



# Patterns in tree squirrel co-occurrence vary with responses to local land cover in US cities

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## Abstract

Urbanization has important effects on the distribution and persistence of wildlife communities. Urbanization may alter not just the distributions of individual species, but also co-occurrence patterns and thus the potential for interspecific interactions (e.g., competition, predation) that structure wildlife communities. Little is currently known about how urbanization alters species co-occurrence or how these changes shape urban species assemblages. Using tree squirrels as a model functional group, we quantified how urbanization alters species occurrence and co-occurrence patterns to shape species assemblages, and how these effects vary within and among cities. We constructed a multi-species, multi-season occupancy model to identify relationships between tree squirrel occupancy and co-occurrence and local land and tree canopy cover and examined variation in these relationships within and among nine US cities. Species' responses to canopy cover were highly variable among, but less variable within cities, suggesting that even common urban wildlife species may respond differently to urban intensity in different landscape contexts. Species co-occurrence was also highly variable among cities and weakly related to canopy cover within a city. These findings provide important evidence that both environmental attributes and species interactions shape urban wildlife communities. Important for management and conservation, they suggest that tree-canopy cover can particularly support forest species co-occurrence and that managing urban forests to provide high canopy cover could contribute to the diversity of urban wildlife communities in forested ecoregions.

**Keywords** Co-occurrence · Eastern gray squirrel · Fox squirrel · Multi-species occupancy model · American red squirrel · Urban

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## Introduction

Urbanization is a key driver of change in wildlife communities. By altering the amount and arrangement (i.e., connectivity) of habitat and introducing new stressors such as human activity and impervious surfaces, urban land-cover conversion leads to change in the distribution of wildlife species and the composition of urban wildlife communities (Newbold et al. 2015). For example, species with large home ranges are often absent due to the lack of contiguous habitat (e.g., large carnivores; Crooks 2002) and urban environments often include similar sets of species across cities that share similar diets and flexible habitat requirements (i.e., biotic homogenization; McKinney 2006). Less is known, however, about how changes in habitat associated with urbanization affect the potential for interspecific interactions (i.e., co-occurrence), such as changes in interaction frequencies among competitors (e.g., Lewis et al. 2015). Thus, we lack a complete understanding of how altered co-occurrence patterns combine with habitat change to shape urban biotic communities. Given that urban areas can be of significant conservation value as wildlife habitat (Derby Lewis et al. 2019), understanding how urbanization leads to and combines with changes to species co-occurrence patterns to structure urban wildlife communities is key to managing cities to stave off global biodiversity loss.

Recent, single-city studies have identified multiple patterns in the co-occurrence of species in urban settings. While some studies suggest that co-occurrence probabilities of competitors increase with urban intensity, for example, for mesocarnivores (Parsons et al. 2019) and lagomorphs (Bach et al. 2023), other studies suggest that co-occurrence exhibits the opposite pattern. Subordinate carnivores, for example, may be less likely to co-occur with larger carnivores, potentially utilizing urban landscapes to avoid larger competitors and potential predators (Mueller et al. 2018). In extreme cases, increasing urbanization can cause a complete breakdown of co-occurrence, with one species replacing the other as urbanization alters environmental conditions in the replacing-species' favor (Sexton 1990; van der Merwe et al. 2005; Peplinski and Brown 2020). On the other hand, habitat patches within cities that maintain tree cover and heterogeneity of vegetation can promote co-occurrence and support diverse communities, for example, of carnivores (Fidino et al. 2019) and small mammals (Cassel et al. 2020). Given the variety of co-occurrence patterns identified in the literature, we lack a complete multi-city understanding of the extent to which patterns of co-occurrence (or lack of co-occurrence) occur across cities and of the factors that drive species co-occurrence. It is likely that all of these patterns occur in cities, potentially mediated by city-, environment-, and species-specific factors that lead them to vary within

and among cities. Given that potential interactions between species are an important but understudied mechanism for determining species distributions (Kraft et al. 2015), this lack of synthesized knowledge regarding urbanization's effects on species co-occurrence prevents us from fully understanding the mechanisms that determine species distributions and community composition in cities (Fidino et al. 2021). The recent availability of broad-scale, long-term datasets (e.g., the Urban Wildlife Information Network, Magle et al. 2019; SnapshotUSA, Cove et al. 2021) make it possible to identify how patterns in the co-occurrence of species vary within and among cities, and the factors that influence co-occurrence.

Tree squirrels (family *Sciuridae*) exemplify common, competing urban wildlife species that often co-occur within a city and have been introduced or naturally dispersed into cities around the world (Tranquillo et al. 2024). In North America, the geographic ranges of eastern gray squirrels (*Sciurus carolinensis*, hereafter 'gray squirrels') and fox squirrels (*S. niger*) overlap extensively, yet these species do not co-occur in all cities within their ranges. The main mechanisms facilitating coexistence of these species in non-urban habitats are behavioral and physiological. Gray squirrels are more efficient foragers and outcompete fox squirrels when food resources are limited; however, fox squirrels' larger body size decreases their predation risk and increases their ability to move between resource patches through more open habitat (Steele and Koprowski 2001). While this mechanism appears to be maintained in some cities (van der Merwe et al. 2005; Larson and Sander 2022), in other cities gray squirrels may replace fox squirrels as tree canopies mature and provide refuge from predation (Sexton 1990). However, we do not currently know whether these findings are generalizable among cities and have not identified the factors that influence co-occurrence. Additionally, fox and gray squirrels have displaced native tree squirrels in cities where they have been introduced (e.g., western gray squirrels *S. griseus*, Muchlinski et al. 2009; European red squirrels *S. vulgaris*, Wauters et al. 2023); thus, understanding the ecology of these species in cities is important for reducing negative impacts on native biodiversity.

American red squirrels (*Tamiasciurus hudsonicus*, hereafter 'red squirrels') also occur in some North American cities. Red squirrels aggressively defend their territories from conspecifics but appear tolerant of other squirrel species (Ackerman and Weigl 1970); thus, urban red squirrels should be able to co-occur with other urban squirrels. However, red squirrels are habitat specialists of coniferous forests (Steele 1998), and in the southern parts of their range where conifers transition to deciduous trees, gray squirrels' larger body size provides a competitive advantage that allows them to forage more efficiently on hardwood mast

and displace red squirrels (Riege 1991). Given that deciduous trees are more common in cities (Clapp et al. 2014), red squirrels may be excluded from urban ecosystems by gray squirrels if gray squirrels can exhaust urban hardwood mast resources. The effects of urbanization on red squirrel populations remain relatively unknown, however, as research on urban red squirrels is sparse, especially regarding potential interspecific interactions.

