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Research Article

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Variation in species-specific responses to habitat fragmentation and land cover structure in urban small mammal communities

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Abstract

Urbanization is a key driver of habitat loss and fragmentation worldwide, yet many urban ecosystems contain vegetated habitat patches that support diverse wildlife communities. Managing urban systems to support robust wildlife communities requires us to understand the mechanisms that drive the response of species to the urban environment. Small mammals are key components of terrestrial ecosystems (e.g., seed predators, prey) and likely also carry out these roles in urban ecosystems; however, the effects of urbanization on small mammal communities are understudied. To identify how species-specific responses to urban environments shape community composition, we quantified both overall community and species-specific changes in small mammal abundance across an urbanization gradient in a Midwestern US metropolitan area. We combined small mammal trapping and land cover data to generate a hierarchical community abundance model. Species diversity increased with increasing proportional cover of human-modified land cover (i.e., impervious surfaces and turfgrass). This finding is driven by high species diversity on sites bordering streams in mowed parks and low diversity on sites with high tree canopy closure. Additionally, modeling results indicated that species responded differently to landscape attributes, leading to variation in small mammal community composition across the urbanization gradient: prairie-associated species tended to be more abundant in tall vegetation bordering mowed parks while habitat generalists tended to be more abundant on sites with greater canopy closure and shrub cover. Our results suggest studies that focus on community-level responses (e.g., species richness) to urbanization may miss important species-specific responses. It may be particularly important to assess both species-specific and community-level responses in cities at ecotones (e.g., between forest and grassland) where species with different habitat requirements may replace one another in different types of green spaces, thereby changing community composition without affecting species diversity or richness. Our findings also indicate that vegetated urban patches, especially patches with tall vegetation cover and low canopy cover, are important habitat for prairie-associated small mammal communities, providing conservation options in heavily altered landscapes.

Key words: urban, rodent, shrew, community, abundance, species richness, habitat fragmentation

Urbanization, the process of urban growth whereby vegetated land cover is replaced with impervious surfaces (i.e., buildings, pavement), is a key driver of habitat loss and fragmentation worldwide (Foley 2005; Seto et al. 2012). The proportion of the Earth's surface covered by urban land is expected to grow as the human population becomes increasingly urban (United Nations 2019), suggesting that these effects will increase. However, urban ecosystems often contain vegetated areas that can support diverse wildlife communities (Parsons et al. 2018), suggesting that urban environments could play a role in the conservation of wildlife. It is also increasingly apparent that wildlife responses to urbanization result from a complex interplay between the characteristics of urban environments and species biology (Aronson et al. 2016; Santini et al. 2019; Fidino et al. 2021), but we do not currently fully understand the mechanisms that drive the response of species to urban environments. Improved understanding of the factors that underlie the varied responses to urbanization exhibited by different species is critical to supporting the conservation of diverse biotic communities in cities.

Small mammals (e.g., small rodents, shrews) are key components of terrestrial ecosystems with roles in seed dispersal, the regulation of both plant and insect prey and predator populations, and the transmission of diseases of importance to both wildlife and human health. Given the central role small mammals play in ecosystem functioning, and the likely sensitivity of these species to urbanization (Cavia et al. 2009), broadening knowledge of the impacts of urbanization on small mammal communities will facilitate the management of cities to further understand these species and the communities of which they are a part. However, urban small mammals have received relatively little attention in the scientific literature. In Europe and South America, where

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these species are best studied, species richness and abundance of small mammals appear to decline as urbanization increases (Dickman 1987; Baler et al. 2003; Castillo et al. 2003; Cavia et al. 2009; Gomes et al. 2011; Klimant et al. 2017). The response of individual species to urbanization may be partially explained by their biology; for example, shrews with lower dispersal ability or specialist habitat requirements were less likely to occur as urbanization increased in both Paris, France (Vergnes et al. 2013) and Chełm, Poland (Łopucki and Kitowski 2017), potentially due to the small size of urban habitat fragments, the lack of preferred habitat for specialists, and their relative isolation. Given their generally low dispersal ability, such fragmentation may particularly restrict the movements of small mammals. While these studies have begun to identify patterns in the distribution of urban small mammals, we still do not know the degree to which these patterns apply across cities and urban settings, particularly outside of Europe and South America.

North American urban small mammals have received little study. A handful of studies have investigated community-level responses to urbanization (e.g., species richness, species diversity), largely identifying a trend of decreasing species richness as urbanization increases, similar to findings elsewhere (Mahan and O'Connell 2005; Johnson and Karels 2016; Viteri and Hadly 2022). While community-level metrics provide useful information, they cannot fully identify aspects of the urban environment to which species are responding nor how community composition changes across urbanization gradients. Additionally, North American cities differ from European and South American cities in their development history (e.g., sprawling vs. compact; Ingram and Carroll 1981; Dong et al. 2019) and species composition, suggesting that patterns in their small mammal communities and drivers of these patterns may differ from those observed on other continents. While previous North American studies have speculated that sensitivity to human activity (Mahan and O'Connell 2005; Viteri and Hadly 2022) and/or reliance on a specific vegetation community (Johnson and Karels 2016) may drive patterns of reduced species richness, no studies have empirically investigated these drivers. Thus, we know little about how individual small mammal species responses shape community-level patterns in small mammal diversity in cities.

In this study, we sought to identify the impacts of urbanization on native small mammals at both the species and community levels. To do so, we quantified changes in small mammal abundance in both the overall community and for specific species across an urban intensity gradient in the Iowa City metropolitan area of the Midwestern United States. We expected that small mammal species richness would decrease with urban intensity (i.e., proportional cover of human-associated land cover types) and fragmentation and increase with proportional native vegetation cover and connectivity. We expected these trends to be driven by the sensitivities of different species to urban development. We further expected that deer mice (*Peromyscus* spp.) and northern short-tailed shrews (*Blarina brevicauda*; hereafter "short-tailed shrews"), both habitat generalists, would not show strong relationships with land cover variables such that neither species would exhibit statistically significant relationships with human-modified land cover. Alternatively, voles (*Microtus* spp.), western harvest mice (*Reithrodontomys megalotis*; hereafter "harvest mice"), and meadow jumping mice (*Zapus hudsonicus*; hereafter "jumping mice"), all prairie-associated species, would show strong negative relationships with human-modified land cover. Thus, species richness and diversity would decrease with increasing urban intensity because prairie-associated species respond negatively to this land cover category, while generalist species are able to remain at all sites.

Materials and methods.

Study area.

This study focused on Iowa City, Iowa, US metropolitan area, including the cities of Coralville and North Liberty, and surrounding rural areas (Fig. 1). This area is characterized by rolling hills and intermittent plains and experiences hot summers (annual average high temperature of 16.6 °C) and cold winters (annual average low temperature of 4.7 °C). Average annual precipitation includes 956 mm of rainfall and 710 mm of snowfall. Prior to European settlement, this area consisted of prairie, oak savannah, and eastern deciduous forest (Anderson 2012). However, current land cover includes 51% row crop and 12% impervious cover with presettlement vegetation cover reduced to 17.5% (Homer et al. 2015). The metropolitan area is approximately 213 km^2 with a human population of 175,732 (U.S. Census Bureau 2021). The metropolitan area has an average cover of 31% impervious, 29% "green" (row-crop agriculture, forest, and herbaceous vegetation), and 38% turf grass cover.

Ten species of small mammal (defined as terrestrial mammals weighing less than 120 g as adults) are known to occur in Johnson County, which contains the Iowa City metropolitan area (Rentz et al. 2018). These include 2 species of shrews, Short-tailed Shrew and Masked Shrew (*Sorex cinereus*); Eastern Chipmunk (*Tamias striatus*); 2 species of deer mice, White-footed Mouse (*Peromyscus leucopus*) and Deer Mouse (*P. maniculatus*); 2 species of voles, Prairie Vole (*Microtus ochrogaster*) and Meadow Vole (*M. pennsylvanicus*); Harvest Mouse, Jumping Mouse, and House Mouse (*Mus musculus*).

