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A small-scale response of urban bat activity to tree cover

Lauren Moretto[1] · Lenore Fahrig[1] · Adam C. Smith[2] · Charles M. Francis[2]

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Abstract
Bats in urban areas depend on trees, and bat activity increases with tree cover. To effectively manage bat habitat in cities, it is important to know the distance to which tree cover most strongly influences bats (i.e., the 'scale of effect'). The aim of this study was to estimate the scale of effect of tree cover on bats in Toronto, Canada. To achieve this, we measured bat activity at 52 sampling sites across the city. We then examined the relationships between bat activity and percent tree cover measured within each of 19 scales, 0.025 to 3.5 km in radius, surrounding each sampling site. We found that the scale of effect of percent tree cover on total bat and individual species activity ranged from 0.025 to 0.25 km among species. Our results suggest that adding or removing urban trees influences bats up to 0.25 km away. Urban tree management decisions should consider the impacts to bats beyond the site of management and within the surrounding landscape of a 250 m-radius scale.

Keywords Bats · Chiroptera · Cities · Tree canopy · Habitat management · Urbanization

Introduction

Areas of primarily natural or semi-natural land cover, even very small ones, provide habitat for wildlife in urban areas, containing resources for feeding, nesting, and refuge from human disturbance (Dixon 2012; Pardee and Philpott 2014; Ferenec et al. 2014; Smith et al. 2014). Although large parks, including ravine systems or woodlots, contain the greatest biodiversity in urban environments (Blair and Launer 1997; Cornelis and Hermy 2004; Avila-Flores and Fenton 2005; Beninde et al. 2015), natural habitat need not be a large, contiguous area to be important. In an urban area, a collection of many small areas of natural habitat can be just as valuable to wildlife as a single large area of the same total size (Fahrig 2017). For example, Smith et al. (2014) found that bird diversity responded as strongly to small residential green spaces (e.g., backyards) as to larger non-residential green spaces, on a per-area basis. In other words, the summed effect of a large number of small green spaces was equivalent to the effect of a large green space of the same total area.

Since areas of natural habitat in urban environments are often small, many species access habitat over a large area to obtain sufficient resources. For example, white-striped free-tailed bat (*Tadarida australis*) in Brisbane, Australia commute nightly between day roosts in tree hollows to feeding areas above floodplains and communal night roosts (Rhodes and Catterall 2008). Big brown bat (*Eptesicus fuscus*) in urban Georgia rely on parcels of forest and various buildings or trees to provide areas for foraging and roosting, respectively (Menzel et al. 2001). The network of nesting sites and foraging grounds between which birds and mammals commute in urban areas often changes seasonally due to changing resource needs or availability. This increases the total area of habitat upon which they rely throughout the year (Law and Dickman 1998). For instance, Menzel et al. (2001) observed that female big brown bat in Georgia foraged in pine forests close to building roosts during parturition, but foraged in hardwood forests with higher prey densities but farther from roosts during lactation to satisfy increased energetic demands. Furthermore, the use of multiple areas of natural habitat by urban species means that adding or removing habitat in an urban landscape may influence species some distance away. For instance, Clark et al. (2007) found that the total amount of green space and number of flowering plants within the surrounding 1 km in urban environments positively affected

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✉ Lauren Moretto
laurenmoretto@hotmail.com

1 Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

2 Canadian Wildlife Service, Environment and Climate Change Canada, National Wildlife Research Centre, Ottawa, ON K1A 0H3, Canada

butterfly species richness. Similarly, Melles et al. (2003) found that urban green space influenced ground- and shrub-nesting bird species occurrence up to 1 km away.

Tree cover comprises a large proportion of the natural habitat in urban environments and is important to urban species, providing food, shelter, and other resources (Dixon 2012; Pardee and Philpott 2014; Ferenec et al. 2014; Smith et al. 2014). Furthermore, knowing the distance to which tree cover influences urban species is informative for management. For example, Pardee and Philpott (2014) found that the total amount of tree cover in the surrounding 500 m and 2 km of backyard gardens positively influenced the abundance of cavity- and ground-nesting bee species, respectively. Similarly, Ferenec et al. (2014) found that species richness of birds at sampling sites was positively related to the proportion of tree cover within 500 m of those sites.

Many urban bats rely on trees to satisfy their requirements for roosts and foraging (van Zyll de Jong 1985). These trees are found throughout cities, in parks, along streets, and on private property such as in front and back yards. Bats move between trees in cities because they often forage some distance away from their roosts (Duchamp et al. 2004; Duchamp and Swihart 2008; Dixon 2012). The resource requirements of bats also change seasonally, so they may rely on different trees throughout the year (Law and Dickman 1998). While a tree in the yard of a residential property may provide an adequate summer roost, a tree in a parcel of forest with less ambient disturbance may be preferred for hibernation. Even bats that roost in buildings commute to trees to forage around their canopies, and may also rely on them to provide an alternate roosting space (Evelyn et al. 2004).

To maintain bat populations in urban areas, it is important to know the spatial extent over which tree cover in the surrounding landscape influences bat activity at a site, that is, the 'scale of effect' (Jackson and Fahrig 2012). When possible, estimating species-specific scales of effect of tree cover can also provide valuable information for management, considering differences between species in life histories and home range sizes (van Zyll de Jong 1985). However, the scale of effect of tree cover on temperate urban bats is not well known. Landscape-scale studies on urban bats often select only a single landscape scale for study, leading to uncertainty that the selected scale is in fact the scale of effect (e.g., Duchamp and Swihart 2008; Threlfall et al. 2012). Some previous studies suggest scales of effect between 0.1 and 3 km for urban bats, but they only compared a small number of scales (i.e., three or fewer; e.g., Dixon 2012; Bazelman 2016; Gallo et al. 2018). Although one European study (Lintott 2015) measured habitat features within seven landscape scales, the scale of effect was not estimated. To date, Fabianek et al. (2011) and Ethier and Fahrig (2011) provide the most precise estimates of the scale of effect for bats in North America, by measuring the relationship between bat activity and land cover within five or more scales. In Montréal, Fabianek et al. (2011) found a 0.1 km scale of effect of forest and non-woody plant cover on urban bats, which was also the smallest landscape scale that they examined. In agricultural eastern Ontario, Ethier and Fahrig (2011) found scales of effect of forest amount on bats of 1 – 5 km, depending on the species. The goal of this study was to estimate the scale of effect of tree cover on bat activity in Toronto, Canada's largest city, to quantify the spatial scale at which bat habitat management may be most effective.