In order to better understand how urban environments influence both species occurrence and co-occurrence, this study sought to identify patterns in urban tree squirrel occupancy and co-occurrence, whether these patterns are consistent among cities, and the factors that influence them. To do so, we combined field-collected species' occurrence data from a large dataset composed of species observations collected using motion-sensitive trail cameras from nine US cities with land-cover data to evaluate relationships between specific land-cover attributes (i.e., areal extents of impervious and vegetated land covers) and species site occupancy and co-occurrence probabilities. Land cover provides a proxy for habitat quality and related factors such as resource availability (Dussault et al. 2005), predation risk (Gaynor et al. 2019), and the presence of competitors (Nelson et al. 2007); thus, land cover serves as an indicator of different environmental processes that may determine community assembly. We predicted that:

1. Fox and gray squirrels would exhibit little variation among cities in their responses to urban intensity as indicated by impervious and turfgrass cover (i.e., occur

in all but the most intensely urban environments) given that these species are relatively generalist in their habitat requirements.

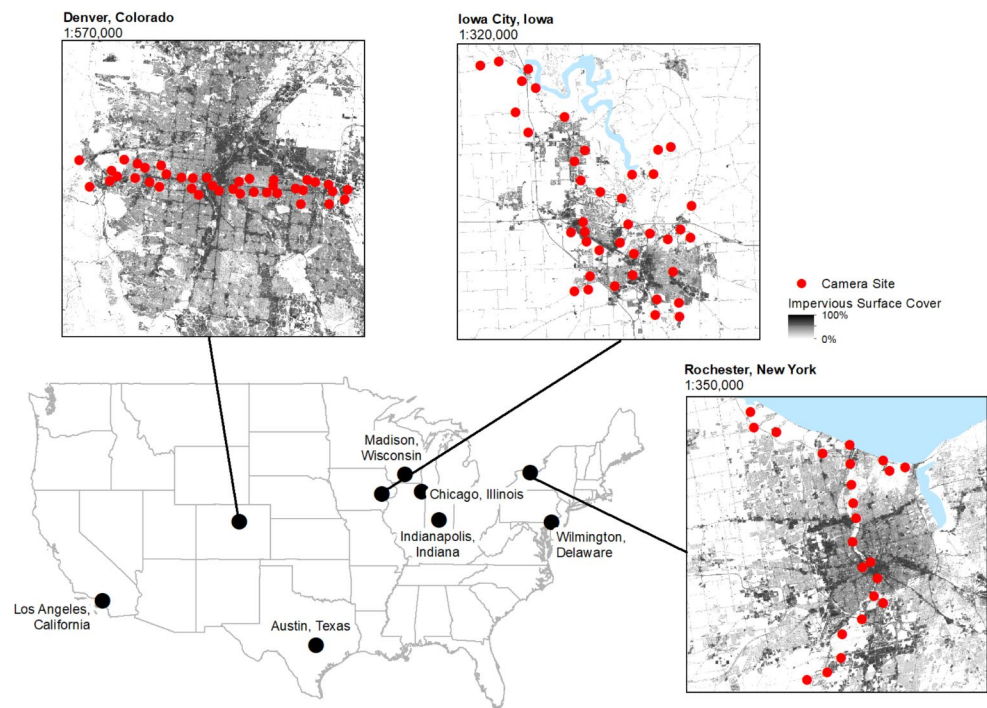
2. Red squirrels would exhibit little variation in their responses to urban intensity (i.e., occur only at low levels of urban intensity) as they are thought to be sensitive to urbanization because of their reliance on coniferous forest for forage and shelter.
3. Co-occurrence of fox and gray squirrels should vary among cities, as co-occurrence patterns identified by past studies exhibit conflicting results, likely because of city-specific attributes such as differences in the proportional cover of different land-cover types that could mediate the co-occurrence of these species.
4. Co-occurrence of red squirrels with both fox and gray squirrels in cities should be uncommon due to red squirrels' negative response to urban intensity and inability to compete with gray squirrels in hardwood-dominated systems.

## Materials and methods

### Study area

We used camera-trapping to sample squirrels in nine United States metropolitan areas (Fig. 1). Our sample included cities with native vegetation characterized by deciduous forest (Chicago, Illinois; Madison, Wisconsin; Indianapolis,

**Fig. 1** Distribution of the nine study metropolitan areas and three representative examples of the distribution of camera trapping sites along each city's respective urbanization gradient



Indiana; Rochester, New York; Wilmington, Delaware), tall-grass prairie (Austin, Texas; Iowa City, Iowa), short-grass prairie (Denver, Colorado), and chaparral (Los Angeles metropolitan area, California, including the cities of Long Beach and Pasadena; Fig. 1; Table 1). These cities vary in their human population density (range: 58–1,034 people/km<sup>2</sup>), average impervious cover (range: 22.2–53.0%), and average canopy cover (range: 3.6–26.9%; Table 1). As such, the study cities include a range of “urban intensities” (e.g., from relatively small cities to megacities) and are situated in many of the US ecoregions inhabited by tree squirrels. Although the Los Angeles metropolitan area is outside the native range of the species analyzed in this study (western gray squirrels were not included in this analysis due to low detection rates; see Sect. 2.2), fox squirrels have been introduced to and established populations in the area (Claytor et al. 2015) and including this city provides additional information about fox squirrels’ responses to urban land cover.

## Data collection

Camera-trapping followed the Urban Wildlife Information Network (UWIN) sampling protocol (Magle et al. 2019). Briefly, each city developed sampling transects that cover an urbanization gradient within that city. Cameras were placed along these transects at sampling locations (hereafter “sites”) that include a wide range of green spaces, among them urban parks characterized by turfgrass with few trees, suburban yards and open spaces with mature trees and shrubs, row-crop landscapes at the urban fringe, and large, natural-area parks with predominantly native vegetation. Sites were separated by at least 1 km (a distance that exceeds the home ranges of many urban mammal species, including tree squirrels; Feldhamer et al. 2003) to reduce double-counting and the potential for spatial

autocorrelation. Because the sampled cities differ in spatial extent and development history, site numbers vary among cities, ranging from 22 (Madison, WI) to 119 (Chicago, IL; Table 1).

One motion-triggered trail camera was attached to a tree or other stationary object on each site for at least 28 days (mean = 33 ± 11 standard deviation after considering malfunctions such as dead batteries) in four separate months: January, April, July, and October (hereafter “seasons”). Cameras were set to operate continuously and take one time-stamped image when a warm object moved in their field of view with 30 s intervals between images if motion sensors were continuously triggered. At the end of each deployment period, photographs were downloaded from cameras. Species in photographs were identified independently by at least two trained observers. A third observer validated species in photographs when observer identifications disagreed to ensure identification of the correct species. Squirrels that could not be identified to species were tagged “Tree Squirrel, Unidentifiable” and excluded from analysis. We analyzed data collected from July 2018 to July 2020. Observations from each season were divided into four, one-week periods (“secondary sampling occasions”; MacKenzie et al. 2002). We compiled binary detection/non-detection histories (1/0) for gray, fox, and red squirrels on each site in each city for each season; western gray squirrels were detected only once at one site and thus were not included in this analysis. For time periods during which a camera was not deployed, entries were marked ‘NA’ (MacKenzie et al. 2002). Our research conforms to the ethical guidelines for conducting research on wild mammals (Sikes 2016), and is approved by Institutional Animal Care and Use Committees where applicable.