Small mammal trapping.

Live-trapping of small mammals occurred on 45, 50-m plots selected to span the gradient of urbanization in the Iowa City metropolitan area. As detailed in MacDougall and Sander (2022), these sites are part of a larger urban wildlife monitoring network designed to sample wildlife with different home range sizes. Network design began with the identification of 3 transects: 1 30-km transect running from northwest to southeast across the metro area; and 2 14-km transects that are perpendicular to the 30-km transect; see Fig. 1 in MacDougall and Sander (2022) to capture the gradient of urban intensity (quantified using proportional impervious surface cover) in the study area. To ensure consistent sampling intensity across the study area, transects were divided into 10, 5 km × 4 km "survey squares" within which sites for 3 to 4 wildlife trail camera locations were selected to represent the land cover composition of each square. Sites are separated by ≥1 km to avoid detecting the same animal on multiple cameras and are used to sample medium- to large-bodied mammals. Given the smaller body and home range sizes of many small mammals, we selected smaller sampling areas within 1 km of each camera to survey small-bodied mammals. We delimited a 1-km buffer around each camera, then selected 3 to 4 random points within each buffer to act as small mammal sampling sites. Resulting trapping sites were separated by a minimum of 168 m, which, given the small home ranges of the species in this study (e.g., Deer Mouse: 405 m^2; Lackey et al. 1985), suggests low potential for double-counting. The 50-m radius area surrounding each of these points acted as our small mammal survey plots.

We used *k*-means analysis to group survey plots into distinct habitat types based on the proportion of cover of several 2016 National Land Cover Database land cover classes (Dewitz et al. 2019). We first used ArcMap version 10.7.1 (ESRI, Redlands, California) to calculate the proportional cover of water (Open Water), herbaceous vegetation (Developed Open Space, Grassland/Herbaceous, Pasture/Hay, and Emergent Wetland Vegetation combined), forest (Deciduous Forest, Coniferous Forest, Mixed Forest, and Woody Wetlands combined),

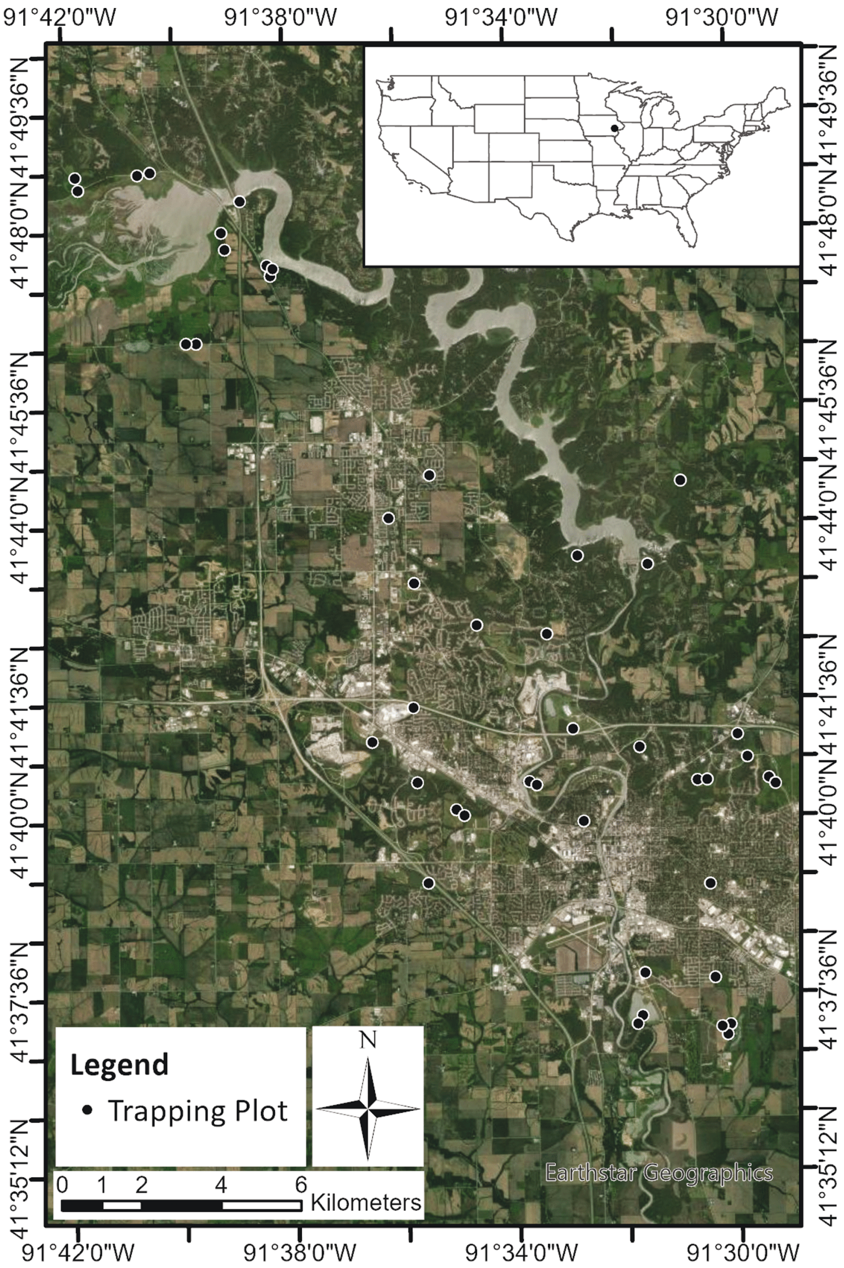

Fig. 1. The Iowa City metropolitan area of Iowa, United States, including the locations of the 45 survey plots where small mammal trapping took place from 2021 to 2022. Inset map shows the location of the study area in the broader context of Iowa and the United States.

developed land (Low-, Medium-, and High-Intensity Developed), and cropland (Cultivated Crops) on each 50-m radius plot. We then used the "kmeans" function in the base R "stats" package (R Development Core Team 2022) to group survey plots into 6 clusters, which we determined was the optimal number of clusters upon inspecting the within-group sum of squares. Dimension 1, which accounted for 45.3% of variation among sites, separated sites with high developed cover (Cluster 1) or a mix of developed and herbaceous cover (Cluster 5) from sites with high forest or herbaceous cover (Clusters 2, 3, 4, and 6). Dimension 2, which accounted for 30.2% of variation among sites, separated sites with high herbaceous cover (Cluster 3) or a mix of herbaceous and crop cover (Cluster 6) from sites with high forest cover (Cluster 4) and sites with mixed forest and herbaceous cover (Cluster 2). To ensure a representative sample, we selected 1 survey plot of each *k*-means cluster type per camera for small mammal trapping, resulting in an initial sample of 52 plots. In some instances, camera trap sites and their associated plots were in areas not conducive to small mammal trapping (e.g., parking lots) or landowners would not provide permission to access their property. These plots were excluded from our analysis, leaving a total of 45 survey plots across the study area (n = 12 in Cluster 1; n = 17 in Cluster 2; n = 2 in Cluster 3; n = 3 in Cluster 4; n = 7 in Cluster 5; n = 4 in Cluster 6).