Methods

We estimated the scale of effect of tree cover on total bat activity and on the activity of individual species using bat recorders at 52 sampling sites across Toronto. We measured the percent tree cover within 19 landscape scales with radii from 0.025 – 3.5 km that were centred on each sampling site. We then modelled the relationship between bat activity and percent tree cover at each spatial extent. We estimated the scale of effect as the radius with both a strong modelled relationship between bat activity and percent tree cover and a strong model goodness-of-fit measure.

Tree cover as bat habitat

We defined bat habitat as the area covered by tree canopies of $2m^2$ or larger. Trees of this size are used as habitat by all seven bat species previously documented in Toronto. Some species roost among the foliage [eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), and tri-colored bat (*Perimyotis subflavus*)], while others roost in cavities or under loose bark [big brown bat (*Eptesicus fuscus*), little brown myotis (*Myotis lucifigus*), northern myotis (*Myotis septentrionalis*), and silver-haired bat (*Lasionycteris noctivagans*) (van Zyll de Jong 1985)]. All species also forage for insects either among trees or above the tree canopy (van Zyll de Jong 1985). Measuring tree cover of trees with a canopy of at least $2m^2$ excluded isolated saplings that we postulated would be too small to provide roosting space for bats (van Zyll de Jong 1985; Kalcounis-Rüppell et al. 2005).

Buildings can be considered habitat for bat species that also roost in artificial structures [big brown bat, little brown myotis, northern myotis, and silver-haired bat (van Zyll de Jong 1985; Whitaker et al. 2006; Geluso and Mink 2009)]. However, our objective was to estimate the scale of effect of tree cover on bats. Therefore, we controlled for percent building cover in site selection (below). Depending on model fit, we also added an additional statistical control for percent building cover to the models of species that roost in buildings.

Sampling site selection and measurement of percent tree cover

The overall objective of site selection was to simultaneously maximize the total number of sampling sites and the range of percent tree cover in the surrounding landscapes across sampling sites, at each of the 19 scales. To achieve this, we first mapped percent tree cover in Toronto using the city's Forest and Land Cover raster dataset (City of Toronto 2009) at a 2 m resolution. We then examined the range in percent tree cover across the city by conducting a moving window analysis in ArcGIS 10.3.1 (ESRI 2015), which calculated percent tree cover around each pixel in the raster dataset for a given window size. For this step, we used a circular window with a radius of 3.5 km, the largest landscape scale we considered. To maximize the range of percent tree cover across sites, we first identified pixels (potential sampling sites) having the highest and lowest percent tree cover in the surrounding 3.5 km-radius landscapes. We considered only pixels in residential backyards with similar local characteristics (i.e., unpaved, with some trees, and without large, artificial structures, including swimming pools). We then verified that these potential sampling sites also maximized the range of percent tree cover at smaller scales. To achieve this, we performed moving window analyses at 1 km and 2 km-radius landscape scales.

The next step in sampling site selection was to add potential sites with intermediate percent tree cover. These were selected such that the number of sites in total was maximized, within the constraint that all selected sites were at least 1.8 km apart to limit spatial autocorrelation in the bat responses. Although other species in our study area are known to travel longer distances while foraging, 1.8 km is the mean commuting distance of big brown bat, which is the most common species in our study area (Brigham 1991). Following this, we adjusted site locations at a fine scale in ArcGIS to ensure that all sites were at least 200 m from major arterial roads and highways. This was to minimize the negative influences of major roads, heavy traffic, and traffic noise on bat activity immediately surrounding the sampling sites (Bennett and Zurcher 2013; Kitzes and Merenlender 2014).

Lastly, we eliminated some sampling sites and fine-tuned the position of the remaining sampling sites in ArcGIS to limit the range in percent building cover in the surrounding landscapes across sampling sites, thus controlling for building roost availability. This resulted in the elimination of thousands of potential sites, since site selection was originally based on the percent tree cover surrounding pixels and there were thousands of pixels in the raster dataset. Older buildings with larger footprints are commonly used by bats for roosting (Soper and Fenton 2007; Neubaum et al. 2007). Our goal was to limit the range in availability of these buildings, but there was no available dataset for building age across the City of Toronto. However, Li and Wilkins (2014) documented a positive relationship between overall building density and bat activity. Therefore, we used percent building cover as a proxy of building roost availability, mapped with the Toronto Building Outlines shapefile (City of Toronto 2014a). We measured percent building cover by converting the building outline polygons into 2 m resolution raster datasets and conducting a moving window analysis with a 3.5 km-radius, circular window to examine the range in percent building cover across the city. We adjusted the sampling site locations such that the surrounding landscapes had a narrow range in building cover, from 14 to 19% of the total landscape, at the 3.5 km-radius scale. This range in percent building cover prevented site placement in the downtown urban core, where building density is very high, and in non-urban areas, such as an agricultural area in the east end of the city.