**Table 1** Summary descriptive information for the cities sampled in this study

City	Metropolitan Area <sup>a</sup>	Camera Sites	Dominant Native Vegetation <sup>b</sup>	Mean Tree Canopy Cover	Mean Impervious Surface Cover	Mean Mowed Turfgrass Cover
Pasadena, CA & Long Beach, CA	Los Angeles – Long Beach – Anaheim, CA	43	California chaparral	3.6%	53.0%	7.7%
Denver, CO	Denver – Aurora, CO	39	Shortgrass prairie	3.9%	39.1%	14.3%
Iowa City, IA	Iowa City, IA	39	Tallgrass prairie	9.0%	31.3%	20.9%
Chicago, IL	Chicago, IL – IN	119	Deciduous forest	9.8%	39.7%	12.8%
Indianapolis, IN	Indianapolis, IN	41	Deciduous forest	10.6%	32.9%	22.9%
Madison, WI	Madison, WI	22	Deciduous forest	14.5%	30.3%	19.9%
Wilmington, DE	Philadelphia, PA – NJ – DE – MD	29	Deciduous forest	24.6%	23.5%	29.3%
Austin, TX	Austin, TX	26	Tallgrass prairie	26.9%	32.9%	15.4%
Rochester, NY	Rochester, NY	23	Deciduous forest	27.7%	22.2%	29.5%

<sup>a</sup>Defined as an “urbanized area” by the United States Census Bureau

<sup>b</sup>As defined by the EPA’s level I ecoregions



## Environmental variables

We calculated a series of environmental predictor variables within a 100 m radius buffer around each camera site. We chose this distance to capture the average home range extents of fox and gray squirrels (area = 3.14 ha, range = 2.39–7.56 ha) in small woodlots and urban settings (Adams 1976; Tounzen et al. 2013). Red squirrel home ranges have not been investigated in urban settings, however, their home ranges in other habitat types are generally below 1 ha (Steele 1998). We calculated the percent cover of mowed turfgrass (i.e., Developed – Open Space) and mean percent impervious cover within each buffer using, respectively, the 2019 National Land Cover Database (NLCD) Land Cover and Percent Developed Imperviousness products (Dewitz and U.S. Geological Survey 2021). We calculated average tree canopy cover using the 2016 NLCD Tree Canopy product (Coulston et al. 2012), as the 2019 data were not yet available. We mean-centered each cover variable for each site in each city to allow for more direct comparison of data among cities. To do so, we first calculated the average mowed turfgrass, impervious, and tree canopy cover for each metropolitan area in our study (Table 1), using the “urbanized area” data from the 2019 TIGER/Line database (U.S. Census Bureau 2019) to delimit the areal extent of each metropolitan area. We then subtracted the metropolitan area’s mean value for each land-cover type from the site-specific proportion of that type; for example, a site in Iowa City that had 20.3% canopy cover would have the Iowa City metropolitan area’s average canopy cover of 9.0% subtracted from that value and the site’s new canopy value would be 11.3%. Environmental covariates were then scaled by their standard deviation prior to analysis. All spatial analysis was performed in ArcMap v10.7.1 (ESRI, Redlands, CA).

## Model specification

We generated a multi-city, multi-species, autologistic occupancy model by modifying the code of Kass et al. (2020) to investigate the effects of local land cover on the occurrence and co-occurrence of squirrel species. Briefly, this model contains first-order parameters that are associated with each species, as well as second-order parameters that are associated with the co-occurrence of species pairs (e.g., fox and gray squirrels). We modeled latent occupancy state  $z_{s, i[j], t}$  of species  $s$  at site  $j$  nested within city  $i$  during season  $t$  using categorical random variables where modeled categories corresponded to the different possible occupancy states. We modeled the log odds a species (or multiple species) occupied a site (i.e., natural parameters  $f_1, f_2, f_3, f_{12}, f_{23}, f_{13}$  where numbers correspond to species; e.g.,  $f_1$  represents the log odds of fox squirrels (“species 1”) occurring as the sole

species on a site while  $f_{12}$  represents the log odds that gray squirrels (“species 2”) and fox squirrels occur together on a site) in the first year as a function of environmental predictors. For example, Eq. (1) describes the natural parameter specification for species 1:

$$f_1 = \beta_{0_i} + \beta_{i x_{i[j]}} \quad (1)$$

where  $\beta_{0_i}$  is the city-specific intercept for city  $i$ ,  $\beta_i$  is a vector of city-specific slope coefficients, and  $x_{i[j]}$  is a vector of conformable environmental predictor variables for site  $j$  within city  $i$ . We used nested indexing here (i.e.,  $i[j]$ ) as the number of sites within cities varies. Because we lacked sufficient observations to model colonization and extinction rates across sites (Mckann et al. 2013), we added a temporal autologistic term to account for temporal dependence in our data. For  $t > 1$  seasons, we modeled the natural parameter for each species  $s$  ( $f_1, f_2, f_3$ ) with an additional autologistic parameter  $\theta_s$ , which was dependent on the occupancy state of species  $s$  at site  $j$  within city  $i$  during the previous season  $t-1$  ( $z_{s, i[j], t-1}$ ) as described in Eq. (2):

$$f_{s,t} = \beta_{0_i} + \beta_{i x_{i[j]}} + \theta_{s z_{s, i[j], t-1}} \quad (2)$$

Autologistic terms can be interpreted as “state persistence” or “state stability” (e.g., a positive autologistic term suggests site occupancy status for a species at a site in one season is correlated with occupancy status in the preceding season). We modeled detection probabilities  $\rho_{s, i[j], k, t}$  for species  $s$  at site  $j$  within city  $i$  during survey  $k$  in season  $t$  as a function of the number of days a camera was active,  $\text{trapDays}_{i[j], k, t}$  as described in Eq. (3).

$$\text{logit}(\rho_{s, i[j], k, t}) = p_{0_i} + p_{1_i} \text{trapDays}_{i[j], k, t} \quad (3)$$

where  $p_{0_i}$  is the city-specific intercept and  $p_{1_i}$  is the city-specific slope for city  $i$ . We partially pooled information among cities by using city-specific random intercepts and slopes for all model parameters. All standard deviation terms were given vague Gamma priors (e.g.,  $\sigma_{\beta_0}^2 \sim \text{Gamma}(1, 1)$ ). Among-city averages were given vague normal priors (e.g.,  $\beta_i \sim \text{Normal}(0, 2)$ ).