We established a 100-m small mammal trapping transect through the plot centroid on each 50-m radius survey plot. Transects were oriented to capture the greatest possible variation in vegetation types on each plot. Plots with homogenous vegetation had transects with either a north/south or east/west orientation and trapping stations were located every 11 m along these transects. Trap stations that were unsuitable or unsafe for trapping (e.g., on a sidewalk) were excluded, reducing the trap station count for that survey plot. We placed 1 small folding Sherman Trap (5 cm × 6 cm × 17 cm; H.B. Sherman Traps Inc., Tallahassee, Florida) within 1 m of each trap station during each sampling bout. Traps were positioned under shrubbery or along fallen logs to increase trap success. If no suitable locations existed within 1 m of a given trap station (e.g., the station was flooded), that station was excluded from that sampling bout. Traps were baited with approximately 1 teaspoon of birdseed mix (sunflower, millet, safflower, peanuts). To reduce mortality, 0.5 teaspoon of peanut butter was added to the bait when overnight temperatures were expected to fall below 7 °C to provide additional calories, similar to other small mammal trapping protocols (Paull et al. 2020), and polyester batting was added to traps as insulating bedding when overnight temperatures were forecast to fall below 18 °C. If a site had high shrew captures (≥20% of individuals) after 1 season of trapping, we added 1 teaspoon of freeze-dried meal worms to the birdseed bait in subsequent seasons to increase the likelihood of shrew survival. All sites were trapped for 3 consecutive nights in the spring (10 April to 26 May), summer (3 July to 14 August), and fall (20 September to 6 November) from spring 2021 to fall 2022. No trapping occurred during the winter (7 November to 9 April) due to logistical complications and high mortality potential when trapping animals in extreme cold and snowy conditions.

Traps were opened at sunset and then checked at sunrise. We recorded moon illumination (proportion full) for each trapping night, the ordinal date, and trap effort. We used the "getMoonIllumination" function from the R package "suncalc" (Thieurmel and Elmarhraoui 2019) to record the proportional fullness of the moon. Trap effort was recorded as the number of traps that were undisturbed (i.e., open) or contained an animal when we checked traps. All captured animals except shrews were taken to a shaded location just off the plot for processing. Individuals were marked with a 3-digit ear tag (Mouse Tag Style 1005-1; National Band & Tag Company, Newport, Kentucky) in their right ear to provide information about recaptures that will be used in additional analyses beyond this study. Chipmunks were not ear-tagged in compliance with our permits and instead marked with nontoxic permanent marker on their chests. All animals were identified to species, sexed, weighed, and measured (right hind foot, ear, tail, and total body measurements). Because *P. leucopus* and *P. maniculatus* are difficult to reliably identify to species through physical characteristics, we labeled all *Peromyscus* captured as "deer mice." We did not handle live short-tailed shrews or masked shrews; live shrew captures were recorded with the date, species, and trap location, then immediately released to prevent mortality. All mortalities (24 short-tailed shrews, 16 deer mice, and 4 masked shrews) were weighed, measured, and stored in individual zipper-top bags at 0 °C before being deposited as voucher specimens at the University of Iowa Museum of Natural History. All trapping protocols followed ASM guidelines for conducting research on wild mammals (Sikes et al. 2016) and were approved by the University of Iowa Animal Care and Use Committee (protocol #0022288) and the Iowa Department of Natural Resources (permit #SC1419).

Urban environmental variables.

We obtained survey plot vegetation characteristics to use as covariates for modeling from field surveys and geographic information systems analysis. To estimate the percent cover of understory vegetation on each plot, we ran 4 evenly spaced 50-m transects from the centroid to the perimeter of each plot. We then recorded the occurrence of non-turfgrass vegetation in 5 height classes (0 to 75, 76 to 150, 151 to 500, 500 to 1,000, and >1,000 cm), turfgrass, and impervious cover at points located every 10 m along each transect. We calculated the percentage of points covered by each vegetation type and impervious cover along each transect to identify the percent cover of that type and averaged percent cover values for all transects on a plot to identify the plot vegetation and impervious cover. We combined the proportional cover of vegetation in the 76 to 150 cm and 151 to 500 cm height classes into a single variable we called "shrub cover," as most of the plants in our study area from these height classes are woody shrubs, e.g., Amur Honeysuckle (*Lonicera maackii*), dogwoods (*Cornus* spp.), and wild rose (*Rosa* spp.). Using a spherical densitometer, we measured canopy closure at the midpoint of each transect 4 times (facing north, south, east, and west), then averaged all measurements to identify plot percent tree canopy closure. We also combined the proportional turfgrass and impervious cover to create a "human-modified land cover" variable.

Because many of these variables were colinear (e.g., canopy closure and human-modified land cover; Pearson's correlation coefficient = −0.5), we used the "prcomp" function in R package "psych" (Revelle 2022) to perform a principal components analysis to create composite variables. The first component (PC1) explained 49.5% of the variation (Table 1). Canopy closure, shrub cover, and tall herbaceous cover (the 0 to 75 cm height class) loaded positively on this axis (0.509, 0.184, and 0.619, respectively) while human-modified land cover loaded negatively (−0.569). Thus, this axis roughly represents a "human-modified" to "naturally vegetated" continuum. We saved the scores of each plot to use as a variable in our community abundance model.

Geographic information system.

In addition to the vegetation characteristics of each plot, we also included the structural connectivity in the surrounding landscape as a model covariate. We delimited a 100-m radius buffer around each survey plot using ArcMap to approximate the average dispersal distance of deer mice (Stickel 1968), which disperse farther than the other species surveyed in this study (e.g., 30 m average dispersal for prairie voles; McGuire et al. 1993). While some individuals can disperse much longer distances, these events are rare and their importance for community abundance is minimal compared to more common dispersal distances. We then used the 2019 National Land Cover Database (Dewitz et al. 2021) to calculate the proportion of vegetated (Developed, Open Space; Developed, Low Intensity; all forest classes; Shrub/Scrub; Grassland/Herbaceous; all planted/cultivated classes; all wetlands classes) and nonvegetated (Open Water; Developed, Medium Intensity; Developed, High Intensity; Barren Land) cover within each plot and its buffer. We used the "lsm_l_contag" function in the R package "landscapemetrics" (Hasselbarth et al. 2019) to calculate a contagion index, which measures the level of dispersion and interspersion of land cover (i.e., pixel) types in a landscape. The metric ranges from 0 to 100, with low values indicating low dispersion of different land cover types (i.e., cell types are clumped) and high values indicating high interspersion (i.e., cells are equally adjacent to all other classes). Thus, contagion roughly represents a "continuous habitat" (low values) to "fragmented habitat" (high values) continuum.

Community abundance model.

We used a dynamic community abundance model (Chandler et al. 2013; MacKenzie et al. 2018) in a Bayesian framework to investigate trends in small mammal community dynamics through time. Dynamic community abundance models are hierarchical models with 2 submodels. One submodel represents the latent, unobservable true abundance (including gains and losses) while the other submodel represents the observed counts as a function of the proportion of the true number of individuals at a site that are captured on any given night.

Species-specific abundance ($\mathbf{N}_{ijt}$) was derived from a Poisson distribution with a mean of λ. Initial abundance of each species i at site

Table 1. Summary of site-level covariates for the dynamic community abundance model describing small mammal communities in the Iowa City, Iowa metropolitan area, United States, 2021 to 2022. Means and standard deviations were calculated using measurements from all 45 trapping sites. "PC1 loading" describes how each variable was loaded on the first axis of a principal components analysis.

