Mammal diversity and metacommunity dynamics in urban green spaces: implications for urban wildlife conservation

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Abstract. As urban growth expands and natural environments fragment, it is essential to understand the ecological roles fulfilled by urban green spaces. To evaluate how urban green spaces function as wildlife habitat, we estimated mammal diversity and metacommunity dynamics in city parks, cemeteries, golf courses, and natural areas throughout the greater Chicago, Illinois, USA region. We found similar α-diversity (with the exception of city parks), but remarkably dissimilar communities in different urban green spaces. Additionally, the type of urban green space greatly influenced species colonization and persistence rates. For example, coyotes (*Canis latrans*) had the highest, but white-tailed deer (*Odocoileus virginianus*) the lowest probability of persistence in golf courses compared to other green space types. Further, most species had a difficult time colonizing city parks even when sites were seemingly available. Our results indicate that urban green spaces contribute different, but collectively important, habitats for maintaining and conserving biodiversity in cities.

Key words: colonization; community ecology; conservation; dynamic community occupancy model; green space; metacommunity; persistence; trail camera; urban wildlife; urbanization.

Introduction

The world's population is growing at nearly 1% per year (United Nations 2015) and for the first time in human history more people live in cities than in rural areas (United Nations 2014). The expansion of cities has significant effects on global biodiversity through near-permanent modifications to natural environments (Farinha-Marques et al. 2011, Beninde et al. 2015). Therefore, to effectively conserve urban biodiversity, it is important to understand the unique ecological processes occurring in cities.

Although urban areas are typically characterized by lower biodiversity (Goddard et al. 2010, Aronson et al. 2014), urban green spaces have the ability to act as important habitat for wildlife. For example, urban green spaces function as surrogate habitats for southwestern birds (Zwartjes and Delong 2005), refuge habitat for bumblebees (McFrederick and LeBuhn 2006), and dispersal and movement corridors for small birds and small mammals (Bolger et al. 2001, Munshi-South 2012). Urban green spaces also provide opportunities for people to recreate and interact with nature; thus increasing human well-being and cultivating an interest in nature conservation (Miller 2005, Dearborn and Kark 2010, Wolch et al. 2014, Soga and Gaston 2016). Given these benefits for both wildlife and humans, it is unsurprising that designing, creating, and managing green spaces has become a recent focus of urban planners and ecologists (Wolch et al. 2014).

Green spaces are often defined broadly (Swanwick et al. 2003), and include all types of urban open space that range from the highly landscaped (e.g., city parks) to remnant natural areas (e.g., an urban forest). Although green spaces likely differ in size, management, and human activity, they all contain some sort of natural or semi-natural vegetation. Starkly different from the surrounding built environment, these varying types of green space are typically generalized in urban ecology studies (Swanwick et al. 2003). However, not all green spaces have the same ecological characteristics. For example, city parks are often small in size, have manicured vegetation, and high human activity (Nielsen et al. 2014). Conversely, golf courses are often large, typically have some semi-natural vegetation and some form of open water, but levels of human activity vary temporally (Boone et al. 2008). On the other end of the spectrum, urban natural areas are typically remnant habitat patches containing complex vegetation composition (Adams and Lindsey 2010). Furthermore, ecological features undoubtedly vary within categories. Thus, habitat variation among and between green spaces should not be ignored when evaluating their role as wildlife habitat.

To understand how green space supports wildlife in highly fragmented and novel landscapes, it is important to consider metacommunity and metapopulation dynamics (i.e., colonization and persistence) between green spaces (Hanski 1998, Holyoak et al. 2005). Persistence rates can indicate the potential habitat available in a patch (Hanski 1998), and colonization rates can signify the effective isolation of habitat patches and the permeability of the matrix (Ricketts 2001). While great

attention has been given to urban bird communities, very little is known about urban mammals. As most mammals lack the mobility of flight, they are more susceptible to the physical barriers that characterize the urban matrix, such as roads, buildings, artificial waterways, and increased human activity (Crooks 2002, McKinney 2002, Ordeñana et al. 2010). Therefore, differences between urban green spaces may play an important role for mammal dynamics. As urban planners look to ecologists for guidance on designing green spaces to benefit wildlife species (Marzluff and Rodewald 2008), it is critical that we acquire a better understanding of not just the distribution of species, but the dynamics of animal communities that use these spaces.

We assessed diversity, community composition, and colonization and persistence probabilities of medium- and large-sized mammals (hereafter referred to as mammals) in urban green spaces by using motion-triggered cameras set in natural areas, city parks, cemeteries, and golf courses in the greater Chicago metropolitan area, Illinois, USA (Magle et al. 2016). We hypothesized that urban natural areas would contain a large proportion of the regional species pool and have higher probabilities of persistence for most species compared to city parks, cemeteries, and golf courses. Due to high human activity and highly manicured understories that characterize city parks (Adams and Lindsey 2010, Vernon et al. 2014), we also hypothesized that city parks would have the lowest species richness and lowest probabilities of persistence. To test our hypotheses, we used a Bayesian multispecies dynamic occupancy model (Dorazio et al. 2010, Kéry and Royle 2016) to estimate and compare mammal diversity and community composition in different types of green space throughout the Chicago metropolitan area and estimate community-level and species-specific probabilities of colonization and persistence across all site types. To our knowledge, this is the most comprehensive study of mammal communities in urban environments to date, and the first study to assess urban mammal dynamics at both the species and community scale. The findings from this study can help guide urban conservation strategies by highlighting differences in mammal communities and dynamics across different types of green spaces in urban areas like Chicago.