The site selection process resulted in a final set of 52 sampling sites (Fig. 1), dispersed across the City of Toronto with a wide range in percent tree cover (15–49%) and a narrow range in percent building cover (14–19%) in the surrounding 3.5 km-radius landscapes. We visited each site to verify the similarity among sites in local characteristics and to obtain the approval of homeowners to set up sampling equipment.

After confirming the sampling site locations, we measured percent tree cover in 19 circular landscape scales in ArcGIS, centered around each site (i.e., 0.025, 0.05, 0.1, 0.2, 0.25, 0.5, 0.75, 1, 1.25, 1.5, 1.75, 2, 2.25, 2.5, 2.75, 3, 3.25, and 3.5 km; Fig. 2a, b) using the Forest and Land Cover raster dataset (City of Toronto 2009). To measure percent tree cover around each site at each landscape scale, we divided the measured number of tree cover pixels in a circular landscape surrounding each site by the maximum possible number of pixels within that landscape scale, and multiplied this value by 100. We also verified that the range of percent tree cover across sites was similar among the 19 scales by using a boxplot to visually compare the ranges among scales (Fig. 1S).

Bat surveys

We surveyed bat activity at each of the 52 sampling sites by recording bat calls using Wildlife Acoustic SM2+ recorders with SMX-U1 microphones. Calls were recorded between May 30 and August 8, 2017, the period of summer residency for Ontario bat species (van Zyll de Jong 1985). At each site, we positioned one recorder two meters above the ground with its microphone angled 45° downwards to protect the microphones from potential rain. We recorded bat calls continuously from sunset to sunrise over two, non-consecutive nights per site.

To ensure that the date of sampling did not confound the effects of tree cover, we sampled bat activity at four sampling sites per night that varied in percent tree cover in the surrounding landscapes. The combination of four sites sampled each night contained one site with low percent tree cover, one site with high percent tree cover, and two sites with intermediate

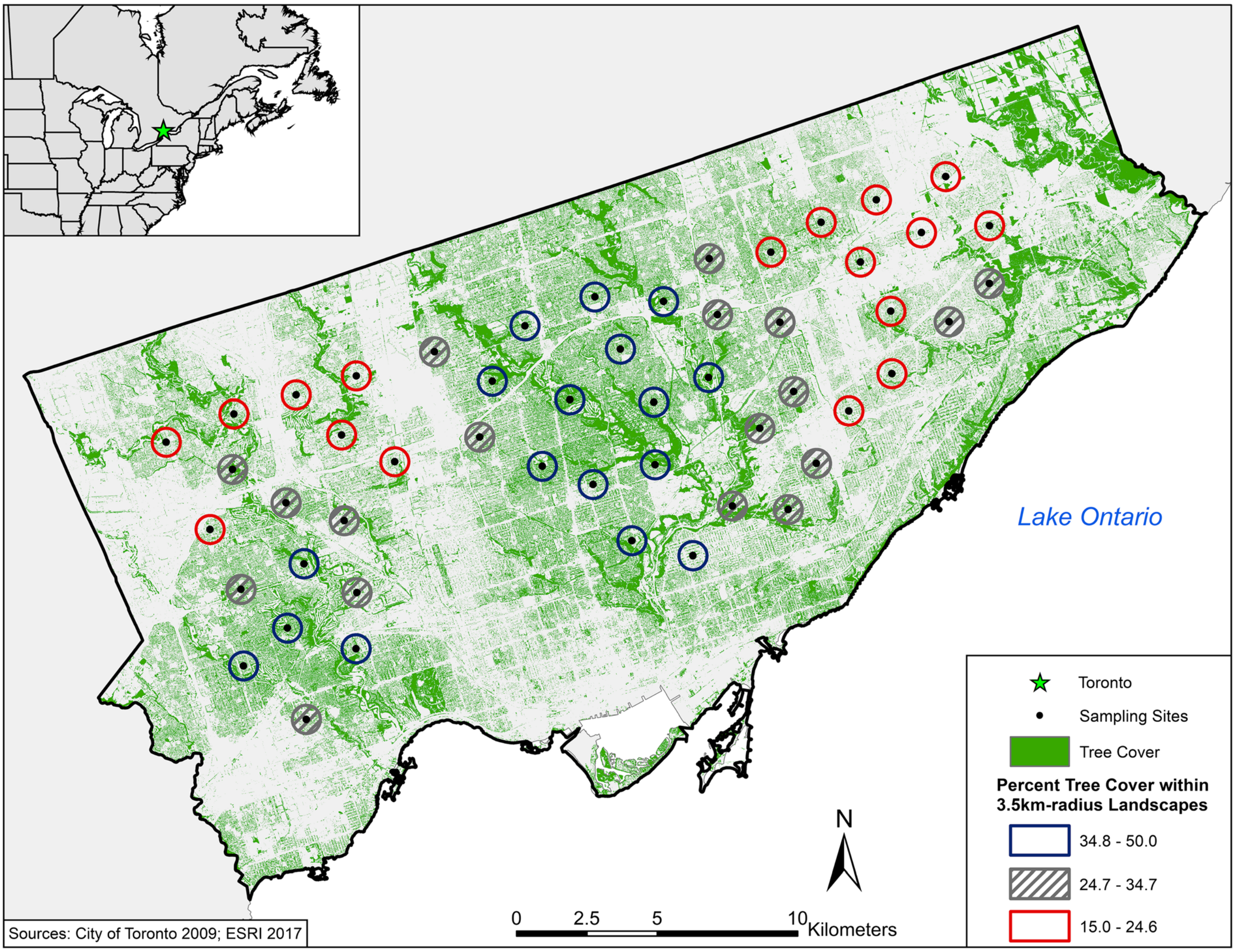

Fig. 1 Locations of 52 bat sampling sites in Toronto, Canada. Sampling sites are indicated as black points. Circles around each site are not to scale, but represent percent tree cover in the surrounding, circular landscape with a 3.5 km radius. Note that percent tree cover was analyzed as a continuous variable in models

percent tree cover at both the 1 km and 3.5 km-radius landscape scales (Fig. 2c–e). After all sites were sampled once, we began a second round of sampling on June 21, 2017. We ensured that each night's combination of sites visited in the second round was different from that of the first round.

