, X. Huang, L. Worledge, H. Miller, J.P. White, H.M. Kaarakka, J.A. Redell, T. Görföl, S.A. Boldogh, D. Fukui, M. Sakuyama, S. Yachimori, A. Sato, M. Dalannast, A. Jargalsaikhan, N. Batbayar, Y. Yovel, E. Amichai, I. Natradze, W.F. Frick, J.T. Foster, J. Feng, and A.M. Kilpatrick. 2020. Environmental reservoir dynamics predict global infection patterns and population impacts for the fungal disease white-nose syndrome. Proceedings of the National Academy of Sciences of the United States of America 117:7255–7262.

Hulgard, K., C.F. Moss, L. Jakobsen, and A. Surlykke. 2015. Big Brown Bats (*Eptesicus fuscus*) emit intense search calls and fly in stereotyped flight paths as they forage in the wild. Journal of Experimental Biology 219:334–340.

IUCN. 2018. Northern Myotis. *Myotis septentrionalis*. The IUCN Red List of Threatened Species. Available online at https://www.iucnredlist.org/species/14201/22064312. Accessed 3 January 2023.

IUCN. 2021. Little Brown Bat. *Myotis lucifugus*. The IUCN Red List of Threatened Species. Available online at https://www.iucnredlist.org/species/14176/208031565. Accessed 3 January 2023.

Ives, A.R. 2015. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution 6:828–835.

Jachowski, D.S., C.A. Dobony, L.S. Coleman, W.M. Ford, E.R. Britzke, and J.L. Rodrigue. 2014. Disease and community structure: White-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. Diversity and Distributions 20(9):1002–1015.

Jin, S., L. Yang, P. Danielson, C. Homer, J. Fry, and G. Xian. 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. Remote Sensing of Environment 132:159–175.

Johnson, J.B., and J.E. Gates. 2008. Spring migration and roost selection of female *Myotis leibii* in Maryland. Northeastern Naturalist 15:453–460.

Johnson, J.S., J.D. Kiser, K.S. Watrous, and T.S. Peterson. 2011. Day-roosts of *Myotis leibii* in the Appalachian Ridge and Valley of West Virginia. Northeastern Naturalist 18:95–106.

Johnson, L.E., and J.S. Johnson. 2024. Preference for hibernacula microclimates varies among 3 bat species susceptible to white-nose syndrome. Journal of Mammalogy 105:1022–1031.

Kalcounis, M.C., and R.M. Brigham. 1995. Intraspecific variation in wing loading affects habitat use by Little Brown Bats (*Myotis lucifugus*). Canadian Journal of Zoology 73:89–95.

Kalcounis, M.C., and R.M. Brigham. 1998. Secondary use of aspen cavities by tree-roosting Big Brown Bats. Journal of Wildlife Management 62:603–611.

Kalda, O., R. Kalda, and J. Liira. 2015. Multi-scale ecology of insectivorous bats in agricultural landscapes. Agriculture, Ecosystems and Environment 199:105–113.

Keeley, B., and M.D. Tuttle. 1999. Bats in American bridges. Bat Conservation International, Resource Publication 4:1–6.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263.

Kramer, A.M., C.S. Teitelbaum, A. Griffin, and J.M. Drake. 2019. Multiscale model of regional population decline in Little Brown Bats due to white-nose syndrome. Ecology and Evolution 9:8639–8651.

Krauel, J.J., and G. LeBuhn. 2016. Patterns of bat distribution and foraging activity in a highly urbanized temperate environment. PLoS ONE 11(12). e0168927.

Kunz, T.H. 1971. Reproduction of some Vespertilionid bats in central Iowa. American Midland Naturalist 86:477–486.

Kunz, T.H., E. Braun de Torrez, D. Bauer, T. Lobova, and T.H. Fleming. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223:1–38.

Kurta, A., G.G.Auteri, J.E. Hofmann, J.M. Mengelkoch, J.P. White, J.O. Whitaker, Jr., T. Cooley, and J. Melotti. 2018. Influence of a large lake on the winter range of a small mammal: Lake Michigan and the Silver-haired Bat (*Lasionycteris noctivagans*). *Diversity 10*(2):24. https://doi.org/10.3390/d10020024. Accessed 10 February 2025.