MATERIALS AND METHODS

Study design and data collection

This study is part of an ongoing wildlife monitoring survey in the greater Chicago metropolitan area (Fidino et al. 2016, Magle et al. 2016). Chicago is the third most populous city in the United States with approximately 2.7 million residents and an average population density of 7,355 people per km^2 (U.S. Census Bureau 2015b). The greater metropolitan area contains an estimated 8.6 million people (U.S. Census Bureau 2015a). Chicago is located on the southwestern shore of Lake Michigan, and

experiences warm summers (average low = 16.8°C), cold winters (average low = 3.6°C), intermediate springs (average low = 8.1°C), and autumns (average low = 4.7°C) (data *available online*).[2]

We delineated three 50 km long transects that radiated out from Chicago's urban center in three cardinal directions (Fig. 1). Each transect was divided into 10 5 km long sections within which we randomly selected sampling sites that fell within 2 km from the transect line (Magle et al. 2016). Selected locations were restricted to sites where landowner permission could be acquired. A maximum of four sites were selected within each section, and locations were separated from one another by at least 1 km (Magle et al. 2016). All sampling sites ($n = 100$) were located in urban natural areas ($n = 38$), city parks ($n = 42$), golf courses ($n = 8$), and cemeteries ($n = 12$). These four types of green space represent the majority of potential wildlife habitat in the Chicago metropolitan area (Fidino et al. 2016). We placed one Bushnell motion-triggered infrared Trophy Cam (Bushnell, Overland Park, Kansas, USA) at each site for approximately 30 d per season (i.e., spring, summer, fall, and winter). In large green spaces (e.g., golf courses or natural areas) we randomly placed a sampling site within the green space boundaries using GIS. In smaller green spaces (e.g., small city parks), we selected a location in the approximate center of the green space or in a location within the green space boundaries that allowed for appropriate camera installation. Each season we placed one synthetic fatty acid scent lure in the line of sight of the camera. Sampling began in fall of 2010 and continued through spring 2013; a total of 11 seasons. Due to logistical constraints not all sites were sampled equally across each season. Detailed descriptions of site selection, study design, and species identification procedures are described in Magle et al. (2016).

Site classification and accounting for urbanization around sites

We classified each site based on its respective land use type. Natural areas were undeveloped woodlands that consisted of secondary growth trees and varying degrees of vegetation composition in their understories (Vernon et al. 2014). Many natural areas in our study were established in the early 1900s when city planners designated an array of protected areas in and around the city of Chicago (Moskovits et al. 2004). City parks consisted of mature native and exotic trees with a predominately turf grass understory, while some larger parks included areas of natural vegetation interspersed throughout the park (Fidino et al. 2016). The creation of individual city parks in our study ranged from the late 1800s to the current decade. However, many of these city parks have been renovated, updated, or changed over the course of their

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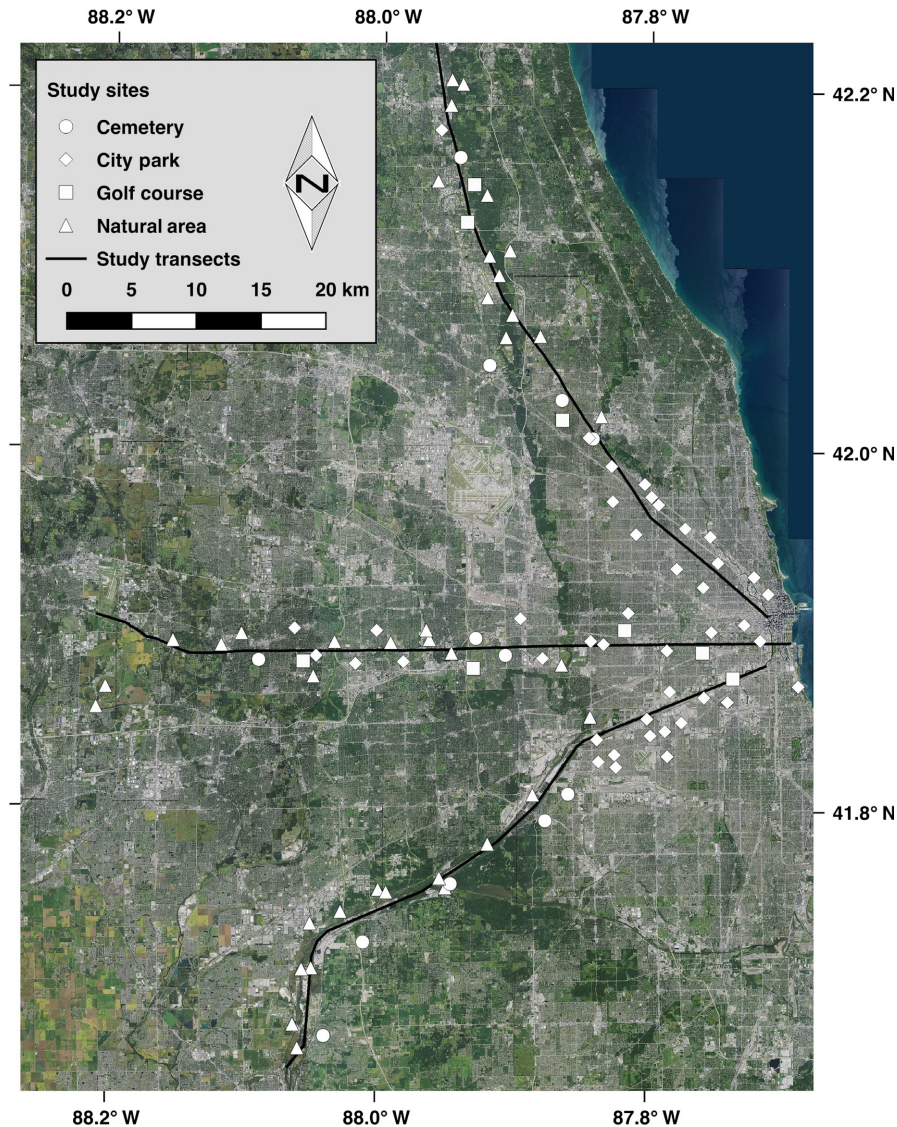[2] https://www.wolframalpha.com/input/?i=chicago+weather+trends

Fig. 1. Map showing the distribution of study sites located in natural areas, city parks, cemeteries, and golf courses in Chicago, Illinois, USA. Sites are depicted at a greater size than the area sampled.

existence. Cemeteries differed with some being large (>2 ha) but similar to small (<2 ha) city parks and others small but directly abutting or containing wooded areas (Fidino et al. 2016). Some cemeteries in our study date back to the mid 1800s with very few modifications over time. Golf courses were large, heavily landscaped, and contained constructed water features (Fidino et al. 2016). However, most golf courses retained some natural areas within and around their periphery (Fidino et al. 2016).