Variable	Mean	Standard deviation	Range	PCA loading, Axis 1
Canopy closure	48%	36%	0% to 98%	0.509
Shrub cover[a]	25%	20%	0% to 85%	0.184
Tall herbaceous cover[b]	56%	24%	10% to 100%	0.619
Human-modified land cover[c]	18%	21%	0% to 85%	–0.569
Turf grass	10%	14%	0% to 60%	—
Impervious surfaces	8%	12%	0% to 42%	—

[a] Cover of vegetation in the 76 to 150 cm and 151 to 500 cm height classes combined.
[b] Cover of vegetation in the 0 to 75 cm height class.
[c] Cover of impervious surfaces and turf grass combined.

j on 1,…,45 sites for time *t* = 1 was made a function of covariates using the log link:

$$N_{i,j,t=1} \sim \text{Poisson}(\lambda_{i,j,t=1})$$
$$\log(\lambda_{i,j,t=1}) = \beta_{0_i} + \beta_{1_i} \times PC1_j$$

where $PC1_j$ is the principal component score of site *j* as described above. In each subsequent sampling period *t* > 1, the abundance of each species *i* was calculated as the sum of survivors ($\mathbf{S}_{ijt}$) and recruits ($\mathbf{R}_{ijt}$) at site *j*. The number of survivors was derived from a binomial trial of abundance in the previous time step and a persistence probability φ for site *j* for time *t*. For each species *i*, the logit-linear function of φ was:

$$N_{i,j,t} = S_{i,j,t} + R_{i,j,t}$$
$$S_{i,j,t} \sim \text{Binomial}(N_{i,j,t-1} \times \varphi_{i,j,t})$$
$$\text{logit}(\varphi_{i,j,t}) = \varphi_{0_i} + \varphi_{1_i} \times PC1_j + \varphi_{2_i} \times CONTAG_j$$

where $CONTAG_j$ is the contagion index of each site as described above. The number of recruits was determined from a Poisson distribution with a mean of γ. For each species *i*, the log-linear function for γ at site *j* for time t was:

$$R_{i,j,t} \sim \text{Poisson}(\gamma_{i,j,t})$$
$$\log(\gamma_{i,j,t}) = \gamma_{0_i} + \gamma_{1_i} \times CONTAG_j + \gamma_2 \times season_t$$

where $season_t$ represents the meteorological season of time *t* (spring, summer, or fall). Season was included to account for population growth in small mammals as young are born throughout the year. We added species-level random effects to the intercept and slope coefficients for each term except "season" in the initial abundance, survival, and recruitment models. Species-specific coefficients were drawn from a normally distributed "community response," e.g., $\gamma_{1_i} \sim \text{Normal}(\mu_{\gamma_1}, \sigma_{\gamma_1})$. This model specification allows rare species to "borrow" information from more common species and improves the accuracy of estimated parameters (Ovaskainen and Soininen 2011).

In our capture probability submodel, the number of individuals captured each night y was derived from a binomial trial based on the true abundance at each site and a capture probability *c*. For each species *i*, the logit-linear function for *c* for site *j*, for nights 1,…,*k*, for time t was:

$$y_{i,j,k,t} \sim \text{Binomial}(N_{i,j,t} \times c_{i,j,k,t})$$
$$logit(c_{i,j,k,t}) = \alpha_{0_i} + \alpha_1 \times moon_{j,k,t} + \alpha_2 \times Date_{j,k,t} + \alpha_3 \times effort_{j,k,t}$$

where $moon_{j,k,t}$ is the proportion fullness of the moon at site *j* on night *k* at time *t*, $Date_{j,k,t}$ was the ordinal date of night *k* at site *j* at time *t*, and $effort_{j,k,t}$ was the number of available (i.e., open, undisturbed) traps at site *j* on night *k* at time *t*. A species-specific random intercept, drawn from a normally distributed "community response," allowed for species-specific capture probabilities. We initially allowed species-level random effects on slope terms; however, all species responded similarly to each variable (e.g., all species capture probabilities decreased with increasing moon fullness). Thus, to reduce the complexity of the model, we removed this species-level effect from the slope terms.

Community responses were given vague normal priors (e.g., $\beta_0 \sim Normal(0, 2)$). All standard deviation terms were given vague Gamma priors (e.g., $\sigma_{\beta_0} \sim Gamma(1, 1)$). Following a 3,500-step adaptation and a 90,000-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).

Species richness and community diversity.

We used the resulting model to calculate average species richness across time at each site by averaging the presence probabilities of each species across all sampling periods. We converted the predicted number of individuals of each species on each site into a "1' if the value was > 0 (i.e., at least 1 individual of a species was predicted to be present), then averaged these presence probabilities across all sampling periods at each site. We then added the average presence probabilities of all species together to calculate average species richness at each site through time. We next used a linear model to assess the relationship between average species richness at a site and its land cover (PC1) and habitat connectivity (contagion). Additionally, we calculated the average number of individuals of each species present on each site by averaging model-predicted abundances across all sampling seasons to measure community diversity. We used a separate linear model to assess the relationship between a site's Shannon-Wiener diversity index (*H*") and its land cover and habitat connectivity. All data processing and modeling were conducted in R version 4.2.2 (R Development Core Team 2022) and JAGS 4.3.1 (Plummer 2003).

Results

We undertook a total of 6,418 trap-nights across 45 trap lines. However, on some nights, traps were unavailable to small mammals (e.g., disturbed by another animal), which reduced the total effort to 5,209 trap-nights. At the individual plot level, trapping effort ranged from 0 to 10 traps (mean ± standard deviation; $\bar{x}$ = 6.6 ± 2.4 SD). A total of 1,742 animals were captured, representing 11 species (Table 2). Of these species, 6 were included in the community occupancy model; the remaining species were either not captured frequently enough to produce accurate models (masked shrews, house mice) or were not target species of this study (eastern chipmunks, a juvenile Virginia Opossum *Didelphis virginiana*, a wren *Troglodytes* spp.).

All Bayesian model estimates are presented as the median value with the 95% credible interval (Table 3). Shared community capture probability was low but highly variable ($\overline{\alpha 0} = 0.19$; CI: 0.06, 0.39; Supplementary Data SD1). Deer mice had the greatest mean capture probability (α_0 = 0.46; CI: 0.41, 0.50), followed by meadow voles (α_0 = 0.26; CI: 0.17, 0.36), short-tailed shrews (α_0 = 0.22; CI: 0.15, 0.31), prairie voles (α_0 = 0.22; CI: 0.12, 0.35), jumping mice (α_0 = 0.08; CI: 0.02, 0.23), and harvest mice (α_0 = 0.05; CI: 0.01, 0.16). Capture

Table 2. Counts of captured animals from the Iowa City, Iowa metropolitan area, United States, 2021 to 2022.

Species	2021			2022			Total
	Spring	Summer	Fall	Spring	Summer	Fall	
Deer mouse (*Peromyscus* spp.)	81	286	357	149	305	246	1,424
Northern Short-tailed Shrew (*Blarina brevicauda*)	1	26	72	0	15	31	145
Meadow Vole (*Microtus pennsylvanicus*)	1	28	16	6	20	4	75
Prairie Vole (*M. ochrogaster*)	1	10	24	2	4	5	46
Meadow Jumping Mouse (*Zapus hudsonicus*)	0	6	0	3	0	4	13
Western Harvest Mouse (*Reithrodontomys megalotis*)	0	1	6	1	2	2	12
Eastern Chipmunk (*Tamius striatus*)	0	3	10	1	1	3	18
Masked Shrew (*Sorex cinereus*)	0	0	0	1	1	4	6
House Mouse (*Mus musculus*)	0	0	0	0	1	0	1
Virginia Opossum (*Didelphis virginiana*)	0	0	1	0	0	0	1
Wren (*Troglodytes* sp.)	0	0	0	0	1	0	1
Total	84	360	486	163	350	299	1,742

probabilities were negatively correlated with moon fullness ($\alpha_1 = -0.27$; 95% CI: –0.36, –0.17) and positively correlated with ordinal date ($\alpha_2 = 0.28$; 95% CI: 0.13, 0.44) and effort ($\alpha_3 = 0.67$; 95% CI: 0.56, 0.78). Average species richness on each site varied from 1.4 to 3.0 species ($\bar{x} = 2.0$). Average species richness was nearly significantly negatively correlated with PC1 ($F_{2,42} = -0.08$, $P = 0.06$) such that sites with greater human-associated land cover may have had greater average species richness than sites with more natural vegetation cover (Fig. 2). Contagion was not a significant predictor of average species richness ($F_{2,42} = -0.05$, $P = 0.41$). Shannon's diversity index was negatively correlated with PC1 ($F_{2,42} = -0.16$, $P < 0.001$) such that sites with greater human-associated land cover had greater species diversity than sites with more natural vegetation. Contagion was not a significant predictor of species diversity ($F_{2,42} = -0.06$, $P = 0.22$).