We tested four candidate models, one model containing each landscape covariate (i.e., turfgrass, impervious, canopy cover; three total models) and one that used a principal components analysis (PCA), conducted using function ‘prcomp’ in R package “psych” (Revelle 2022), to summarize all three environmental covariates. We retained the first two PCA components, which explained 86% of the variation in these data. The loadings of the first metric, PC1, were impervious (0.66), canopy (-0.59), and grass (-0.46). Thus this metric represents a gradient of urban intensity such that negative

values represented locations higher in canopy and grass cover, and positive values represented locations higher in impervious cover. The loadings of the second metric, PC2, were canopy (0.54), grass (-0.83), and impervious (-0.10). Thus, PC2 separated vegetated sites with high canopy cover from sites with high grass cover.

We selected our best-fit model from the list of candidate models by calculating the conditional predictive coordinate (CPO) of each data point at each Markov chain Monte Carlo (MCMC) step (Geisser 1993). Overall model performance was evaluated with the summary statistic  $-\sum_{k,t} \log(\text{CPO}_{k,t})$  for data point  $k$  and MCMC step  $t$ ; the lowest value indicates the best relative fit (Hobbs and Hooten 2015). Following a 500-step adaptation and a 50,000-step burn-in, we sampled all model parameters 20,000 times across 3 chains for a total of 60,000 samples. To assess model convergence we inspected traceplots of all model parameters to assess proper mixing and ensured that all Gelman-Rubin diagnostics for each parameter were  $< 1.10$  (Gelman et al. 2013). All analyses were performed in R version 4.2.2 (R Core Team 2022) and JAGS version 4.3.1 (Plummer 2003). Following convention in multi-species occupancy modeling (Rota et al. 2016), we calculated marginal occupancy (i.e., the probability a species occurs on a site regardless of occupancy by other species;  $\psi^M$ ) and conditional occupancy (i.e., site occupancy probability of a species conditional on the presence/absence of another species;  $\psi^C$ ) from a randomly-selected 10,000 sample subset of the full posterior. We compared “expected co-occurrence” (i.e., the marginal occupancies of each pair of species multiplied together, thus calculating the probability of co-occurrence if species are distributed randomly with respect to each other) to conditional occupancy to determine the strength of the effect of the presence/absence of another species on occupancy. To determine the extent to which species occurrence and co-occurrence patterns from our top model varied across urban environments, we calculated 95% and 50% credible intervals to see if they overlapped zero. If the 95% credible interval did not contain zero this was considered “strong evidence”, and if the 50% credible interval did not contain 0 this was considered “weak evidence” (Kass et al. 2020).

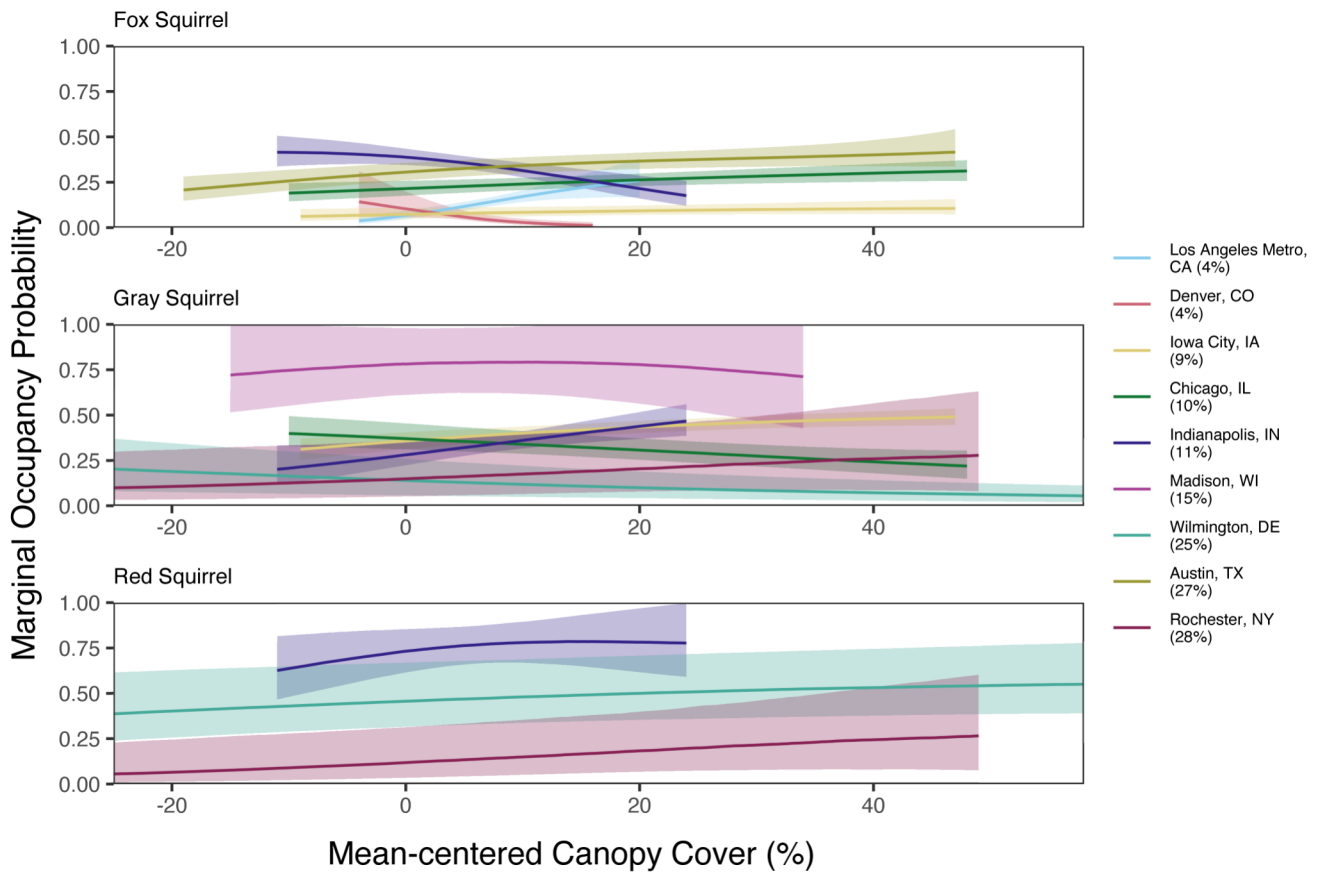
## Results

We recorded a total of 5,475 detections of squirrels across all surveyed cities, including 3,285 detections of gray squirrels in 6 cities, 2,108 detections of fox squirrels in 6 cities, and 82 detections of red squirrels in 3 cities. Gray squirrels were detected at 224 (61.2%), fox squirrels at 203 (55.5%), and red squirrels at 30 (8.2%) of the 366 sites across all cities. Fox squirrels were not detected in Madison,

Rochester, or Wilmington; gray squirrels were not detected in Austin, Denver, or Los Angeles; and red squirrels were only detected in Indianapolis, Rochester, and Wilmington. Our most-competitive model (CPO=30,756.79) included canopy cover, while next-best performing models included impervious (CPO=31,408.01) or the PCA-derived variables (CPO=34,946.98). The model including turfgrass cover was the least competitive model (CPO=41,818.08). The full model summary is available in Online Resource 1.