Our study sites fall along an urban to exurban gradient (Fig. 1). To control for the influence that varying levels of urbanization may have on the colonization and persistence rates of species, we created three urbanization covariates using QGIS ver. 2.14 (QGIS Development Team 2009), mean tree cover, mean impervious cover, and mean housing density, each within a 500-m buffer

around each site (Fidino et al. 2016, Magle et al. 2016). To reduce the dimensionality of these three parameters, we used principal components analysis (PCA) to create orthogonal principal components and used the first principal component, accounting for 77.31% of the variation in the data, as a covariate in our model. Positive values of this parameter indicate sites with higher mean canopy cover, while negative values indicate sites with higher housing densities and impervious cover.

A dynamic community occupancy model

Estimating and comparing community dynamics among different types of urban green space poses two unique challenges: (1) variation exists in patch size, shape, vegetation composition, historical land use, and

human activity, both among and between types of green space and (2) not all species are easily detected by cameras, and some species may be missed although present at a site. To account for these challenges and test our hypotheses, we developed a Bayesian dynamic multi-species occupancy model (MacKenzie et al. 2006, Dorazio et al. 2010) that accounts for an individual species' response to the variation within each type of green space. We then modified this model using parameter expansion and data augmentation (Dorazio et al. 2010, Kéry and Royle 2016) to account for "missed species," those present at a site but never detected. Using this model, we estimated the gamma (γ)-diversity of mammals in the Chicago metropolitan area, compared alpha (α)- and beta (β)-diversity between each type of green space, and estimated community-level and species-specific probabilities of colonization and persistence at each site type.

Parameter expansion and data augmentation.—To account for species that may have been missed or rarely detected by our camera trap efforts, we used data augmentation and parameter expansion as described in Kéry and Royle (2016). More specifically, we added eight hypothetically unobserved species (nz) to our data set and gave these species all-zero observations. This set of hypothetical species was based on known species that occur in the Chicago metropolitan area. Rather than analyzing only the observed species ($N = 8$, see Appendix S1: Table S1), we analyzed the augmented data set ("metacommunity"; $M = nz + N$) consisting of 16 species. We then incorporate into our hierarchical model, Eq. 6 and 7, an indicator for each species that takes a value of 1 if the species is part of the observed community and 0 if they are not (Carrillo-Rubio et al. 2014). Each indicator follows a Bernoulli process

$$w_k \sim \text{Bernoulli}(\Omega) \qquad (1)$$

where w_k is the indicator for species k ($k = 1,2,\ldots,M$) and Ω is the probability that M species are in the regional pool (Kéry and Royle 2016). This approach allows us to estimate the probability that an unobserved species should be included in the regional species pool and extend our inference to any species that may have been available for detection but happened to be missed (Kéry and Royle 2016).

Species-specific response to variation among types of green space.—To account for differences in species-specific responses to the different types of green spaces, we modeled a species-level mean response, μ.sp, for species k to site type s (i.e., natural area, city park, cemetery, or green space) as the following normal distribution:

$$\mu.\text{sp}_{ks} \sim \text{N}(\mu.\text{global}_s, \sigma_s) \qquad (2)$$

where $\mu.\text{global}_s$ specifies the community-level mean response of all species to site type s and assumes a semi-informed N(0,3) hyperdistribution (Gelman et al. 2008).

σ_s is the variance among species-level responses from the community-level mean at site type s. We assumed that σ_s follows a semi-informed Inv–Gamma(3,2) hyperdistribution (Gelman 2006).

To further account for variability between sites of type s, we added another level to the model

$$\theta_{ki} \sim \text{N}(\mu.\text{sp}_{ks[i]}, \sigma_{ks}) \qquad (3)$$

where $s[i]$ is the site type of the ith site ($i = 1,2,\ldots I$). Thus, each species has its own estimated response to an individual site that is informed by their mean response to the site's respective green space type, $\mu.\text{sp}_{ks[i]}$, and is allowed to vary by σ_{ks}. We assumed a semi-informed Inv–Gamma(3,2) hyperdistribution for σ_{ks}.

The above model specification allows us to calculate four quantities of ecological interest: (1) how the community-level colonization and persistence rates differ across site types ($\mu.\text{global}_s$), (2) how species-specific colonization and persistence rates vary across site types ($\mu.\text{sp}_{ks[i]}$), (3) how much individual species vary from the community-level response, and (4) to what extent sites of the same type vary in quality for a single species. Following MacKenzie et al. (2006), we define colonization as the probability a site is occupied given it was unoccupied in the previous time step, and persistence as the probability a site remains occupied given it was occupied in the previous time step. To estimate the third and fourth quantities, we calculated variance to mean ratios (VMR) from draws of the posterior distributions to determine (1) how much species differ from the community mean in their probability to persist and colonize a site type ($\text{VMR}_s = \sigma_s^2/\mu.\text{global}_s$) and (2) how sites of the same type differentially influence a species' probability to persist or colonize a site type ($\text{VMR}_{ks} = \sigma_{ks}^2/\mu.\text{sp}_{ks}$). A $\text{VMR}_s > 1$ indicates that individual species within the community respond differently from the community mean. This would suggest that a particular type of green space has varying effects on different species and does not generalize well across the mammalian community. However, a $\text{VMR}_s < 1$ suggests that species in the community respond relatively similarly and effects from a particular type of green space may be generalized for the entire community. A $\text{VMR}_{ks} > 1$ indicates that sites of a particular type vary in quality for an individual species, while $\text{VMR}_{ks} < 1$ suggests little variation among sites. Therefore, like VMR_s, one could determine how general the effect of a particular type of green space is on an individual species' ability to colonize or persist. For each VMR, we calculated the proportion of the posterior distribution that was >or <1 to assess significance.

Modified dynamic multi-species occupancy model.—We incorporated our hyperparameters accounting for variation within green spaces and our community indicator variables into a standard formulation of a Bayesian dynamic occupancy model (MacKenzie et al. 2006, Dorazio et al. 2010) as follows: our data, y_{kit}, are the

total number of detections for all species, including nz, at site i during season t ($t = 1,2,\ldots T$). Our data then arise as a binomial random variable

$$y_{kit}|z_{kit}, p_{kt} \sim \text{binomial}(j_{it}, z_{kit}p_{kt}) \qquad (4)$$

where j_{it} is the number of sampling occasions per site per season, and p_{kt} is the species- and season-specific detection probability. Previous studies have shown that season is an important factor influencing the probability of detecting mammals on trail cameras in the Chicago area (Fidino et al. 2016, Magle et al. 2016). Therefore, we modeled detection probability as a function of the northern meteorological season (i.e., spring, summer, fall, and winter) for which sampling took place using the logit link

$$\text{logit}(p_{kt}) = \alpha_{0k} + \alpha_k \text{season}_t \qquad (5)$$

with species-specific effects given by α_{0k}.