Shared community persistence probability was highly variable ($\overline{\varphi 0} = 0.23$, 95% CI: 0.03, 0.62; Fig. 3). Deer mice had the highest average persistence probability ($\varphi_0 = 0.67$; CI: 0.56, 0.76), followed by jumping mice ($\varphi_0 = 0.24$; CI: 0.01, 0.91), harvest mice ($\varphi_0 = 0.21$; CI: 0.00, 0.89), prairie voles ($\varphi_0 = 0.17$; CI: 0.01, 0.48), meadow voles ($\varphi_0 = 0.13$; CI: 0.01, 0.34), and short-tailed shrews ($\varphi_0 = 0.10$; CI: 0.00, 0.38), We did not detect an effect of PC1 ($\overline{\varphi 1} = -0.13$; 95% CI: –1.05, 0.76) or contagion ($\overline{\varphi 2} = 0.10$; 95% CI: –1.09, 1.34) on community persistence probability. Although not significant at the overall community level, PC1 did have significant effects on the persistence of deer mice ($\varphi_2 = 0.19$; 95% CI: 0.00, 0.39) and prairie voles ($\varphi_2 = -0.63$; 95% CI: –1.58, –0.01) such that deer mice had greater persistence at sites with more natural vegetation cover while prairie voles had greater persistence at sites with more human-associated land cover.

Mean community recruitment was low but highly variable ($\overline{\gamma 0} = 0.3$ individuals, 95% CI: 0.2, 0.9; Table 2; Fig. 4). On average across sites and seasons, deer mice populations recruited the most individuals ($\gamma_0 = 1.6$; CI: 1.2, 2.2), followed by short-tailed shrews ($\gamma_0 = 0.6$; CI: 0.4, 0.9), meadow voles ($\gamma_0 = 0.3$; CI: 0.2, 0.3), harvest mice ($\gamma_0 = 0.2$; CI: 0.1, 0.7), prairie voles ($\gamma_0 = 0.2$; CI: 0.1, 0.3), and jumping mice ($\gamma_0 = 0.1$; CI: 0.0, 1.4). We were unable to detect an effect of contagion on community recruitment ($\overline{\gamma 1} = -0.50$; 95% CI: –0.66, 0.56); however, contagion did have a significant effect at the species level for short-tailed shrews ($\gamma_1 = -0.47$; 95% CI: –0.75, –0.20) and deer mice ($\gamma_1 = 0.17$; 95% CI: 0.00, 0.34) such that short-tailed shrews had greater recruitment at sites with greater connectivity, whereas deer mice had greater recruitment at sites with lower connectivity. Compared to fall, fewer individuals were recruited into the community in spring ($\gamma_2 = -1.78$; 95% CI: –3.88, –0.75) but more individuals were recruited in the summer ($\gamma_2 = 0.33$; 95% CI: 0.05, 0.67; Fig. 4).

Discussion

We sought to identify how species-specific responses of small mammals to aspects of the urban environment shaped community-level metrics. Overall, we found that species diversity increased as human-modified land cover increased, an unexpected finding that differs from previous studies. In general, we saw a shift from a community dominated by deer mice to a more diverse community with prairie-associated species as urbanization increased. Our most species-diverse locations were typically sites with tall vegetation next to mowed turfgrass or water features (e.g., streams), which likely mimic the species-diverse edge habitats found in many ecosystems. While more diverse than the more naturally vegetated sites, it is possible that these human-modified sites represent low-survival population sinks, although additional studies are needed to identify population-level effects on small mammals in human-modified environments. Our findings also did not support our hypothesis that generalist species would not show strong relationships with land cover; rather, both deer mice and short-tailed shrews demonstrated significant relationships with land cover. Small mammals, including both generalist species that theoretically should be adaptable to urban environments and habitat specialists, thus appear to be sensitive to urbanization.

We predicted that species richness and diversity would be lower on sites with higher proportions of human-modified land cover. Our results did not support this prediction. Rather, sites with the highest proportional human-modified land cover had, on average, 1.5 more species than sites with the highest natural vegetation cover. This relationship appears to be driven by sites located near streams in turfgrass parks and in stormwater collection channels next to housing developments, both of which tend to be surrounded by tall, dense vegetation in our study area. Previous research in southwestern Iowa has shown that the grass-dominated, low-canopy-cover habitat bordering channelized streams tended to have higher small mammal species richness than upland habitat (Geier and Best 1980), similar to our results. Vegetation surrounding streams and stormwater channels may also provide important habitat or movement corridors for urban small mammals (Mahan and O'Connell 2005;

Table 3. Median coefficients and 95% Bayesian credible intervals for the dynamic community abundance model describing small mammal communities in the Iowa City, Iowa metropolitan area, United States, 2021 to 2022. PC1 is the principal components score of a site, ranging from high cover of impervious surfaces and turfgrass (negative values) to high cover of natural vegetation (positive values). The contagion index of a site is a measure of habitat fragmentation with low values indicating low dispersion of different land cover types (i.e., high connectivity) and high values indicating high interspersion (i.e., low connectivity).

	Median	Lower 95% CI	Upper 95% CI
Capture probability			
Intercept			
Community mean (μ_{α_0})	–1.48	–2.67	–0.46
Community variance (σ_{α_0})	1.11	0.61	2.33
Northern Short-tailed Shrew (*Blarina brevicauda*)	–1.24	–1.75	–0.78
Prairie Vole (*Microtus ochrogaster*)	–1.25	–2.00	–0.61
Meadow Vole (*M. pennsylvanicus*)	–1.07	–1.61	–0.59
Deer mouse (*Peromyscus* spp.)	–0.18	–0.38	0.01
Western Harvest Mouse (*Reithrodontomys megalotis*)	–2.98	–4.72	–1.67
Meadow Jumping Mouse (*Zapus hudsonicus*)	–2.45	–3.94	–1.22
Moon illumination (α_1)	–0.27	–0.36	–0.17
Ordinal date (α_2)	0.28	0.13	0.44
Effort (α_3)	0.67	0.56	0.78
Initial abundance			
Intercept			
Community mean (μ_{β_0})	–2.90	–5.15	–1.09
Community variance (σ_{β_0})	1.80	0.94	4.20
Northern Short-tailed Shrew	–3.59	–6.35	–1.92
Prairie Vole	–3.45	–6.32	–1.70
Meadow Vole	–3.42	–5.90	–1.85
Deer mouse	0.11	–0.36	0.51
Western Harvest Mouse	–3.90	–8.71	–1.39
Meadow Jumping Mouse	–3.98	–8.83	–1.24
PC1 (human-modified vs. naturally vegetated)			
Community mean (μ_{β_1})	0.05	–0.99	1.13
Community variance (σ_{β_1})	0.87	0.49	1.86
Northern Short-tailed Shrew	–0.75	–1.81	0.40
Prairie Vole	0.41	–0.93	2.14
Meadow Vole	0.07	–0.95	1.36
Deer mouse	0.66	0.37	0.98
Western Harvest Mouse	–0.15	–1.66	1.76
Meadow Jumping Mouse	–0.07	–1.42	1.71
Persistence			
Intercept			
Community mean (μ_{φ_0})	–1.22	–3.55	0.49
Community variance (σ_{φ_0})	1.43	0.72	3.57
Northern Short-tailed Shrew	–2.16	–5.82	–0.51
Prairie Vole	–1.59	–4.42	–0.10
Meadow Vole	–1.89	–5.17	–0.68
Deer mouse	0.71	0.26	1.16
Western Harvest Mouse	–1.35	–5.90	2.13
Meadow Jumping Mouse	–1.16	–5.29	2.35
PC1 (human-modified vs. naturally vegetated)			
Community mean (μ_{φ_1})	–0.13	–1.05	0.76