Lemieux-Labonté, V., N.A.S.-Y. Dorville, C.K.R. Willis, and F.-J. Lapointe. 2020. Antifungal potential of the skin microbiota of hibernating Big Brown Bats (*Eptesicus fuscus*) infected with the causal agent of white-nose syndrome. Frontiers in Microbiology 11:1776.

Lilley, T.M., J.S. Johnson, L. Ruokolainen, E.J. Rogers, C.A. Wilson, S.M. Schell, K.A. Field, and D.A.M. Reeder. 2016. White-nose syndrome survivors do not exhibit frequent arousals associated with *Pseudogymnoascus destructans* infection. Frontiers in Zoology 13:1–8.

Linsley, J.H. 1842. A Catalogue of the Mammalia of Connecticut, arranged according to their natural families; Furnished for the Yale Natural History Society. American Journal of Science and Arts 43:345–354.

Lowry, H., A. Lill, and B.B.M. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88:537–549.

Mackey, R.L., and R.M.R. Barclay. 1989. The influence of physical clutter and noise on the activity of bats over water. Canadian Journal of Zoology 67:1167–1170.

McGuire, L.P., C.G. Guglielmo, S.A. Mackenzie, and P.D. Taylor. 2012. Migratory stopover in the long-distance migrant Silver-haired Bat, *Lasionycteris noctivagans*. Journal of Animal Ecology 81:377–385.

Metzler, K.J., and R.W. Tiner, Jr. 1992. Wetlands of Connecticut. DEP Maps and Publication, Hartford, CT. 44–64 pp.

Moore, M.S., K.A. Field, M.J. Behr, G.G. Turner, M.E. Furze, D.W.F. Stern, P.R. Allegra, S.A. Bouboulis, C.D. Mustante, M.E. Vodzak Biron, M.B. Meierhofer, W.F. Frick, J.T. Foster, D. Howell, J.A. Kath, A. Kurta, G. Nordquist, J.S. Johnson, T.M. Lilley, B.W. Barrett, D.M. Reeder. 2017. Energy conserving thermoregulatory patterns and lower disease severity in a bat resistant to the impacts of white-nose syndrome. Journal of Comparative Physiology B 188:163–176.

Moosman, P.R., D.P. Warner, R.H. Hendren, and M.J. Hosler. 2015. Potential for monitoring Eastern Small-footed Bats on talus slopes. Northeastern Naturalist 22:NENHC1–13.

Moretto, L., and C.M. Francis. 2017. What factors limit bat abundance and diversity in temperate, North American urban environments? Journal of Urban Ecology 3:1–9.

Morningstar, D.E., C.V. Robinson, S. Shokralla, and M. Hajibabaei. 2019. Interspecific competition in bats and diet shifts in response to white-nose syndrome. Ecosphere 10:e02916. 10.1002/ecs2.2916.

Moss, C.F., C. Chiu, and A. Surlykke. 2011. Adaptive vocal behavior drives perception by echolocation in bats. Current Opinion in Neurobiology 21:645–652.

Oksanen, J., F. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, R. O'Hara, G. Simpson, P. Solymos, M. Stevens, E. Szoecs, and H. Wagner. 2018. vegan: Community ecology package. Available online at https://cran.r-project.org/package=vegan.

Patriquin, K.J., and R.M.R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

Peixoto, F.P., P.H.P. Braga, and P. Mendes. 2018. A synthesis of ecological and evolutionary determinants of bat diversity across spatial scales. BMC Ecology 18:18.

Procheş, Ş. 2005. The world's biogeographical regions: Cluster analyses based on bat distributions. Journal of Biogeography 32:607–614.

Rainho, A., and J.M. Palmeirim. 2011. The importance of distance to resources in the spatial modelling of bat foraging habitat. PLoS ONE 6(4):e19227.

Rodhouse, T.J., K.T. Vierling, and K.M. Irvine. 2011. A practical sampling design for acoustic surveys of bats. Journal of Wildlife Management 75:1094–1102.

Russo, D., and L. Ancillotto. 2015. Sensitivity of bats to urbanization: A review. Mammalian Biology 80:205–212.