We then modeled the initial occupancy state (in time period 1) for the kth species at the ith site (z_{ki1}) as a Bernoulli processes and introduced our latent indicator variable from Eq. 1 into our occurrence model

$$z_{ki1}|w_k, \psi_{ki1} \sim \text{Bernouli}(\psi_{ki1}w_k) \qquad (6)$$

where ψ_{ki1} is the probability of species k initially occurring at site i during the first season. Note that if $w_k = 0$ then $z_{ki1} = 0$ with probability 1; thus if species k is not a member of the observed community of N species, then the occupancy state of species k must equal zero. Following the first time period, we assume that future occupancy rates in the next season ($t + 1$) are dependent on the occupancy state at time t via a mixture of local colonization (γ) and persistence (ϕ) probabilities (MacKenzie et al. 2006)

$$z_{kit}|z_{kit-1}, w_k, \phi_{kit}, \gamma_{kit} \sim \text{Bernoulli}(w_k(z_{kit-1}\phi_{kit} + (1 - z_{kit-1})\gamma_{kit})) \text{ for } t \text{ in } 2,\ldots,T. \qquad (7)$$

Here we again incorporate w_k and now θ_{ki} from Eq. 3 as part of the linear predictor for ϕ_{kit} and γ_{kit} using the logit link. As θ_{ki} is included and estimated separately for ϕ_{kit} and γ_{kit}, we add a third subscript to denote which process is being estimated such that θ_{ki1} indicates persistence and θ_{ki2} indicates colonization. We also include a time-varying intercept for both processes and the first principal component representation of urbanization (u_i) to control for the potential influences of varying levels of urbanization along the study transects

$$\text{logit}(\phi_{kit}) = b_{0kt} + \theta_{ks[i]1} + v_k u_i \qquad (8)$$

$$\text{logit}(\gamma_{kit}) = c_{0kt} + \theta_{ks[i]2} + d_k u_i \qquad (9)$$

where v_k and d_k are the estimated effect that u_i has on species k. We assumed a N(0,σ_k) prior distribution for v_k and d_k and an Inv–Gamma (3,2) hyperdistribution for

σ_k. We then calculated the 95% predictive interval of species means from $\mu.\text{global}_s$ and σ_s^2. This allows us to estimate the interval that the mean probability of both colonization and persistence would be expected to fall 95% of the time for an unobserved species.

Model estimation.—Posterior distributions of model parameters were estimated using a Markov chain Monte Carlo (MCMC) algorithm implemented in JAGS (see Data S1) using the jagsUI package (Kellner 2016) in R (R Core Team 2016). Six parallel chains were run from random starting values for 150,000 iterations with a thinning rate of 1 out of 20. The first 50,000 model iterations were discarded as burn in. We retained a total of 30,000 samples. Model convergence was assessed by checking that the Gelman-Rubin diagnostic statistic for each parameter was <1.1 (Gelman and Rubin 1992) and by visually inspecting the trace plots of MCMC samples.

Estimating gamma, alpha, and beta diversity.—The above model provides a detection-error-corrected estimate of occurrence for each species at each site during each sampling season, and an estimate of the latent variable w_k for every species in the metacommunity M. To estimate the total species pool during our study in the Chicago metropolitan area (γ-diversity), we summed across $\mathbf{w}$. To estimate site-specific species richness (α-diversity) during each season, we summed across the values of $\mathbf{Z}$ (a three-dimensional array of occupancy states across all potential species, sites, and seasons) $N_{it} = \sum_{k=1}^{M} z_{kit}$. We further summarized the posterior distributions of $\mathbf{Z}$ to identify the most common community compositions observed in each type of green space. Finally, to estimate the mean similarity of species occurring between site types (β-diversity) we estimated the Jaccard's similarity indices comparing each non-natural area site to each natural area site separately during each season

$$\text{Jaccard}_{ift} = \frac{\sum_{k=1}^{N} z_{kft}z_{kit}}{\sum_{k=1}^{N} z_{kft} + \sum_{k=1}^{N} z_{kit} - \sum_{k=1}^{N} z_{kft}z_{kit}}$$ where $\mathbf{f}$ is a vector that indexes which of the sites in $\mathbf{i}$ are natural areas. Each site type was indexed in a similar fashion to $\mathbf{f}$ and mean similarity was computed such that $\overline{\text{Jaccard}_t} = \text{Jaccard}_{uft}$, where $\mathbf{u}$ is a vector that indexes which of the sites in $\mathbf{i}$ are of a particular type.

RESULTS

Between fall of 2010 and spring 2013, we obtained 116,357 photographs of 16 species (see Appendix S1: Table S1), not including human, domestic dog, or livestock, during a total of 23,108 trap nights.