Table 3. Continued

	Median	Lower 95% CI	Upper 95% CI
Community variance ($\sigma_{\varphi 1}$)	0.77	0.44	1.68
Northern Short-tailed Shrew	–0.30	–1.25	0.82
Prairie Vole	–0.63	–1.58	–0.01
Meadow Vole	0.25	–0.64	1.31
Deer mouse	0.19	0.00	0.39
Western Harvest Mouse	–0.21	–1.82	1.51
Meadow Jumping Mouse	–0.13	–1.87	1.49
Contagion index			
Community mean ($\mu_{\varphi 2}$)	0.10	–1.09	1.34
Community variance ($\sigma_{\varphi 2}$)	0.86	0.46	2.02
Northern Short-tailed Shrew	–0.24	–1.77	1.32
Prairie Vole	0.24	–1.27	1.65
Meadow Vole	0.56	–0.90	2.14
Deer mouse	–0.12	–0.51	0.25
Western Harvest Mouse	0.25	–1.78	2.62
Meadow Jumping Mouse	–0.07	–2.33	2.23
Recruitment			
Intercept			
Community mean ($\mu_{\gamma 0}$)	–1.11	–2.16	–0.09
Community variance ($\sigma_{\gamma 0}$)	1.06	0.64	2.10
Northern Short-tailed Shrew	–0.52	–0.94	–0.12
Prairie Vole	–1.86	–2.45	–1.30
Meadow Vole	–1.30	–1.76	–0.82
Deer mouse	0.49	0.14	0.80
Western Harvest Mouse	–1.63	–2.68	–0.33
Meadow Jumping Mouse	–2.05	–3.19	–0.90
Contagion Index			
Community mean ($\mu_{\gamma 1}$)	–0.50	–0.66	0.56
Community variance ($\sigma_{\gamma 1}$)	0.63	0.39	1.22
Northern Short-tailed Shrew	–0.47	–0.75	–0.20
Prairie Vole	0.22	–0.19	0.60
Meadow Vole	–0.07	–0.41	0.24
Deer mouse	0.17	0.00	0.34
Western Harvest Mouse	–0.10	–0.78	0.45
Meadow Jumping Mouse	–0.03	–0.65	0.60
Season (γ_2)—Spring	–1.78	–3.88	–0.75
Season (γ_2)—Summer	0.33	0.05	0.67

Łopucki and Kitowski 2017) and could concentrate activity into a small area. Additionally, these sites may have additional resources present, such as anthropogenic structures in which to nest or food subsidies (e.g., bird seed), which could support more diverse communities of small mammals (Hansen et al. 2020). Predation risk on higher-intensity urban sites may also be lower, as has been demonstrated for urban songbirds (Eötvös et al. 2018). However, predation risk for urban small mammals is relatively poorly quantified (but see Moll et al. 2020); thus, this hypothesis warrants future investigation. We also found that sites with low species richness had high canopy closure and sparse understory vegetation. Many of the species present in our study area are prairie-associated species for whom forested environments are not suitable habitat. These sites would thus likely have low species richness regardless of urbanization. Our findings suggest that heterogeneity in vegetation (from forest to tall herbaceous vegetation) helps to maintain species diversity in urban small mammal communities in the Midwestern United States.

Contrary to our prediction, our results indicate that species richness and diversity are not significantly related to habitat connectivity. This finding may be indicative of an extinction debt, such that small mammal populations that were recently isolated by

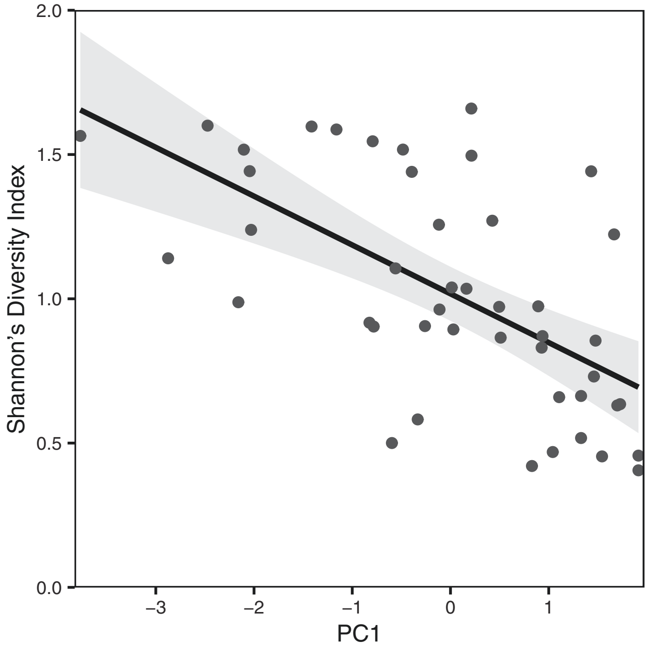

Fig. 2. Small mammal species diversity as a function of a principal component score (PC1) describing land cover characteristics (sites with more negative scores have higher cover of imperviousness and turfgrass and sites with more positive scores have higher canopy closure with greater shrub and herbaceous cover) in the Iowa City, Iowa metropolitan area, United States, 2021 to 2022. Dark gray dots are species diversity for individual sites, the black line is the model-estimated mean, and the light gray ribbon is the standard error around the model mean.

urbanization are on a trajectory toward extinction but have not yet experienced sufficient negative effects of isolation and small population size to cause extinction. Although extinction debts have not been documented in urban small mammals, they have been documented for urban plants (du Toit et al. 2020), butterflies (Soga and Koike 2013), and songbirds (Haddou et al. 2022). It is thus possible that small mammals also experience this negative outcome of urbanization. An extinction debt may particularly exist for our prairie-associated species, which tend to occur in small patches of grassland along the boundary between forest or agriculture and urbanized environments. Long-term monitoring of urban small mammal diversity could help elucidate whether urban populations are stable or decline through time.

Alternatively, the lack of a significant relationship between species richness and connectivity could indicate that small mammal movement is not significantly impacted by urbanization in our study area. Our results suggest that sites with high species richness may themselves act as corridors that facilitate connectivity among populations, such as vegetation surrounding streams in turfgrass parks. It is also possible that this finding is caused by a scale mismatch, either in the grain size of the NLCD or the distance at which landscape variables impact connectivity. Landscape elements of importance for small mammal dispersal may exhibit a finer grain size than the 30-m pixel size of the NLCD. Elucidating such effects may not only require a finer spatial grain, but also a more detailed thematic representation (i.e., a more detailed land cover classification system) than the NLCD provides. Additionally, although 100 m represents average dispersal distances and we were primarily interested in the probability of animals being recruited (i.e., dispersing into) populations, urban small mammal