Potential confounding variables

The main objective of the study was to identify the scale of effect of tree cover on bat activity in an urban environment. However, bat activity around a recorder is likely to be influenced by variables other than tree cover, which might obscure the relationship between bat activity and surrounding tree cover. We controlled for this by collecting data only during good weather (i.e., no rain, average wind speed below 20 km/h, average wind gusts below 25 km/h, and average nightly temperature above 9 °C), and by ensuring minimal human disturbance during data collection (i.e., avoiding sampling overnight on Fridays, Saturdays, and holidays). At each site, we also deployed one Onset HOBO Pendant Temperature and Light Data Logger and one Digi-Sense Data Logging Light Meter to measure temperature (°C) and light intensity (lux) at 10 min increments during the recording period.

Although we had tried to minimize variation in the surrounding building cover among sampling sites during site selection, there was a greater range in percent building cover at smaller landscape scales than at larger landscape scales (Fig. 1S). Percent building cover was also negatively correlated ($r = 0$ to -0.65) with percent tree cover (Fig. 2S). Because both building cover and tree cover may be habitat for many bat species, and they were negatively correlated in our sample, we included percent building cover to avoid biasing our estimate of the effect of tree cover (i.e., suppressor effects, see Smith et al. 2009).

Quantifying bat activity and identifying bat species

Bat activity was indexed as the number of bat passes per sampling site. A bat pass is a grouping of echolocation pulses

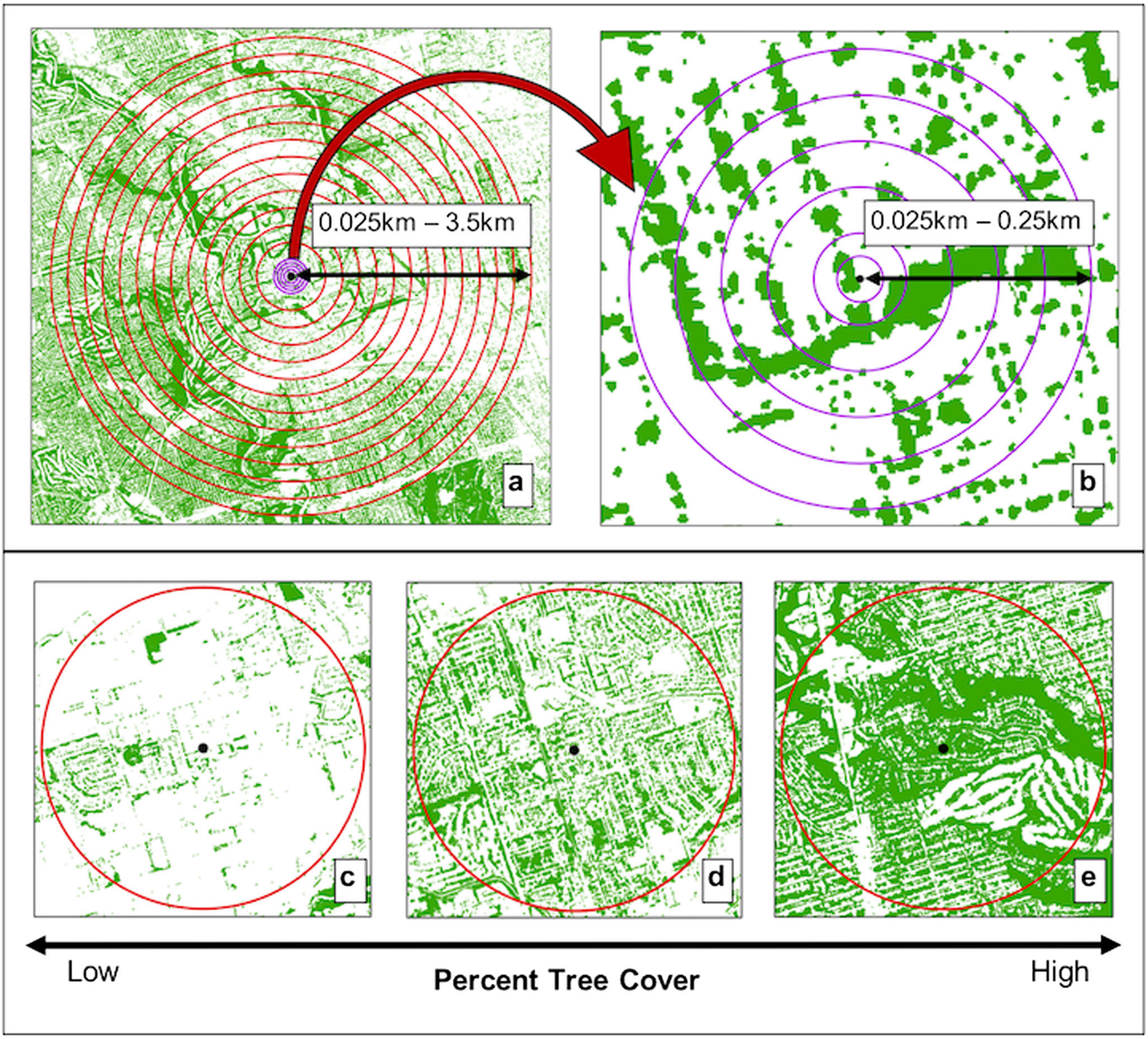

Fig. 2 (**a**) An example sampling site surrounded by the 19 circular landscapes in which percent tree cover was measured. Landscapes ranged between 0.025 km and 3.5 km in radius. (**b**) A closeup of the smallest landscape scales in **(a)** measuring between 0.025 km and 0.25 km in radius. Examples of landscapes with **(c)** low, **(d)** medium, and **(e)** high percent tree cover within 1 km of the sampling site, and less than 20% of tree cover in parks

separated by at least one second of silence from the next pulse (Coleman and Barclay 2012; Griffin et al. 1960; see supplementary material Fig. 3S for more information).