Diversity

Estimated γ-diversity was 15.5 (95% CI 14–16) species in the Chicago metropolitan area. The α-diversity varied by site type with city parks having the lowest species richness, and natural areas having the highest (Fig. 2).
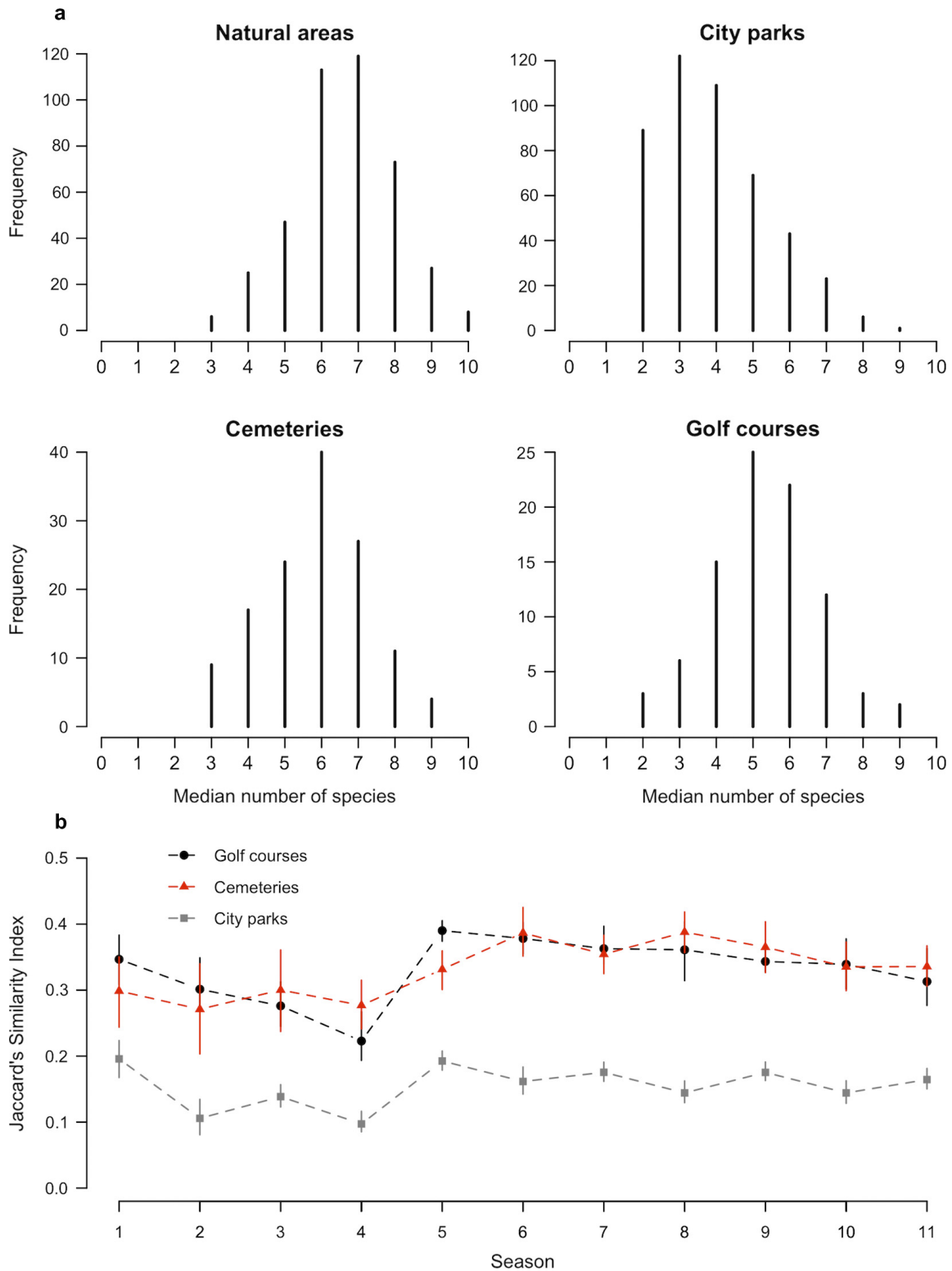
Fig. 2. (a) α-diversity: histogram of median values of species richness at each site across 11 seasons, grouped by natural areas, city parks, cemeteries, and golf courses in Chicago, Illinois, USA. (b) β-diversity: Jaccard's similarity indices between city parks, cemeteries, and golf courses compared to natural areas across 11 seasons of camera trap data in Chicago. Jaccard's similarity index of 1 indicates that the communities are exactly the same, while an index of 0 indicates they share no species in common.

Jaccard's similarity indices comparing natural areas to other types of green space were low (<0.5); indicating a profound difference in β-diversity between natural areas and city parks, golf courses, and cemeteries (Fig. 2). City parks were significantly less similar to natural areas than both golf courses and cemeteries (Fig. 2 and Appendix S1: Table S2). The most common mammal community composition observed in natural areas was coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), Virginia opossum (*Didelphis virginiana*), and raccoon (*Procyon lotor*; Fig. 3). The absence of any species was observed most often in city parks and cemeteries, and coyote and raccoon was the most common composition observed at golf courses (Fig. 3).

Species-specific colonization and persistence

Colonization and persistence differed greatly between species and between site types (Fig. 4). Domestic cat (*Felis catus*), Eastern cottontail (*Sylvilagus floridanus*), striped skunk (*Mephitis mephitis*), and red fox (*Vulpes vulpes*) all showed a low probability of colonization (<30%) in natural areas; whereas raccoons showed a high probability of colonization in natural areas (>70%). All species, with the exception of Eastern cottontail, had a low probability of colonization in city parks (Fig. 4). Eastern cottontail, striped skunk, red fox, and deer had a low probability of colonizing cemeteries, and domestic cat, Eastern cottontail, striped skunk, red fox, and deer had a low probability of colonizing golf courses (Fig. 4). Coyotes, raccoons, and deer all showed a high probability of persistence in natural areas (Fig. 4). Striped skunk showed a low probability of persistence in city parks, Eastern cottontail a low probability in cemeteries, and deer a low probability in golf courses (Fig. 4). Raccoons and coyotes had a high probability of persisting in golf courses (Fig. 4). The urban gradient had a positive effect on raccoon, red fox, striped skunk, and white-tailed deer colonization and raccoon persistence (Table 1).