### First order parameters (marginal occupancy & persistence of individual species)

Marginal occupancy of all squirrels was highly variable among cities (Fig. 2). Gray squirrels had the least variable responses across cities, as measured by the standard deviation of the among-city intercept ( $\sigma_{\beta_0}^2 = 1.60$ , 95% CI: 0.71, 3.19) and canopy coefficient ( $\sigma_{\beta_{canopy,gray}}^2 = 0.71$ , 95% CI: 0.44, 1.30) while red squirrels had the most variable responses ( $\sigma_{\beta_0}^2 = 2.18$ , 95% CI: 1.20, 4.29;  $\sigma_{\beta_{canopy,red}}^2 = 0.76$ , 95% CI: 0.45, 1.48). The range of marginal occupancy values at average canopy cover (i.e., the intercept  $\beta_0$ ) for all squirrels was similar; occupancy in the highest-probability city, Indianapolis (0.39, 95% CI: 0.27, 0.54), was approximately five to six times greater than in the lowest-probability city, Los Angeles (0.07, 95% CI: 0.02, 0.18). At the among-city level we failed to detect a relationship between marginal occupancy and canopy cover for fox and red squirrels, while there was weak evidence of a negative relationship among all cities for gray squirrels ( $\beta_{canopy,gray} = -0.29$ , 50% CI: -0.51, -0.07). In individual cities, however, there was weak evidence for contrasting responses to canopy cover for all species. We found weak evidence of a positive relationship between canopy cover and fox squirrel occupancy in Chicago ( $\beta_{canopy,Chicago} = 0.29$ , 50% CI: 0.08, 0.52) and Los Angeles ( $\beta_{canopy,Los\ Angeles} = 0.44$ , 50% CI: 0.12, 0.77), and a negative relationship in Denver ( $\beta_{canopy,Denver} = -0.74$ , 50% CI: -1.27, -0.24). We found weak evidence of a negative relationship between canopy cover and gray squirrel occupancy in Chicago ( $\beta_{canopy,Chicago} = -0.42$ , 50% CI: -0.62, -0.22) and Wilmington ( $\beta_{canopy,Wilmington} = -0.52$ , 50% CI: -0.78, -0.26), and a positive relationship in Iowa City ( $\beta_{canopy,Iowa\ City} = 0.40$ , 50% CI: 0.22, 0.59). We found weak evidence of a positive relationship between red squirrel occupancy and canopy cover in Indianapolis ( $\beta_{canopy,Indianapolis} = 0.60$ , 50% CI: 0.21, 1.01). Persistence (i.e., the autologistic term  $\theta$ ) was, on average among cities, positive for all species, indicating species tended not to go extinct from camera sites between sampling seasons (i.e., occupancy patterns were stable through time). The exception to this trend was a negative relationship for red squirrels in Indianapolis ( $\theta = -3.23$ , 95% CI: -5.96, -1.53),



**Fig. 2** Marginal occupancy across canopy cover gradients in each city of (a) fox squirrels, (b) gray squirrels, and (c) red squirrels. Solid lines are median estimates and shaded polygons are 50% credible intervals. Numbers in parentheses identify average canopy cover for a given city (Table 1)

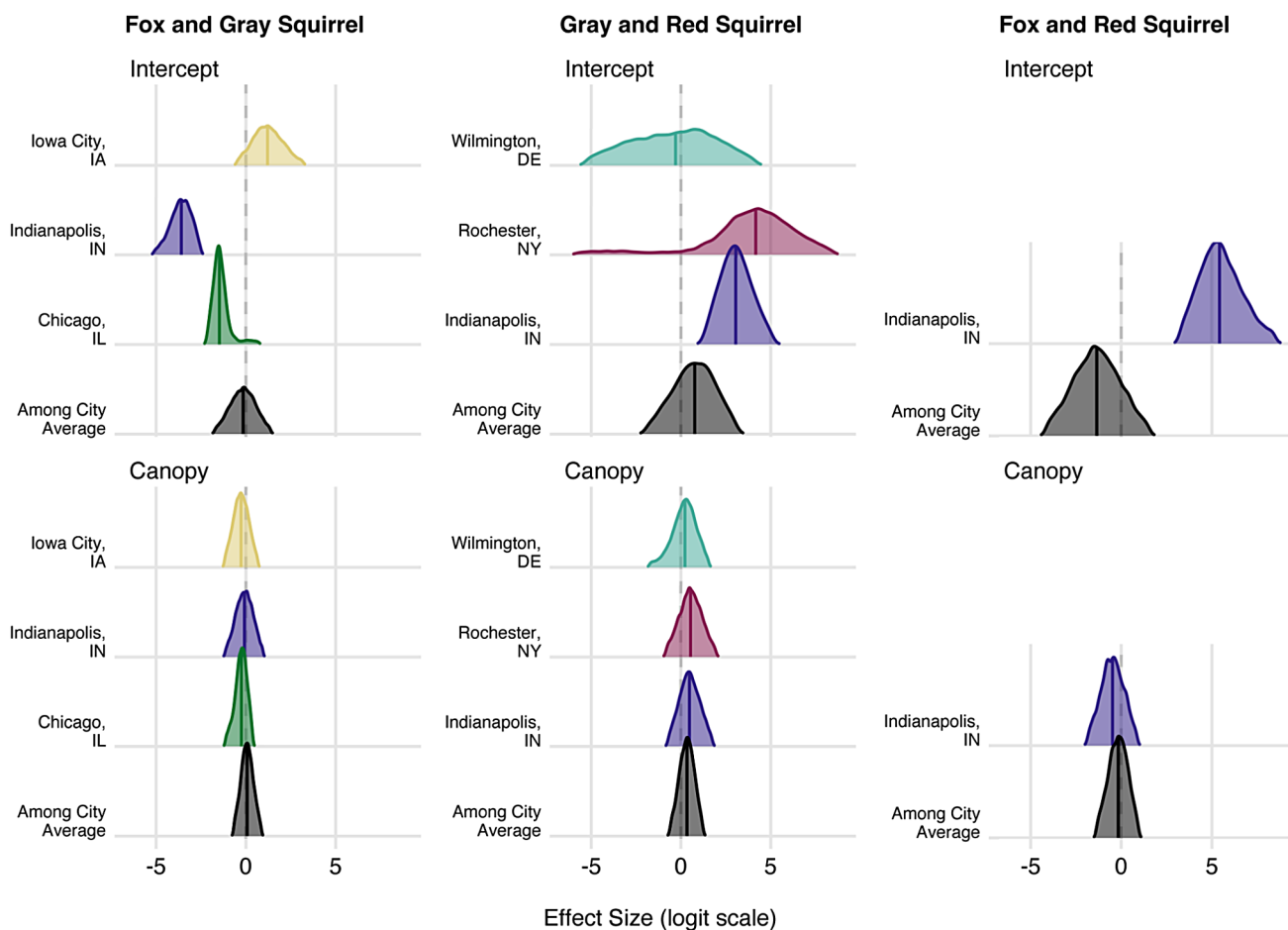
indicating sites were more likely to become unoccupied in the following season if red squirrels were present.