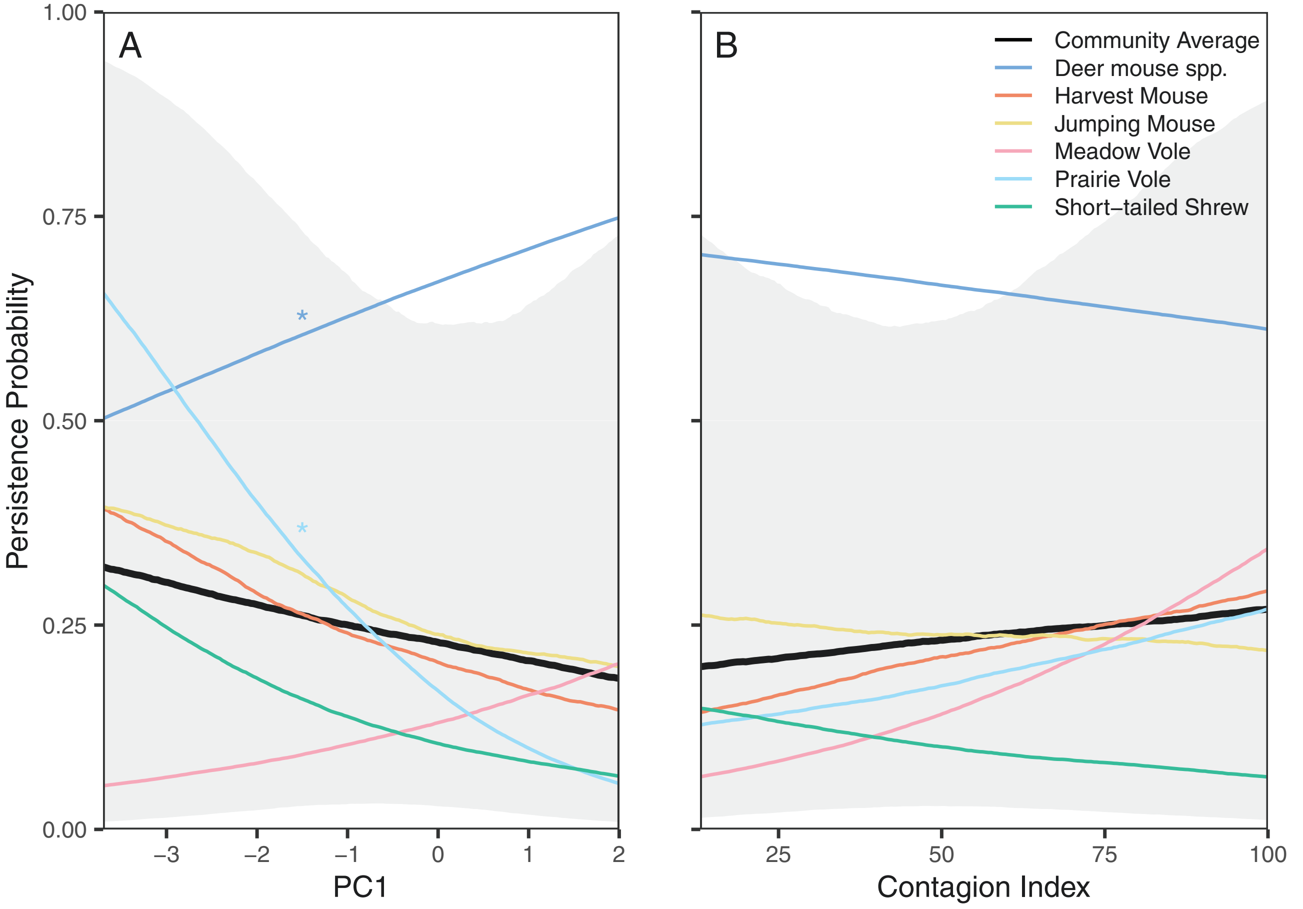

Fig. 3. Persistence probability of the small mammal community on average and species-specific estimates in the Iowa City, Iowa metropolitan area, United States, 2021 to 2022. PC1 (A) is the principal components score of a site, ranging from high cover of impervious surfaces and turfgrass (negative values) to high cover of natural vegetation (positive values). The contagion index (B) of a site is a measure of habitat fragmentation with low values indicating low dispersion of different land cover types (i.e., high connectivity) and high values indicating high interspersion (i.e., low connectivity). Colored lines are species-specific responses; the black line is the community mean response. Gray ribbon is the 95% credible interval for the community mean. Species with statistically significant relationships have their lines labeled with an asterisk.

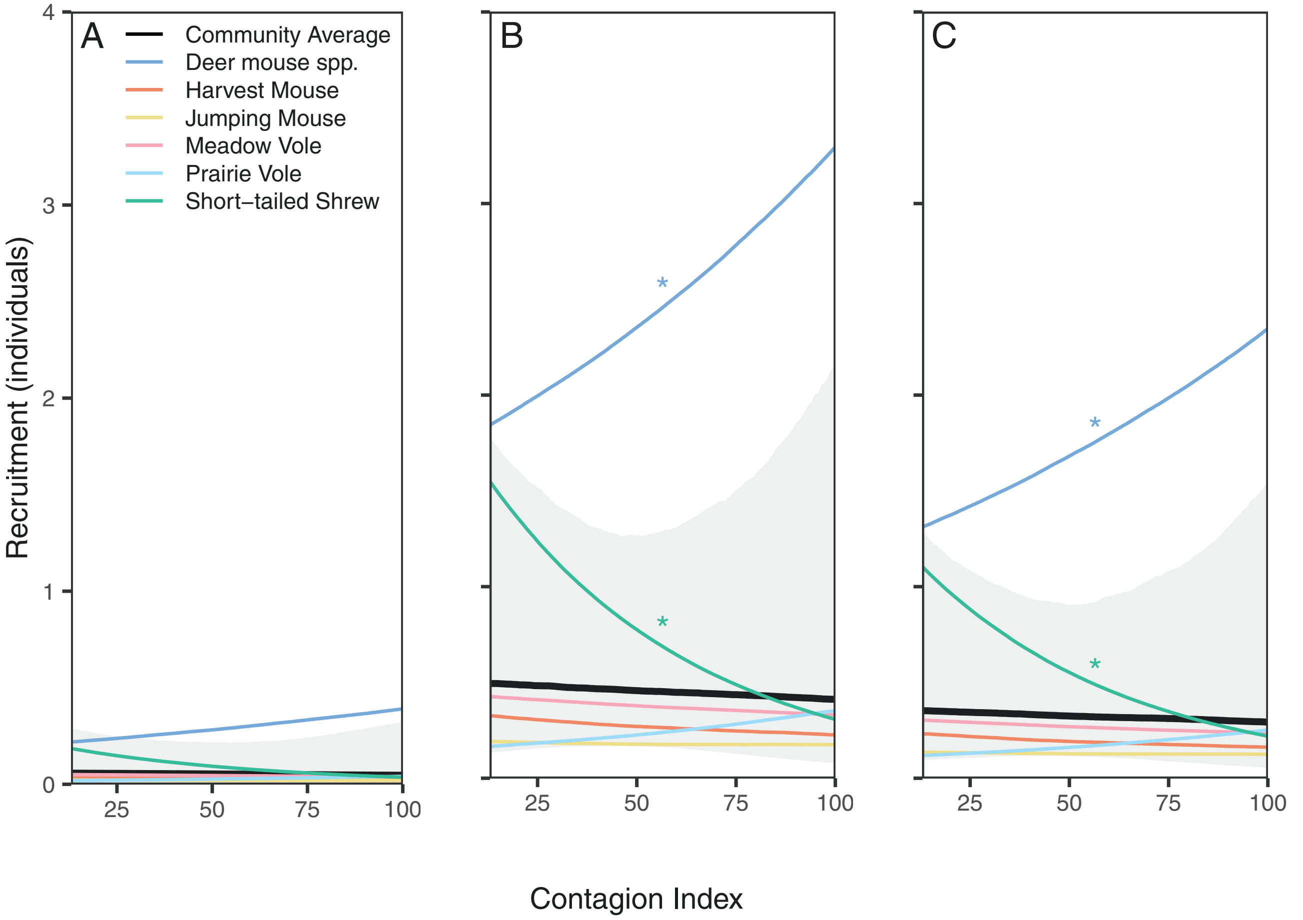

Fig. 4. Population gain (recruitment) of small mammals during (A) spring, (B) summer, and (C) fall in the Iowa City, Iowa metropolitan region, United States, 2021 to 2022. The contagion index measures habitat fragmentation with low values indicating low dispersion of different land cover types (i.e., high connectivity) and high values indicating high interspersion (i.e., low connectivity). Colored lines are species-specific responses; the black line is the community mean response. Gray ribbon is the 95% credible interval for the community mean. Species with statistically significant relationships have their lines labeled with an asterisk.

population connectivity may respond more strongly to variables measured over larger or smaller distances. Future studies could assess the importance of connectivity and identify exactly what constitutes connectivity for small mammals by tracking animal movements or by using finer spatial and thematic resolution geospatial data.