Bats can be identified to species using the acoustic characteristics of the echolocation pulses. To identify each pass to species, we compared the results of two identification software programs to account for discrepancies in their identification algorithms (Lemen et al. 2015), and reviewed each pass manually to confirm the identity. These were the Bats of North America 3.1.0 classifier package in Kaleidoscope Pro 3.1.1. (Wildlife Acoustics 2015) and a quadratic discriminate function analysis model (QDFA) created by Ethier and Fahrig (2011), which used reference calls from the Fenton Laboratory (Hooton and Adams, unpublished data, University of Western Ontario). We included only the seven species of bats that have been documented in Toronto as possible outcomes for each program [i.e., big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), little brown myotis (*Myotis lucifugus*), northern myotis (*Myotis septentrionalis*), and tri-colored bat (*Perimyotis subflavus*)].

We analysed bat activity for all bats combined, as tree cover is used by all of the species in our study, and the aim of our study was to provide information about the scale at which tree cover might be managed for bats. The activity of all species combined is also a relevant measure for bat conservation, as it may be an index of arthropod suppression by bats, an important ecosystem service that they provide (Kunz et al. 2011). In addition, by using total bat activity we were able to include unidentified passes in the analysis. We also analysed the activity of two individual species (big brown bat and eastern red bat), and a species group containing passes of hoary bat and silver-haired bat. We were conservative in our identification of bat passes to species, and did not identify a pass unless we were confident in its identity. We combined hoary bat and silver-haired bat because we had difficulty discriminating their passes in our recordings, as they were often not confidently identified by the identification software programs (A. Adams, personal communication). We note that they have often been grouped in previous studies due to similar features of their low frequency calls (Humbolt State University Bat Lab 2011; Baerwald and Barclay 2011; Nagorsen et al. 2014), and both species commonly use trees as roosts (van Zyll de Jong 1985). Due to the low numbers of calls identified to little brown myotis, northern myotis, and tri-colored bat, these species were only included in the analyses of total bat activity.

Statistical analysis

We used generalized linear mixed models (GLMM) to estimate the relationship between each of the four bat activity response variables (total bat activity and activity of each of the species and species group) and percent tree cover measured within each of the 19 spatial scales. Therefore, for each bat response variable there were 19 models, one for each landscape scale. Since bat activity was surveyed twice at each sampling site, models contained a random effect of site, to account for repeated sampling within sites. Each model also contained the potential confounding effects of standardized mean nightly temperature (°C) and Julian date. The light-intensity loggers did not register any variance in light intensity (lux) among sites and nights, so lux was not included in any models. We included percent building cover at the 1 km-radius landscape scale in the GLMM as a statistical control based on both model fit and the roosting behaviour of each species. Firstly, we controlled for percent building cover at the 1 km-radius scale because the AIC values of the 19 models with building cover included at this scale were lower overall than those with percent building cover included at other scales (e.g., 0.5 km or 1.5 km). Then, for each bat activity response variable, we compared AIC values of the 19 models with and without the control for percent building cover at the 1 km scale. AIC values were lower in models without percent building cover for eastern red bat, a species that does not roost in buildings, so percent building cover was not included in further analyses for this species. We modeled bat activity with a negative binomial error and a log link function, based on the distributions of the response variables in histograms and residual plots.

Then, we estimated the scale of effect of percent tree cover for each response variable by evaluating both the model fit (AIC values) and the strength of the relationship between a bat activity response variable and percent tree cover (regression coefficients) of each model. AIC values were examined first and indicated the scales at which the data best fit the model. All scales with a ΔAIC of 2 or less were identified as important scales (Burnham and Anderson 2004), but the scale with the largest regression coefficient was deemed the scale of effect. We examined the regression coefficient to verify that the selected model also showed a strong relationship between a bat activity response variable and percent tree cover. We used Moran's *I* tests to determine whether the residuals of the models were spatially autocorrelated. All analyses were conducted in R version 3.4.1. (R Core Team 2017), using the MASS, glmmADMB (Bolker et al. 2012), ape (Paradis et al. 2017), psych (Revelle 2017), ggplot2 (Wickham and Chang 2016), dplyr (Wickham et al. 2017), and corrplot (Wei et al. 2017) packages.

Finally, we evaluated the importance of park trees to total bat activity at the scale of effect of percent tree cover. To achieve this, we used Toronto's Zoning By-law layer (City of Toronto 2014b) to measure the percent tree cover within parks around each sampling site at the scale of effect in ArcGIS, and correlated this to total bat activity.

Results

We recorded 7593 bat passes. Forty-nine percent of these were identified as big brown bat (*Eptesicus fuscus*), 6% as eastern red bat (*Lasiurus borealis*), 21% as hoary bat (*Lasiurus cinereus*)/ silver-haired bat (*Lasionycteris noctivagans*), and 1% as little brown myotis (*Myotis lucifugus*)/ northern myotis (*Myotis septentrionalis*)/ tri-colored bat (*Perimyotis subflavus*). Twenty-three percent of passes (i.e., 1741 passes) could not be identified to species or species group. The average number of bat passes per sampling site was 73 (range 7–296), with an average of 8.1 passes per hour (range 0.8–31.6). Including Myotis species and tri-colored bat, on average, there were 3 species and/or species groups per site (range 1–4).