Community response to green spaces

The community-level probability of colonization of natural areas was 0.21 (95% CI = 0.10–0.42), with a 95% predictive interval (PI) between 0.03 and 0.74
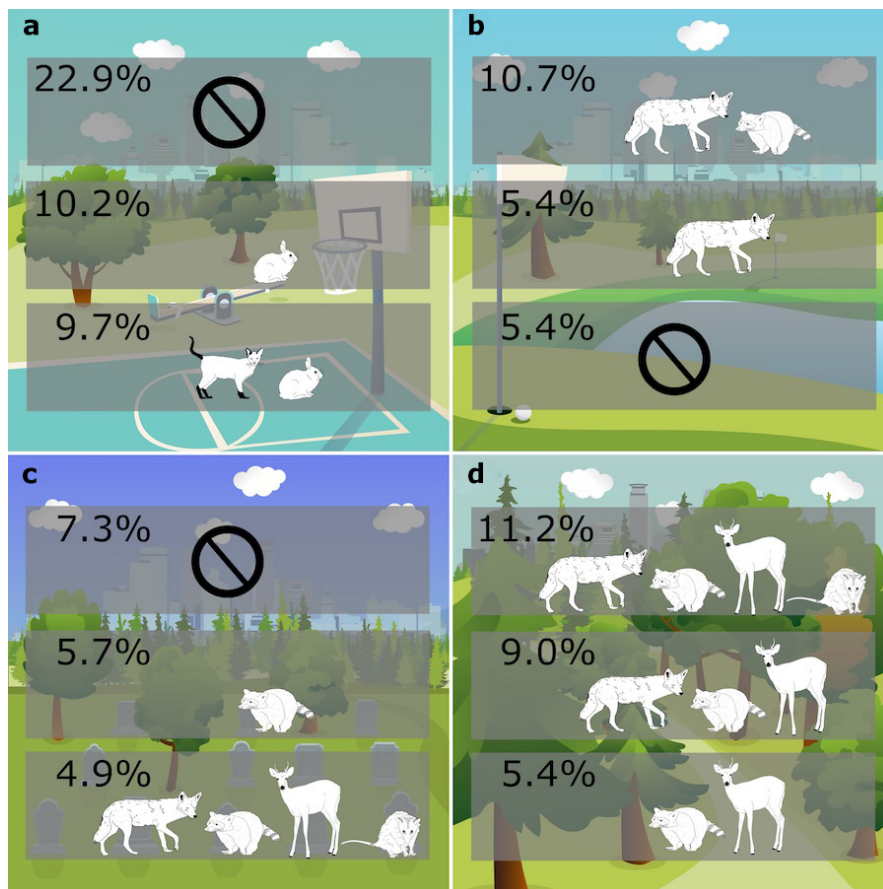

Fig. 3. The three most common mammal community compositions found in (a) city parks, (b) golf courses, (c) cemeteries, (d) and natural areas and the percentage of times they were observed in 11 seasons worth of surveys in Chicago, Illinois, USA. Crossed out circles indicate that no species were present.
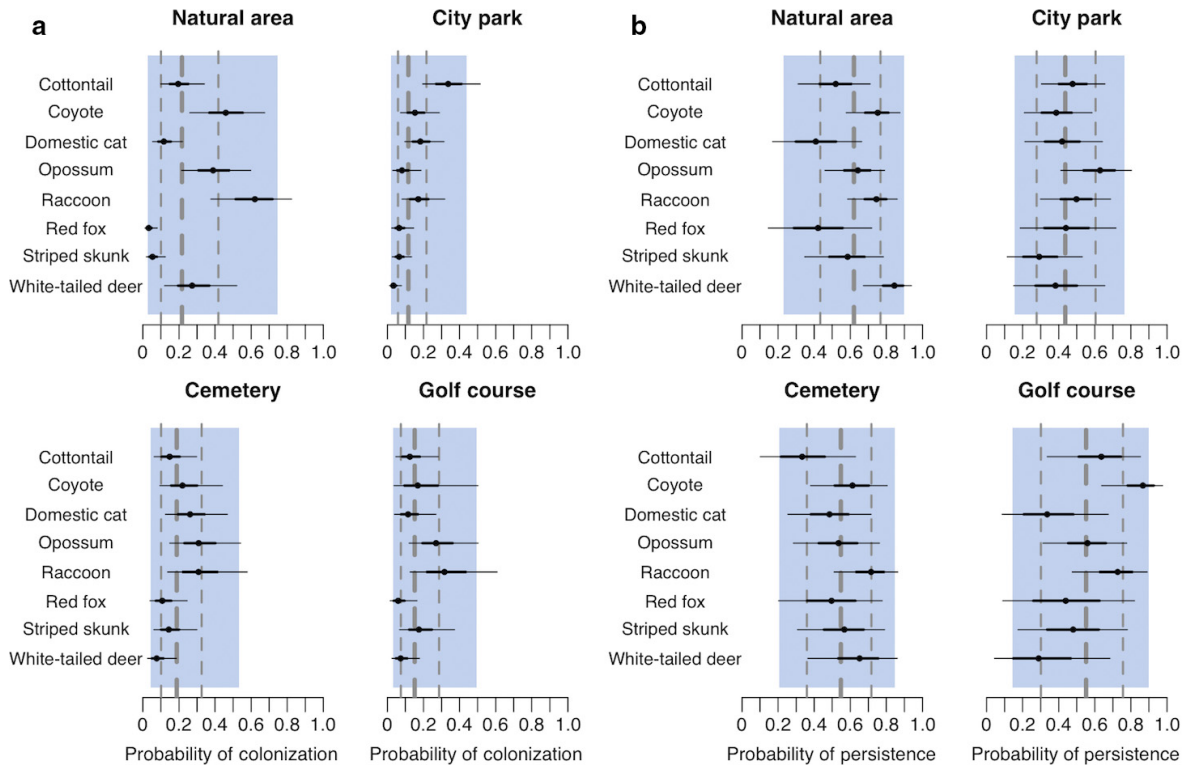
Fig. 4. Community and species-specific probabilities of (a) colonization and (b) persistence in natural areas, city parks, cemeteries, and golf courses in Chicago, Illinois, USA. The median probability values (point), 95% (thin line), and 80% (thick line) credible intervals for each species are displayed horizontally. Vertical dashed lines indicate the median probability value and 95% credible intervals for the mammal community. The background box indicates the interval in which the mean probability an unobserved species is expected to fall 95% of the time.

TABLE 1. Median posterior distribution values and 95% credible intervals for the model coefficient of the effect that the urban gradient (u_i) had on species-specific colonization and persistence probabilities in different green spaces in the Chicago metropolitan area, Illinois, USA.

Species	Median	95% Credible interval	
		Lower	Upper
Colonization			
Coyote	0.35	−0.03	0.77
Domestic cat	−0.28	−0.57	0
Eastern cottontail	−0.24	−0.56	0.06
Raccoon	0.61	0.22	1.02†
Red fox	0.59	0.2	1.01†
Striped skunk	0.66	0.28	1.06†
Virginia opossum	0.19	−0.17	0.59
White-tailed deer	0.66	0.2	1.15†
Persistence			
Coyote	0.17	−0.17	0.5
Domestic cat	−0.28	−0.72	0.14
Eastern cottontail	−0.16	−0.5	0.18
Raccoon	0.48	0.15	0.83†
Red fox	−0.06	−0.76	0.63
Striped skunk	−0.36	−0.96	0.22
Virginia opossum	0.22	−0.16	0.61
White-tailed deer	0.41	−0.12	0.99

†Indicates 95% CI that do not overlap zero.