Our results contrast with the results of previous studies that found declining small mammal richness with increasing urbanization in cities in North America and on other continents. The development history of Iowa City may partially explain this finding. Iowa City was founded in 1939, making it a relatively young (i.e., founded later in history) city. European cities are considerably older; for example, Chełm, Poland—the site of past urban small mammal research—dates back from at least the 9th century. Thus, European small mammals have likely already experienced any negative effects of urbanization over longer time periods, potentially leading to the realization of the extinction debts discussed above. South American urban small mammal research has also occurred in comparatively old cities (e.g., Bueno Aires, Argentina, established in 1580), indicating that Southern American small mammals may also have realized extinction debts. Additionally, the Iowa City metropolitan area is characterized by highly intermixed impervious and vegetated land covers (Table 1), especially compared to larger North American cities. This high interspersion of vegetation across the landscape likely provides habitat for small mammals and could maintain connectivity between habitat patches. Iowa City generally lacks the expansive, intensely impervious locations found in larger cities and these sites likely have very low species diversity. For example, our maximum impervious cover on any site was 42%, while studies in cities that found negative impacts of urban intensity on small mammals generally had sites with greater impervious cover (e.g., Nitra City, Slovakia; and Buenos Aires, Argentina with maximums of over 50% impervious; Cavia et al. 2009; Klimant et al. 2017). Thus, our results likely indicate patterns in small mammal diversity in small, low-density cities, particularly cities in grassland ecoregions. Additional studies of small mammal communities in other North American cities, especially cities with a high proportional impervious cover, and cities of varying extents and intensities globally would help to further identify the generalizability of the patterns we identified.

Contrary to our prediction, deer mice exhibited strong relationships with human-modified land cover. Deer mice were more likely to persist on sites with high levels of naturally vegetated cover that was less fragmented. Tree canopy is an important indicator of Deer Mouse habitat in both urban and nonurban systems (Munshi-South 2012; Cassel et al. 2020) and higher population persistence in these habitats is likely related to food provisioning and protection from predation. Lower persistence on sites with high human-modified land cover may thus be related to lower food availability, a lack of cover, or the high likelihood of predator occurrence (e.g., domestic cats, *Felis catus*; Cove et al. 2023). Further work that quantifies the availability of food for urban small mammals and the relative strength of predation pressure and competition in urban environments could clarify these responses and their drivers. Lower persistence probabilities on sites with low connectivity may be related to higher recruitment rates on these sites (Fig. 4). Thus, isolated patches in urban environments may be inhabited by dispersing individuals, although more research on Deer Mouse movement through urban environments is needed.

Although we predicted and found that short-tailed shrews did not have a strong relationship with human-modified land cover, our results indicate that short-tailed shrews are sensitive to habitat connectivity as evidenced by lower shrew persistence and recruitment on sites with lower connectivity. Greater white-toothed shrews (*Crocidura russula*), a similar species from Eurasia, were less likely to occur in gardens located farther from corridors (Vergnes et al. 2013), potentially indicating that large-bodied shrews in general are sensitive to urban fragmentation. This phenomenon may be explained by the semi-fossorial behavior of shrews and their reliance on a leaf-litter layer for nesting and movement (George et al. 1986). Shrews may thus be more reluctant or less able than other small mammals to disperse in urban landscapes due to the lack or fragmentation of such habitats. Our results demonstrate that even habitat generalists such as shrews that should theoretically fare well in urban environments still experience negative effects of urban intensity, potentially as a result of urban vegetation management practices (e.g., removing leaf litter, mowing herbaceous vegetation) that reduce the availability of preferred microhabitats.

We predicted that voles, harvest mice, and jumping mice would exhibit strong relationships with human-modified land cover; however, we only found support for this prediction in prairie voles, who had higher persistence probabilities in environments with high human-modified land cover. These higher persistence probabilities may be related to the low canopy closure on these sites. As a grassland-associated species, prairie voles select habitat with low canopy cover and tall vegetation (Stalling 1990), such as prairie patches with turfgrass borders present in our study area. Although not statistically significant, we also found that harvest mice persistence increased as human-associated land cover increased. Our results thus point to the importance of preserving grassland habitat within cities to support grassland-associated species.

Our research should be considered in the light of certain limitations. Nonsignificant relationships observed for rarer species (e.g., harvest mice, jumping mice, meadow voles) may represent true ecological relationships, but more likely result from low capture rates for those species which reduced statistical power. Harvest mice often weigh less than the minimum weight required to trigger a Sherman trap (10 g); thus, we likely did not detect harvest mice at all locations where they were present. Jumping mice were hibernating during portions of our survey period (e.g., March to April and October to November), reducing their overall capture probability. Additionally, because these rarer species "borrow" information from more common species in our model, and these more common species exhibited opposing responses, responses of rare species may be "pulled" toward a nonsignificant response. However, if the more common species act as umbrella species in terms of habitat conservation, rarer species likely still benefit even if their exact responses to urbanization are unclear.

Our findings highlight the importance of investigating species-specific responses to urban environments to understand the drivers of changes in community composition across urbanization gradients. In using this approach, we were able to demonstrate that increases in species diversity seen on more urban sites are not the result of adding new species, but rather result from the replacement of a depauperate community with a more diverse one comprised of different species. Based on our findings, urban habitat patches with tall vegetation likely have high conservation value for the diverse, prairie-associated small mammal communities of the Midwestern United States, where the once-expansive tallgrass prairie landscape has largely been lost. These urban small mammal communities may even have the potential to act as source populations in the restoration of tallgrass prairie communities in other parts of the state. We further found that adaptable, generalist species (e.g., deer mice) can exhibit strong, negative relationships with human-associated land cover and experience negative effects of urban development. This may have important implications for disease dynamics, as deer mice and other rodents are important vectors of several zoonotic diseases and changes in abundance along a gradient of urban intensity likely alter exposure risk for humans and domestic animals. Future research that investigates the relative consistency of these patterns both within and among cities will help to better identify whether the impacts of urbanization on North American small mammals that we found in our study area pertain broadly or vary with city attributes such as size, development history, and ecoregion. Our work demonstrates that urban environments, particularly environments with diverse vegetation, can support diverse small mammal communities, providing conservation options for small mammals in heavily altered landscapes.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Capture probability of small mammals in Iowa City is negatively correlated with (A) moon illumination and positively correlated with (B) ordinal date and (C) trapping effort (number of available traps per site). Colored lines and dots are species-specific responses, black lines and dots are the community mean responses. Gray ribbons (moon illumination and ordinal date) and black bars (trap effort) are the 95% credible interval for the community mean.

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Author contributions

RNL conceived of and designed the study, collected the data, performed the analyses, made all figures, and wrote and edited the manuscript. HAS provided oversight of the study and reviewed and edited all versions of the manuscript.

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Conflict of interest

None declared.

Data availability

A public repository of data and code used in these analyses is available at https://github.com/RLarson92/UrbanSmammalCommunity.

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