Total bat activity most strongly related to percent tree cover within the 0.2 km-radius landscape scale, though tree cover was also important at the 0.15 and 0.25 km-radius scales (Fig. 3a, Table 1, 1S). Total bat activity increased by 44% for each 10% increase in tree cover, with the predicted total number of passes ranging from 22 to 287. Including site-level random effects and percent building cover at the 1 km scale in the models strengthened the relationship between total bat activity and percent tree cover at this scale of effect (i.e., 0.2 km) when compared to this relationship without these variables included (Fig. 4). The scale of effect of percent tree cover differed among species/ species groups. Big brown bat and hoary

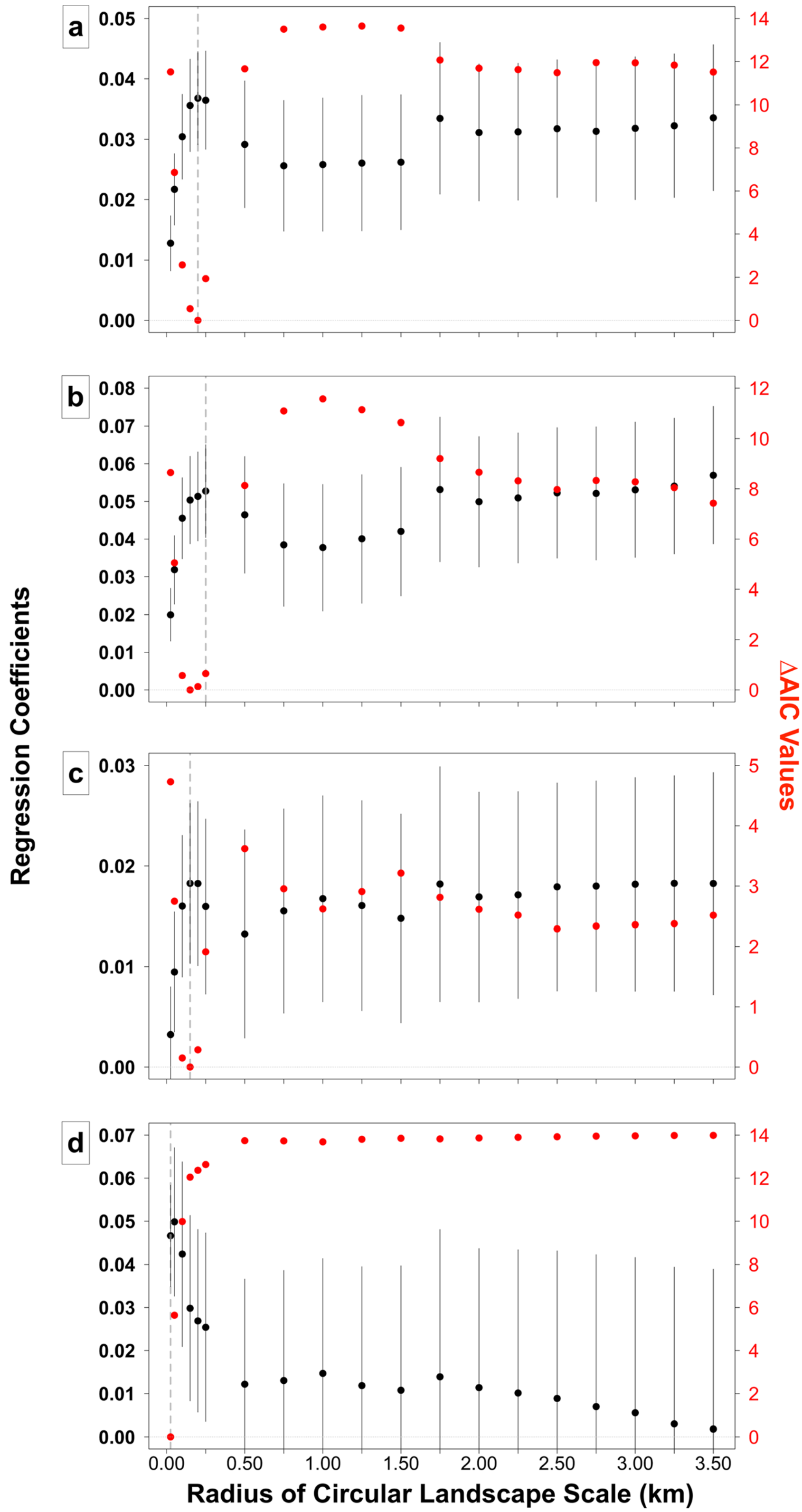

Fig. 3 Regression coefficients (black dots) ± SE (vertical lines) and ΔAIC values (red dots) from generalized linear mixed models of the relationship between the percent tree cover in landscapes and **(a)** total bat, **(b)** big brown bat, **(c)** hoary bat/ silver-haired bat, and **(d)** eastern red bat activity. Bat activity was measured at 52 sampling sites distributed across Toronto, Canada. Percent tree cover was measured within each of 19 circular landscape scales with radii between 0.025 km and 3.5 km surrounding the sampling sites. The scale of effect (vertical dashed line) was selected based on the model AIC value and regression coefficient of percent tree cover

bat/ silver-haired bat showed strongest relationships at 0.25 km and 0.15 km, respectively (Fig. 3b, c), although tree cover was generally important between 0.1 and 0.25 km-radius landscapes for these species. Eastern red bat had a smaller scale of effect at 0.025 km (Fig. 3d), the only landscape scale at which tree cover was important to this species. There was also a positive effect of percent building cover within a 1 km-radius landscape on total bat activity, big brown bat, and hoary