**Second order parameters: (species co-occurrence)**

The estimated variance of co-occurrence of each pair of species (for both the intercept and slope terms) was greater than the variance estimated for each species separately. Log-odds difference of co-occurrence was most variable for fox and red squirrels ( $\sigma_{\beta_{0_{fox+red}}}^2 = 5.16, 95\% \text{ CI: } 2.72, 11.21$ ) and least variable for fox and gray squirrels ( $\sigma_{\beta_{0_{fox+gray}}}^2 = 2.18, 95\% \text{ CI: } 1.35, 3.95$ ). Both fox and red squirrel ( $\sigma_{\beta_{canopy}^{fox+red}}^2 = 0.83, 95\% \text{ CI: } 0.46, 1.84$ ) and fox and gray squirrel ( $\sigma_{\beta_{canopy}^{fox+gray}}^2 = 0.83, 95\% \text{ CI: } 0.46, 1.60$ ) co-occurrence had similar variance in among-city response to canopy cover; while gray and red squirrel co-occurrence had the least variable response ( $\sigma_{\beta_{canopy}^{gray+red}}^2 = 0.75, 95\% \text{ CI: } 0.48, 1.54$ ). At the among-city level we did not find evidence that species co-occurrence was related to canopy cover for all combinations of species, except for weak evidence of a positive relationship with canopy cover for gray and red squirrel co-occurrence ( $\beta_{canopy} = 0.33, 50\% \text{ CI: } 0.03, 0.64$ ; Fig. 3). In individual cities,

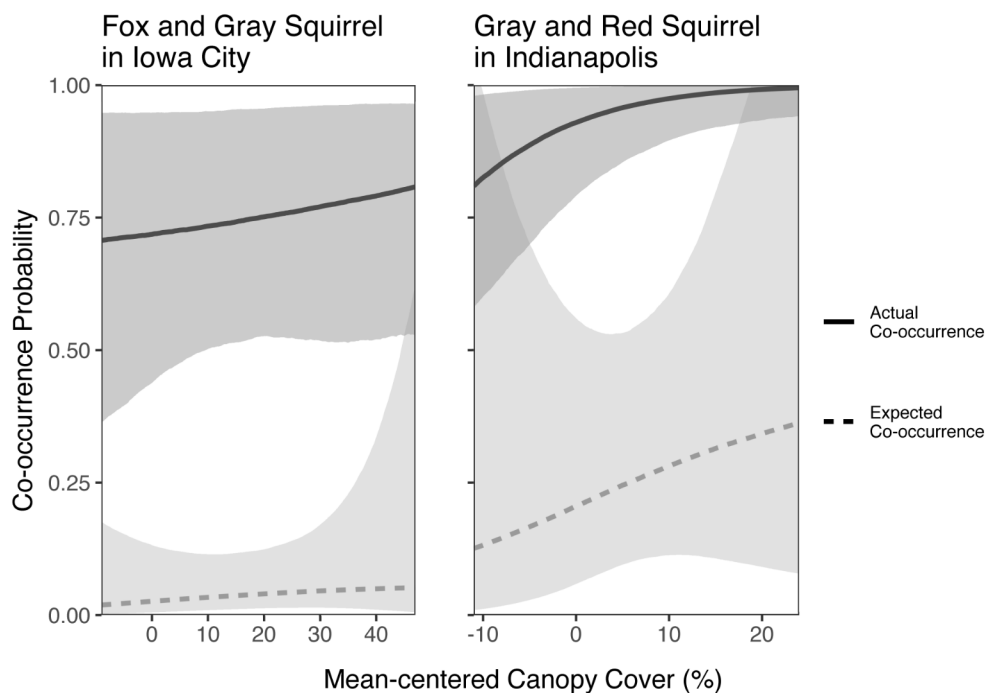
however, weak evidence suggested contrasting responses to canopy cover. There was weak evidence of positive relationships between gray and red squirrel co-occurrence and canopy cover in Indianapolis ( $\beta_{canopy, Indianapolis} = 0.44, 50\% \text{ CI: } 0.10, 0.79$ ) and Rochester ( $\beta_{canopy, Rochester} = 0.54, 50\% \text{ CI: } 0.09, 1.01$ ), and weak evidence of negative relationships between fox and gray squirrel co-occurrence and canopy cover in Chicago ( $\beta_{canopy, Chicago} = -0.25, 50\% \text{ CI: } -0.49, -0.02$ ) and between fox and red squirrel co-occurrence and canopy cover in Indianapolis ( $\beta_{canopy, Indianapolis} = -0.47, 50\% \text{ CI: } -0.93, 0.00$ ).

At the among-city level we found no deviation from the trend that fox and gray squirrels co-occurred together as expected if each species was distributed randomly with respect to the other at average canopy cover (expected  $\psi = \psi_{fox}^M \times \psi_{gray}^M = 0.03, 95\% \text{ CI: } 0.00, 0.76$ ). While this trend was true in Chicago and Indianapolis, in Iowa City, gray squirrels were significantly more likely to occur with fox squirrels than expected (Fig. 4; Online Resource 2). In Indianapolis (the only city with both fox and red squirrels), fox squirrels occurred with red squirrels as expected, while red squirrels were 1.4 times more likely to occur with fox



**Fig. 3** Density plots of the posterior estimates of intercept and canopy coefficients for (a) fox and gray squirrel, (b) gray and red squirrel, and (c) fox and red squirrel co-occurrence. Plots are 95% credible intervals, colored vertical lines inside plots are median estimates

**Fig. 4** Expected co-occurrence (i.e.,  $\psi_{species 1}^M \times \psi_{species 2}^M$ ) and actual (i.e., model-estimated) co-occurrence of (a) gray squirrels with fox squirrels in Iowa City and (b) red with gray squirrels in Indianapolis. Lines are median estimates and shaded ribbons are 95% credible intervals





squirrels than without. Among cities, we found no deviation from the trend of gray and red squirrels co-occurring together as expected, although expected co-occurrence was highly variable (expected  $\psi = 0.03$ , 95% CI: 0.00, 1.00). The only exception to this was Indianapolis, where red squirrels were 1.2 times more likely to occur with gray squirrels than without.