(Fig. 4). The community-level probability of colonization of city parks was 0.11 (95% CI = 0.06–0.21), with a 95% PI between 0.02 and 0.44 (Fig. 4), and 0.19 (95% CI = 0.06–0.21) for cemeteries with a 95% PI between 0.05 and 0.53. The community-level probability of colonization of golf courses was 0.15 (95% CI = 0.07–0.29) with a 95% PI between 0.03 and 0.50 (Fig 4). Natural areas had a colonization $VMR_s > 1$, which indicates that individual species had different colonization rates in natural areas compared to the community mean response. City parks, cemeteries, and golf courses all had colonization $VMR_s < 1$ (Table 2), suggesting that individual species responses to these sites types varied little from that of the community.

The community-level probability of persistence in natural areas was 0.62 (95% CI = 0.43–0.77) with a 95% PI between 0.23 and 0.90 (Fig. 4). The community-level probability of persistence in city parks was 0.44 (95% CI = 0.23–0.61) with a 95% PI between 0.16 and 0.77 (Fig. 4), 0.55 (95% CI = 0.36–0.71) for cemeteries with a 95% PI between 0.21 and 0.85, and 0.55 (95% CI = 0.30–0.75) with a 95% PI between 0.14 and 0.90 in golf courses. All four types of green space had a persistence $VMR_s > 1$ (Table 2), which indicates greater variation in the responses between individual species and the community mean.

TABLE 2.　Variance to mean ratios (VMR) comparing how species differ from each other within the community at natural areas, city parks, cemeteries, and golf courses, and comparing how species respond to sites of the same type.

Species	Natural area		City park		Cemetery		Golf course	
	Median	Pr($\neq$1)	Median	Pr($\neq$1)	Median	Pr($\neq$1)	Median	Pr($\neq$1)
Colonization								
Community	1.14	0.59	0.42	0.94†	0.46	0.90†	0.45	0.90†
Eastern cottontail	0.72	0.72	1.22	0.61	0.51	0.82	0.39	0.91†
Coyote	1.90	0.75	0.82	0.64	0.68	0.68	0.90	0.53
Domestic cat	0.44	0.93†	0.41	0.95‡	0.85	0.58	0.61	0.74
Virginia opossum	2.17	0.83	1.45	0.74	0.87	0.57	0.73	0.65
Raccoon	1.34	0.62	0.72	0.73	1.20	0.57	0.91	0.54
Red fox	0.26	0.99‡	0.36	0.95‡	0.50	0.82	0.30	0.94†
Striped skunk	0.69	0.76	0.24	1.00‡	0.41	0.90†	0.54	0.80
White-tailed deer	1.22	0.58	0.20	1.00‡	0.33	0.92†	0.25	0.98†
Persistence								
Community	1.55	0.71	1.92	0.78	2.26	0.83	3.18	0.90†
Eastern cottontail	2.63	0.86	1.94	0.78	1.00	0.50	1.40	0.62
Coyote	1.33	0.67	1.92	0.79	1.58	0.68	0.40	0.86
Domestic cat	3.05	0.90†	5.11	0.99‡	2.00	0.77	1.12	0.54
Virginia opossum	1.15	0.57	1.69	0.70	4.40	0.94†	1.95	0.76
Raccoon	0.69	0.72	3.60	0.93†	0.70	0.67	1.01	0.50
Red fox	1.54	0.66	1.77	0.71	1.90	0.74	1.25	0.58
Striped skunk	1.94	0.75	0.84	0.58	2.22	0.78	1.99	0.76
White-tailed deer	1.00	0.50	1.64	0.70	1.54	0.65	0.87	0.54

Notes: Community VMR > 1 indicates that individual species within the community respond differently from the community mean, and <1 indicates that species in the community respond relatively similar to a type of green space. A species-specific VMR > 1 indicates that sites of a particular type vary in quality for an individual species, and <1 suggests little variation among sites.

†Indicates a $\geq$ 90% probability that the posterior distribution does not contain 1.

‡Indicates a $\geq$ 95% probability that the posterior distribution does not contain 1.

DISCUSSION

As urbanization expands and intensifies, urban green spaces are becoming important components of the management and conservation of urban wildlife (Gilbert 1989). We found profound differences in the mammal community composition using different types of green spaces, and many species varied greatly in their ability to colonize and persist at these locations. While city parks were relatively depauperate of mammal species, we found that golf courses, cemeteries, and natural areas contributed important habitats for maintaining urban biodiversity (Fig. 2). Thus, collectively, urban green spaces provide important habitats for different portions of the regional γ-diversity.

We estimated the overall γ-diversity of mammals in the Chicago metropolitan area to be ~16 species. While natural areas are often considered optimal urban habitat (Adams and Lindsey 2010) they contained, most often, half of the total regional γ-diversity (Fig. 2). Similarly, golf courses and cemeteries also contained less than half of the total γ-diversity, and city parks fell well short (Fig. 2). Although golf courses and cemeteries had similar α-diversity to natural areas, the mammal communities using these green spaces were profoundly different (Fig. 2 and 3). While human-constructed green spaces such as golf courses and cemeteries have very different characteristics

compared to natural areas (e.g., complexity of vegetation structure), habitat heterogeneity is known to increase animal diversity (Rosenzweig 1995, Tews et al. 2004). Perhaps the combination and collection of these different green spaces synergistically form important habitats for maintaining mammal diversity in urban environments.

While estimating species richness allows us to assess the mammal communities that occupy urban green spaces, it provides little insight into how green spaces may function as habitat. Our model provides some insight into this by estimating species persistence within each type of green space (Hanski 1998). More specifically, persistence $VMR_{sk} > 1$ infers that individual sites within a particular type of green space vary greatly in their influence on a species' mean persistence; the greater the number, the greater this discrepancy. As estimates are made for the individual site, these parameters can be further inspected to denote sites of high and low habitat potential for a species. For example, red fox had a low probability of persistence in natural areas (Fig. 4), but a high VMR_{sk} (1.54); indicating high variation in persistence levels across sites, with red foxes actually persisting well in some natural areas. Understanding the drivers of this variability (e.g., site-level vegetation complexity, prey availability, human activity levels, and surrounding urban development) would provide important information for habitat management.