Table 1 AIC, ΔAIC, relative likelihood, and AIC weights from the five best-fitting generalized linear mixed models (GLMM) examining the relationship between percent tree cover measured within a landscape scale, specified below, and **(a)** total bat activity and **(b – d)** species-specific activity. For each bat activity response variable, models are ranked by ΔAIC, and all values are bolded for important models (i.e., GLMM with a ΔAIC of 2 or less). A * indicates the scale with the top model, designated the scale of effect. The ΔAIC, relative likelihoods, and AIC weights reflect the best-fitting model with respect to inclusion of the building cover control (i.e., with percent building cover at 1 km included as a statistical control for total bat activity, big brown bat, and hoary bat/ silver-haired bat, and without percent building cover included for eastern red bat). Furthermore, AIC values are shown for GLMM without a statistical control for percent building cover, and with a statistical control for percent building cover included separately in models at the 0.5 km, 1 km, or 1.5 km-radius landscape scales

Bat activity response variable	Landscape scale (km)	ΔAIC	Relative likelihood	AIC weight	AIC			
					No building control	0.5 km building	1 km building control	1.5 km building control
(a) total bat activity	**0.2***	**0**	**1.000**	**0.403**	**1081.324**	**1075.964**	**1064.656**	**1070.504**
	0.15	**0.542**	**0.763**	**0.307**	**1080.198**	**1075.312**	**1065.198**	**1069.844**
	0.25	**1.938**	**0.379**	**0.153**	**1082.018**	**1077.028**	**1066.594**	**1072.106**
	0.1	2.576	0.276	0.111	1078.478	1075.604	1067.232	1068.978
	0.05	6.860	0.032	0.013	1077.898	1077.196	1071.516	1071.632
(b) big brown bat	**0.15**	**0**	**1.000**	**0.273**	**906.332**	**903.318**	**894.554**	**899.948**
	0.2	**0.132**	**0.936**	**0.255**	**907.682**	**904.442**	**894.686**	**900.956**
	0.1	**0.574**	**0.751**	**0.205**	**904.296**	**902.740**	**895.128**	**898.280**
	0.25*	**0.652**	**0.722**	**0.197**	**908.042**	**904.706**	**895.206**	**901.612**
	0.05	5.050	0.080	0.022	904.042	904.430	899.604	900.786
(c) hoary bat/ silver-haired bat	**0.15***	**0**	**1.000**	**0.144**	**741.356**	**737.834**	**734.710**	**736.080**
	0.1	**0.150**	**0.928**	**0.134**	**740.828**	**737.850**	**734.860**	**735.486**
	0.2	**0.286**	**0.867**	**0.125**	**741.686**	**738.438**	**734.996**	**736.602**
	0.25	**1.912**	**0.384**	**0.055**	**741.972**	**740.066**	**736.622**	**737.844**
	0.05	2.748	0.253	0.036	741.170	739.952	737.458	737.412
(d) eastern red bat	**0.025***	**0**	**1.000**	**0.921**	**383.172**	**384.746**	**385.102**	**384.716**
	0.05	5.642	0.060	0.055	388.814	389.278	390.420	389.926
	0.1	9.982	0.007	0.006	393.154	393.666	394.556	394.132
	0.15	12.044	0.002	0.002	395.216	395.932	396.772	396.558
	0.2	12.364	0.002	0.002	395.536	396.210	397.064	396.890

bat/ silver-haired bat at the scale of effect of percent tree cover for these bat activity responses (Table 1S). There was no significant spatial autocorrelation of the residuals for total bat activity, or for any species or the species group.

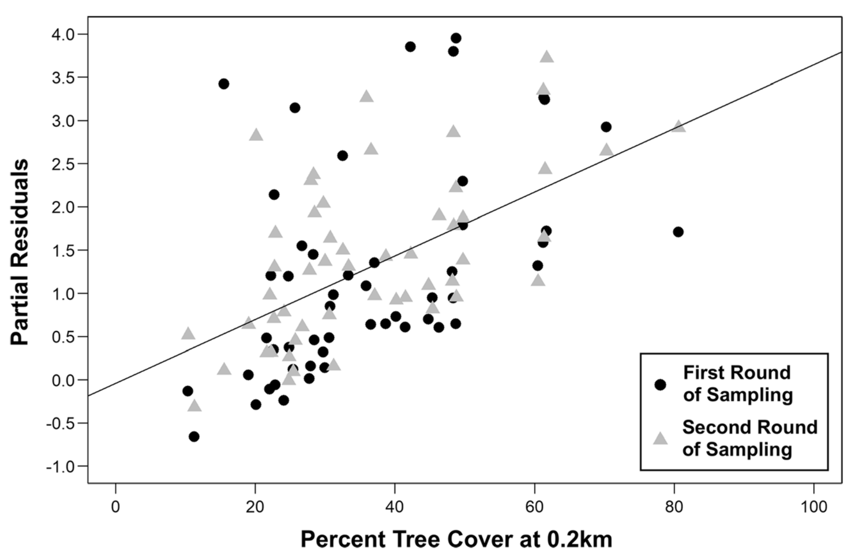

Fig. 4 Percent tree cover at the scale of effect for total bat activity, 0.2 km in relation to partial residuals from the 0.2 km generalized linear mixed model of the relationship between percent tree cover measured around each of the 52 sampling sites and total bat activity. Shapes of points indicate the round of bat sampling, and the dark, solid line is a fitted line

At the scale of effect of percent tree cover on total bat activity (0.2 km), we found that greater than 70% of tree cover was located outside of parks for 48 of 52 sampling sites, and there was no tree cover in parks around 17 of those sites. In addition, there was only a weak correlation between total bat activity and the percent tree cover within parks at the 0.2 km scale (r = 0.02).