## Discussion

Overall, we found occupancy and co-occurrence of all species was highly variable among cities, but less variable with respect to canopy cover within a city. We did, however, find weak evidence that canopy cover was associated with co-occurrence in some cities and, surprisingly, the direction of this relationship among cities was not the same. These findings support the idea that urban squirrels spatially partition urban habitat. Most combinations of species occurred together as often as expected; however, some pairs of species occurred together more frequently than expected but the relationship was not the same in all cities. The variability in species co-occurrence patterns among cities suggests that potential interactions among species also vary among cities, even for common urban wildlife species, and likely contributes to differences in urban wildlife community assemblages found in this and other studies (Fidino et al. 2019; Parsons et al. 2019; Bach et al. 2023).

### Marginal occupancy was highly variable among, but less variable within, cities

We predicted that fox and gray squirrel responses to urban intensity would be similar among cities and our results provide some support for this prediction. Fox and gray squirrels exhibited less variation in both their average occupancy probability and responses to canopy cover than red squirrels. Although variation of model estimates was lower for these species, the direction and magnitude of the effect of canopy cover on fox and gray squirrel occupancy differed among cities. The relative availability of vegetated habitat may underlie these differences. For example, in a previous multi-city study, both fox and gray squirrel occupancy positively covaried with increasing housing density in cities with  $\geq 25\%$  green space; below this level, both species responded negatively to housing density (Fidino et al. 2021). The cities in our study had a large range of average canopy cover (4–28%); therefore, landscape-scale differences in canopy cover or green space availability among cities may explain the variable city-specific responses of fox and gray squirrels to canopy cover in our study. Additionally, our sampling

tends to occur on trees, so there may be preferential bias towards areas where squirrels are located within a city.

Fox squirrels had the weakest relationship with canopy cover of all squirrel species. This finding is likely related to attributes of this species' morphology and behavior which allow fox squirrels to use habitats with low canopy cover because their larger body size protects them from predation and facilitates movement between resource patches (Koprowski 1994a). However, we found weakly significant relationships between occupancy and canopy cover for some cities. Fox squirrel occupancy was negatively correlated with canopy cover in Denver, and positively correlated with canopy cover in Chicago and Los Angeles. Los Angeles is located outside the native range of fox squirrels and southern California, where Los Angeles is located, is a chaparral ecosystem with low canopy cover except along riparian corridors. Thus, fox squirrels, which were introduced to this city by humans, likely select for urban habitat patches with greater canopy cover to provide nesting locations and food resources. High-canopy-cover sites are also the preferred habitat of western gray squirrels, and fox squirrels have contributed to the decline of the western gray squirrel by displacing them from these habitats (Muchlinski et al. 2009). Reducing the negative effects of fox squirrels on western gray squirrels in southern California will require careful management of the urban canopy to reduce fox squirrel habitat without sacrificing habitat for western gray squirrels. Alternatively, canopy cover may be correlated with additional, unmeasured environmental variables (e.g., human activity, predator presence) to which fox squirrels may be responding.

We were surprised to find weak evidence for decreasing gray squirrel occupancy with increasing canopy cover at the among-city level. Given that gray squirrels typically prefer relatively closed-canopy environments in natural and semi-natural landscapes (Koprowski 1994b), their absence from these habitats may be the result of competitive exclusion through interspecific competition. However, we did not find evidence of increased occupancy probability at higher levels of canopy cover for the other species in our study, with the exception of fox squirrels in Chicago. Although gray squirrels may prefer closed-canopy environments as stated above, they are also relatively flexible in their habitat requirements (Koprowski 1994b) and thus may not be very sensitive to changes in canopy cover along urbanization gradients. Alternatively, gray squirrels may be responding to increased food resources in low-canopy urban habitats. Gray squirrels will consume anthropogenic foods (e.g., garbage; Rimbach et al. 2023) and may forage in low-canopy habitats to take advantage of this resource, especially if they perceive the surrounding habitat as less risky (Bowers and Breland 1996). Gray squirrels may also have been

more detectable on low-canopy sites, as they can occur at greater abundances in urban environments (Engel et al. 2020) and the lack of understory vegetation likely increases visibility. A negative relationship with canopy cover was not detected in all cities with gray squirrels, however, further highlighting the importance of multi-city investigations into the effects of urbanization on wildlife. Even common urban wildlife species, such as fox and gray squirrels, can have highly variable responses to the urban environment across cities.

We predicted consistent negative responses to urban intensity by red squirrels, and our results were equivocal as to this prediction. We were unable to detect a relationship between red squirrel occupancy and canopy cover at the among-city and within-city levels (except for weak evidence of a relationship within Indianapolis). Red squirrels also exhibited greater variation in their estimated model parameters compared to other squirrel species, likely due to the small number of red squirrel detections in our study which reduced the precision of model estimates. Red squirrels are territorial (Steele 1998), which could reduce local abundance and, in turn, detection and occupancy. Additionally, red squirrels are more arboreal than both fox and gray squirrels (Steele 1998), which could also reduce detection rates as our set-up is aimed at capturing terrestrial mammals. Thus, our estimates of site occupancy by red squirrels should be considered conservative. Increasing red squirrel detections by sampling over additional seasons or in additional cities where red squirrels are known to occur, or by using additional cameras deployed in tree canopies, could increase the precision of model estimates. Given that red squirrels are important seed dispersers for coniferous trees and may be important dispersers of fungal spores (Pauli et al. 2019), their presence in (or absence from) cities could have implications for urban forest processes.

### **Co-occurrence of species is highly variable and only weakly related to canopy cover**

We predicted that co-occurrence of fox and gray squirrels would vary across cities, and our results both support and refute this prediction. Fox and gray squirrels appear to spatially partition urban habitat, as suggested by stable site occupancy patterns (i.e., positive autologistic terms) and low probabilities of co-occurrence. This finding is similar to published reports of local-scale habitat partitioning among gray and fox squirrels from other urban and non-urban ecosystems (Armitage and Harris 1982; Brown and Batzli 1985; Conner et al. 1999; van der Merwe et al. 2005). However, this trend was not universally observed in all study cities. In Iowa City, fox and gray squirrels were more likely to occur together than expected. This finding could

be related to the distribution of intense row-crop agriculture and urbanization, which could confine squirrel activity in this city to remaining forest patches and force these species to use other adaptations (e.g., temporal partitioning; Larson and Sander 2022) to maintain coexistence. Fox and gray squirrel co-occurrence was more variable among cities than within, as we found little evidence of an effect from a city's canopy cover gradient. There was, however, some evidence that fox and gray squirrels occurred together less frequently than expected as canopy cover increased in Chicago. Fox squirrels may displace gray squirrels from sites with greater canopy cover, as fox squirrel occupancy increased while gray squirrel occupancy decreased as canopy cover increased. Alternatively, as described above, gray squirrels may be better able to persist in low-canopy environments if food resources are scarce given their greater foraging efficiency over fox squirrels, as van der Merwe et al. (2005) previously reported in Chicago. Canopy cover may also be correlated with an unmeasured environmental variable (e.g., predator presence) to which gray and fox squirrels respond. Both hypotheses warrant future investigation. Nevertheless, variation in canopy cover within a city appears to help to maintain a diverse squirrel community. These results highlight the need for multi-city analysis of co-occurrence trends to capture variance in species' responses to urbanization and the presence of potential competitors, even for common urban wildlife species.