Schielzeth, H., N.J. Dingemanse, S. Nakagawa, D.F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N.A. Dochtermann, L.Z. Garamszegi, and Y.G. Araya-Ajoy. 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. Methods in Ecology and Evolution 11:1141–1152.

Sedgeley, J.A., and C.F.J. O'Donnell. 1999. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. Biological Conservation 88:261–276.

Seewagen, C.L., and A.M. Adams. 2021. Turning to the dark side: LED light at night alters the activity and species composition of a foraging bat assemblage in the northeastern United States. Ecology and Evolution 11:5635–5645.

Simonis, M.C., L.K. Hartzler, J. Campbell, T.C. Carter, L.N. Cooper, K. Cross, K. Etchison, T. Hemberger, R.A. King, R.J. Reynolds, Y. Samar, M.R. Scafini, S. Stankavich, G.G. Turner, and M.A. Rúa. 2023. Long-term spring through fall capture data of *Eptesicus fuscus* in the eastern USA before and after white-nose syndrome. Data in Brief 49:109353.

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.

Skog, N. 2021. Bats in urban Sweden: A multiple regression analysis of bats' relationship to urbanization. M.S. Thesis. Södertörn University, Huddinge, Sweden. 31 pp.

Sleep, D.J.H., and R.M. Brigham. 2003. An experimental test of clutter tolerance in bats. Journal of Mammalogy 84:216–224.

Tablado, Z., and L. Jenni. 2017. Determinants of uncertainty in wildlife responses to human disturbance: Modulators of wildlife response to recreation. Biological Reviews 92:216–233.

Treitler, J.T., O. Heim, M. Tschapka, and K. Jung. 2016. The effect of local land use and loss of forests on bats and nocturnal insects. Ecology and Evolution 6:4289–4297.

U.S. Fish and Wildlife Service (USFWS). 2023. Endangered and threatened wildlife and plants; Endangered species status for northern long-eared bat; Delay of effective date. Available online at https://www.federalregister.gov/documents/2023/01/26/2023-01656/endangered-and-threatened-wildlife-and-plants-endangered-species-status-for-northern-long-eared-bat. Accessed July 16, 2024.

U.S. Fish and Wildlife Service (USFWS). 2024. National domestic listing workplan. Available online at https://www.fws.gov/sites/default/files/documents/2024-05/national-domestic-listing-workplan-2024.pdf. Accessed July 16, 2024.

Walters, B.L., C.M. Ritzi, D.W. Sparks, and J.O. Whitaker, Jr. 2007. Foraging behavior of Eastern Red Bats (*Lasiurus borealis*) at an urban-rural interface. American Midland Naturalist 157:365–373.

Wheeler, A.R., K.A. Fulton, J.E. Gaudette, R.A. Simmons, I. Matsuo, and J.A. Simmons. 2016. Echolocating Big Brown Bats, *Eptesicus fuscus*, modulate pulse intervals to overcome range ambiguity in cluttered surroundings. Frontiers in Behavioral Neuroscience 10:125

Wilcox, A., L. Warnecke, J.M. Turner, L.P. McGuire, J.W. Jameson, V. Misra, T.C. Bollinger, and C.K.R. Willis. 2014. Behaviour of hibernating Little Brown Bats experimentally inoculated with the pathogen that causes white-nose syndrome. Animal Behaviour 88:157–164.

Willis, C.K.R., and R.M. Brigham. 2004. Roost switching, roost sharing and social cohesion: Forest-dwelling Big Brown Bats, *Eptesicus fuscus*, conform to the fission-fusion model. Animal Behaviour 68:495–505.

Willis, C.K.R., and R.M. Brigham. 2005. Physiological and ecological aspects of roost selection by reproductive female Hoary Bats (*Lasiurus cinereus*). Journal of Mammalogy 86:85–94.

Willis, C.K.R., K.A. Kolar, A.L. Karst, M.C. Kalcounis-Rueppell, and R.M. Brigham. 2003. Medium- and long-term reuse of trembling aspen cavities as roosts by Big Brown Bats (*Eptesicus fuscus*). Acta Chiropterologica 5:85–90.

WNSRT (White Nose Syndrome Response Team). 2024. Bats affected by WNS. Available online at https://whitenosesyndrome.org/static-page/bats-affected-by-wns. Accessed 16 July 2024.