We found that species persistence varied among the different types of urban green spaces and among sites within a green space type (Fig. 4). Raccoons were the only species that had persistence $VMR_{sk} < 1$ for natural areas and cemeteries, meaning that individual sites within these green spaces were relatively equal in terms of raccoon persistence. These results, combined with relatively high probabilities of persistence (Fig. 4) suggest that natural areas and cemeteries are good urban habitat for raccoons. These results are consistent with previous findings, which found that raccoons are often found in forested parks and cemeteries (Pedlar et al. 1997), and prefer sites with mature trees for denning (Endres and Smith 1993, Rosatte 2000). Striped skunks had an extremely low probability of persistence in city parks (Fig. 4), and were the only species to have a persistence $VMR < 1$ for city parks, suggesting that city parks in general are poor habitat for striped skunks. Skunks primarily consume insects and fruits (Greenwood et al. 1999). It is possible that the highly maintained landscapes of city parks (e.g., removal of woody plants, leaf litter removal, and reduction of other microhabitats) reduce the diversity and abundance of food sources for striped skunks. Coyotes and white-tailed deer both had a persistence $VMR < 1$ for golf courses. Coyotes had the highest and deer had the lowest probability of persistence in golf courses compared to all other types of green space (Fig. 4). To our knowledge coyotes and deer are not actively managed on the golf courses that we sampled. Therefore, these results demonstrate that golf courses are valuable habitat for coyotes, but poor habitat for white-tailed deer. Golf courses typically have semi-natural vegetation on their peripheries and are interspersed with open areas (i.e., fairways and greens); habitat heterogeneity that is typically preferred by deer (Beier and McCullough 1990). However, these open areas are a monoculture of turf grass and offer little variety in available forage for deer. Therefore, the lack of continuous habitat that characterizes most golf courses may discourage deer from using these sites in urban areas. On the other hand, coyotes are capable of occurring in relatively small habitat fragments and their habitat use is mostly limited by human activity and urban development (Gehrt 2010). Golf courses are often large, contain some vegetation for cover, and human activity is typically limited to daytime use. Therefore, golf courses may provide suitable habitat for coyotes within cities. An enhanced understanding of species-specific differences, such as these, would benefit urban wildlife conservation and human-wildlife conflict management.

It is important to note that colonization and persistence are not mutually exclusive, as a species must first colonize a site in order to persist (Hanski 1998). We found that most species, as well as the entire mammalian community, had low colonization probabilities in all four types of urban green spaces (Fig. 4). These results are unsurprising for species characterized by high persistence, because a species cannot colonize a site they already occupy. However, we found that most species had low probabilities of both colonization and persistence in city parks (Fig. 4). Further, colonization VMR_s for all species, with the exception of Virginia opossum and Eastern cottontail, were < 1 in city parks (Table 2). These results demonstrate that most species had an equally difficult time colonizing city parks even when potential sites were seemingly available. Given that most species had low colonization rates across all non-natural types of green space (Fig. 4), future wildlife-friendly, urban designs should include connectivity among green spaces to soften the matrix and increase the ability for new individuals to colonize potential habitat.

While the built environment may be difficult to abruptly alter in favor of wildlife species, urban green spaces are continuously being built or transformed to improve aspects utilized by animals (Marzluff and Rodewald 2008). Therefore, understanding the habitat characteristics within green spaces that favor or discourage mammals is critical for future green space planning. In some cases, we found that persistence VMR_s were extremely high, indicating that persistence rates for these species are dependent on the characteristics of an individual site. In our study, raccoon and Virginia opossum had high persistence VMR_s in city parks and cemeteries, respectively (Table 2). These results illustrate that the ability of raccoon and opossum to persist is likely a function of smaller scale processes (e.g., tree cover or food availability). Future research should explore the mechanistic relationships between habitat characteristics and colonization and persistence, focusing on those species with VMR_s greater than one. Understanding these mechanisms will help managers recognize why some sites are more or less favorable than others, and this information could be incorporated into urban planning scenarios.

Although we did not specifically address habitat quality (i.e., space, food, water, and shelter), we generated site-specific estimates for colonization and persistence that were partially informed by their respective site type mean. This approach can be used to identify sites that perform better or worse than an average site of a particular type of green space. Therefore, our modeling approach could be used to inform future hypotheses related to habitat quality within cities. These hypotheses could then be tested using specific habitat characteristics. As cities are extremely heterogeneous, our approach provides a foundation for future research.

We found that sites with a combination of higher tree cover and lower housing density and impervious cover (urbanization metric) had higher rates of colonization and persistence for some species (Table 1). Due to multicollinearity among variables, we are unable to make inference about these individual variables in our analysis. However, these results demonstrate that landscape level patterns of urbanization influenced habitat use for these species. While some species may have the ability to colonize or persist in urban green spaces, they may be sensitive to the level of urbanization surrounding the site

(Ordeñana et al. 2010). Future studies of mammal habitat use in urban green spaces should consider broad-scale features of the environment surrounding each site (e.g., population density, impervious cover, habitat connectivity).

An important shortcoming of our analysis is that we did not directly assess species interactions (e.g., interspecific competition) and their influence on metacommunity dynamics. Interactions, such as competitive exclusion, may also help to explain low colonization rates across most green space types. Species interactions are an influential component of any metacommunity (Holyoak et al. 2005) and likely added to the variation in colonization and persistence rates in our study. Although challenging, species interactions should be assessed in future urban wildlife research.

Urban green spaces have the ability to act as important habitat in highly heterogeneous and fragmented urban landscapes. We found that, collectively, golf courses, cemeteries, and natural areas contributed important wildlife habitats for different portions of regional γ-diversity. We also found that colonization and persistence rates could be generalized across certain types of green spaces and for particular species. To effectively conserve urban biodiversity it is fundamental that we understand the ecological roles fulfilled by urban habitat. Our study provides important insight and analytical tools to assess the ecology of urban green spaces.

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