Discussion

We found that percent tree cover most strongly influenced the activity of urban bats over a small landscape scale. Percent tree cover within 0.2 km from our sampling sites (i.e., the scale of effect) had the strongest influence on total bat activity, though tree cover was also important between 0.15 and 0.25 km. Previously documented scales of effect for temperate bats ranged from 0.1 – 5 km (Ethier and Fahrig 2011; Fabianek et al. 2011; Dixon 2012; Bazelman 2016; Gallo et al. 2018), although 0.1 km was the smallest scale measured in two of those studies (Fabianek et al. 2011; Dixon 2012).

It is possible that the small scale response of urban bats to tree cover reflects the general influence of urban environments on bat activity and life histories. Since urban infrastructure, such as major roads, heavy traffic, and artificial lighting, can disrupt the movement of bats (Russell et al. 2009; Bennett and Zurcher 2013; Moretto and Francis 2017), this could confine bat foraging activity, and reduce the scale over which tree cover influences bat activity. It is also possible that the tendency of insects to aggregate in urban environments (e.g., around trees or lights) drives localized bat foraging activity. Insectivorous bats frequently forage around insect aggregations (Müller et al. 2012), and most bats in Toronto forage within 40 m of tree canopies (Janzen and Fenton 2013). Street trees and trees on private property in cities are often spaced for aesthetics, providing ample area for insects to aggregate and bats to forage. Tree cover farther away may not be as important to bats if tree cover in the vicinity is sufficient to provide insects. Future research should evaluate how insect distributions influence the small-scale response of bats to tree cover in urban areas.

Individual species also showed small-scale responses to percent tree cover, mostly ranging between 0.1 and 0.25 km. Eastern red bat showed an even smaller-scale response to percent tree cover, with a scale of effect at 0.025 km. We speculate that the differences in scale of response to tree cover among species may relate to different uses of habitat features in urban environments. Both big brown bat and silver-haired bat roost in artificial structures (van Zyll de Jong 1985; Whitaker et al. Whitaker et al. 2006; Geluso and Mink 2009), and we found a strong, positive influence of percent building cover within 1 km of our sampling sites for these species (Table 1). These were also the species with the largest-scale responses to percent tree cover. It is possible that this larger-scale influence of tree cover reflects their use of the landscape over a larger extent, perhaps commuting between roosts in buildings and trees for foraging or alternative roosts. Eastern red bat do not roost in buildings, so it is possible their smaller scale of effect reflects a shorter commute between tree roosts and foraging grounds. Hoary bat are also tree-roosting obligates and silver-haired bat commonly roost in trees (van Zyll de Jong 1985), which may have contributed to the slightly smaller scale of effect for hoary bat/ silver-haired bat (0.15 km) in comparison to big brown bat (0.25 km). The strong influence of building cover on the activity of building-roosting species also suggests that buildings may be critical habitat features to bats in urban environments.

Although not the primary goal of this study, our results also suggest that the total urban tree cover, not just that in parks, influences bats within 0.2 km. All sampling sites in this study were in residential backyards, surrounded mostly by trees outside of parks at the 0.2 km scale (i.e., > 70% of tree cover was outside of parks for 48 of 52 sites). We found a weak correlation (r = 0.02) between total bat activity and the percent tree cover within parks at this scale. This suggests that non-park trees (i.e., street trees and trees on private property) are the main drivers of the overall positive relationship between tree cover and bat activity.

Although there are no North American studies that directly compare the importance of trees within parks and outside of parks to bats, our results are supported by other studies that have noted the importance of all local tree and vegetation cover in residential neighbourhoods to invertebrates, amphibians, birds, and other wildlife (Fernandez-Juricic 2000; Sperling and Lortie 2010; Lerman and Warren 2011; Scheffers and Paszkowski 2013; Pardee and Philpott 2014; Belaire et al. 2014; Smith et al. 2014). Conversely, one study in Vitória, Brazil that compared the influence of parks to other treed space on urban bat diversity found a much stronger effect of parks than wooded streets (Opera et al. 2009). This difference might be because most of the captured bats (92%) in their study were not insectivores, while all of the bat species in our study are insectivores. Resources for insectivorous bats are often more abundant throughout urban environments than are resources for other bats (Bredt and Uieda 1996; Silva et al. 1996). It is possible that resources for non-insectivorous bats were concentrated in urban parks in Vitória.

This study provides information useful for the management of bat habitat in cities. Firstly, the small scale responses of bats to tree cover suggests that land management decisions should consider the impacts of the addition or removal of tree cover not just at the site of addition or removal, but within approximately the surrounding two residential city blocks. To supplement our understanding of the small-scale responses of bats to tree cover, future research should examine the influence of prey distributions on bat activity in urban areas. Furthermore, while our study was not designed to evaluate the influence of building cover on bats, our finding of a strong, positive effect of building cover for two species (i.e., big brown bat and silver-haired bat) suggests that building roosts may be a limiting factor for these species. Artificial roosts could be explored for enhancing urban habitat for these species. Previous studies (e.g., Soper and Fenton 2007; Neubaum et al. 2007) have identified ideal characteristics of artificial roosts, but additional research is needed to evaluate their optimal placement and effectiveness in urban areas. Lastly, our results suggest that all urban trees, including privately-owned trees and street trees, and not just trees in parks, are important for bats. Private and public trees are often managed separately, and management of urban trees often occurs on a tree-by-tree basis (Carreiro et al. 2008). As the landscapes in our study primarily included privately-owned trees in residential neighbourhoods, this emphasizes the potential for small groups of property owners (e.g., the houses on a single residential street) to increase local bat activity. Management for bats in cities could therefore include education of property owners about the value of bats themselves and of their trees for bats, and could even include a requirement for permission to remove trees on their property, as is the case in some jurisdictions (e.g., City of Toronto by-law No. 248–2013; City of Ottawa by-law No. 2009–200).

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