Finally, our results did not support our prediction that red squirrels would rarely co-occur with other squirrel species. Rather, red squirrels occurred with another squirrel species as often as predicted by chance such that co-occurrence probabilities ranged from 0.48 with gray squirrels in Wilmington to 1.00 with fox squirrels in Indianapolis. Given the rarity of red squirrels in our cities, our sample size was likely too small to explore variation in co-occurrence with this species, resulting in model predictions of red squirrel co-occurrence with other species at probabilities that would be expected if co-occurrence were random. Red squirrel co-occurrence with other squirrels may be moderated by canopy cover as, on average among cities, gray and red squirrels co-occur more frequently than expected at sites with increasing canopy cover. This pattern likely results from the preference of both species for habitats with high canopy closure (Koprowski 1994b; Steele 1998), and the potential for high canopy cover sites to take the form of larger forest fragments that could support multiple squirrel species. Conversely, we found some evidence that fox and red squirrels occurred together less frequently than expected as canopy cover increased. Fox squirrels, with their larger body size, are more tolerant of the predation risk associated with open canopy habitat (Koprowski 1994a), and may outcompete red squirrels in those habitats. Alternatively, red

squirrels are more sensitive to canopy cover than fox squirrels and may thus be less likely to use open canopy habitat. Model estimates for red and fox squirrel co-occurrence were also highly variable, most likely because these species only co-occurred in one city; thus, interpretation of our results warrants caution. Nevertheless, red squirrel co-occurrence with other squirrel species was highly variable within cities and less variable among cities. Our results provide some encouraging evidence that patterns in urban red squirrel co-occurrence with other squirrel species resemble co-occurrence patterns in rural environments where different habitat preferences for canopy cover and foraging tree species best predict co-occurrence probabilities (Riege 1991; Fisher and Merriam 2000).

### Limitations & future directions

Our findings should be considered in light of certain limitations. First, we evaluated variation in patterns of species occupancy, a relatively coarse metric, which addresses spatial overlap but not fine-scale mechanisms that may contribute to co-occurrence, such as temporal partitioning. Future studies could use timestamp information from camera images to assess variation in activity timing across urbanization gradients, or variation in spatial overlap at certain times of year (e.g., during the fall hoarding season) in different urban habitats. As our analysis focused at the site level, we could not determine how the dispersal of individuals could influence co-occurrence patterns or whether co-occurrence states were temporary or long-lasting. Future research could assess how the different dispersal abilities of species and connectivity among urban habitat patches combine to influence occupancy patterns, for example, using circuit theory models (Grafius et al. 2017). Connectivity may be particularly important for red squirrels, which are more arboreal than fox and gray squirrels and rely on connected tree canopy cover for dispersal (Steele and Koprowski 2001). Additionally, we included cities that are not within the known range of all three species (e.g., Los Angeles), causing the model to struggle to estimate certain co-occurrence probabilities (e.g., for fox and red squirrels, which are absent from Los Angeles). As a result, these specific co-occurrence estimates have high variation and large, uninformative confidence intervals (Online Resource 1). However, these cities still provide important information regarding species responses to the urban environment for the species that do occur in them, improving model estimates for those species. Future studies could use the approach of Magle et al. (2021) to add a ‘distance to range edge’ covariate to address co-occurrence estimation issues resulting from species being absent from some cities. As discussed throughout this study, competition could predict tree squirrel occupancy patterns,

but wildlife cameras cannot directly measure competition between species. Although species must co-occur in some capacity to compete, and our results provide estimates of co-occurrence, co-occurrence is not direct evidence of competition. Behavioral observations or data from GPS collars would provide evidence to elucidate the role of direct competition. Additionally, predation is known to be an important mediating factor in the co-occurrence of species; future occupancy models could include the presence of predators (e.g., mammalian carnivores, domestic cats/dogs) at each site to assess the role of predation and address the possibility of tree squirrel habitat partitioning as apparent competition (*sensu* Holt 1977).

### Conclusion

Our research suggests tree squirrel co-occurrence both within and among cities is considerably more variable than any single species’ occurrence. This finding suggests that environmental filtering associated with urbanization shapes wildlife communities differently in different landscape contexts. Evidence from this and other studies indicates that highly-urban environments can and do support tree squirrels (e.g., in Chicago, see above). Managing urban habitats to provide sufficient resources, particularly by providing tree canopy cover, would better support diverse forest species communities and the biotic interactions that maintain those communities, which warrant particular consideration in implementing conservation in formerly-forested regions. Our research also demonstrated temporal fluctuations (i.e., changes from season to season) in occupancy for red squirrels, suggesting that the occurrence of red squirrels in urban areas could rely on colonization and extinction (e.g., source-sink dynamics) and that maintaining connectivity within and among cities and exurban areas may be critical to urban red squirrels. Changes in occurrence and co-occurrence patterns across space and through time mimic niche partitioning among competing species in natural ecosystems, indicating that interspecific interactions play an important role in structuring urban wildlife communities. Changes in spatial overlap along urbanization gradients could lead to a loss of interactions, a precursor to declines in ecosystem function and species loss (Valiente-Banuet et al. 2015). Urban ecosystems are also key areas for biodiversity conservation (Aronson et al. 2014; Ives et al. 2016); thus, increasing our understanding of the effects of urbanization on processes that structure wildlife communities, such as species co-occurrence and interactions, will be critical to maintaining biodiversity in and beyond cities.

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**Author contributions** R.N.L. and H.A.S. developed the initial study proposal, covariate collection methods, and wrote the initial drafts of the manuscript. R.N.L. and M.F. wrote the R scripts for data analyses. R.N.L. made the figures. All authors (R.N.L., H.A.S., M.F., J.L.A., S.H.H., S.B.M., K.C.M., C.M.S., T.S., K.T., L.B., A.M.D., D.D., L.H., P.R.S., A.R., T.S., J.W., & A.J.Z.) collected camera data and reviewed and edited the manuscript.

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**Data availability** The data that support the findings of this study and the model code are openly available on Zenodo at <https://doi.org/10.5281/zenodo.11132184>.

## Declarations

**Competing interests** Coauthor Seth B. Magle is on the editorial board for Urban Ecosystems.

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