Living in the concrete jungle: carnivore spatial ecology in urban parks

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ABSTRACT

People and wildlife are living in an increasingly urban world, replete with unprecedented human densities, sprawling built environments, and altered landscapes. Such anthropogenic pressures can affect processes at multiple ecological scales from individuals to ecosystems, yet few studies integrate two or more levels of ecological organization. We tested two competing hypotheses, humans as shields versus humans as competitors, to characterize how humans directly affect carnivore spatial ecology across three scales. From 2017-2020, we conducted the first camera survey of city parks in Detroit, Michigan, and obtained spatial occurrence data of the local native carnivore community which included coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). We constructed single-species occupancy models to discriminate parks into areas of

low and high human presence using the average human occupancy as the threshold. At the community level, carnivores were spatially aggregated at both high and low human use sites, though aggregation was stronger at sites with high human occupancy, indicating that other factors such as available resources rather than human presence might influence community segregation. Three carnivore species pairs changed from positive association at low human occupancy to negative association at high human occupancy, two subordinate species pairs aligning with the humans as competitors hypothesis, and an apex-subordinate pair consistent with the humans as shields hypothesis. At the individual level, human hotspots of high site use did not overlap with any carnivore activity hotspots, similarly lending support to the humans as competitors hypothesis. Overall, we found inference on anthropogenic impacts on carnivore spatial ecology varied depending on the scale of ecological organization. Our findings demonstrate how urban carnivores are exploiting spatial refugia in the cityscape.

Keywords: city, co-occurrence, distribution, community structure, camera survey, Detroit, human shield, coyote, overlap

INTRODUCTION

Cities are highly heterogeneous landscapes of risk and reward, borne of unique interactions between anthropogenic and ecological processes (Alberti et al., 2003; Liu et al., 2007). As urbanization and land cover conversion rates continue to increase worldwide, cities have emerged as a new and unique habitat for wildlife. By 2050, over half of the global human population will live in a city while urban development is projected to grow by 120 million hectares globally by 2030 (McDonald et al., 2018; United Nations, 2018). Cities can be a source or a sink for mammal species, a duality driven by both increases in availability of food sources and risks of mortality (Bateman, & Fleming, 2012; Lepczyk et al., 2017). For example, black bears (*Ursus americanus*) in urban areas of Nevada had higher birth rates than their rural and protected area counterparts, but also experienced higher age-specific mortality rates, which significantly decreased fitness (Beckmann, & Lackey, 2008). Cougars (*Puma concolor*) in an urban-wildland system in Colorado successfully exploited anthropogenic food sources, yet faced a 6.5% increase in mortality risk in developed areas (Moss et al., 2016). Wildlife responses to the built environment are unsurprisingly driven by humans themselves and their induced modifications to landscapes through food provisioning, artificial habitat and light, and roads (Clucas, & Marzluff, 2011; Gaston et al., 2017; Riley et al., 2014).

Anthropogenic pressures affect wildlife at multiple levels of ecological organization, from community structure and intraguild interactions down to behavioral shifts in individual species. Perturbations to higher trophic levels can have cascading impacts on ecosystem processes, which underscores the need to understand how carnivores respond to human activities (Ripple et al., 2014b; Terborgh, 2010). A study in the city of Chicago found that raccoons (*Procyon lotor*) comprised a larger relative proportion of the mesopredator community in urban

compared to rural sites, irrespective of patch size (Prange, & Gehrt, 2004). Intraguild interactions are also mediated by anthropogenic pressure the human shield effect (Berger, 2007; Gallo et al., 2019; Muhly et al., 2011). Red foxes (*Vulpes vulpes*) have been shown to exploit highly developed core urban areas as spatial refugia to avoid their dominant coyote (*Canis latrans*) competitors (Moll et al., 2018). Individual species responses to human activity are varied and depend on each species' biology and tolerance to human encounters. Cottontail rabbits (*Sylvilagus floridanus*) in an urban area were more vigilant at sites where coyotes were absent, suggesting humans are a third "player" in a predator-prey-human system (Gallo et al., 2019). Striped skunk (*Mephitis mephitis*) occupancy was greatest near urban areas, but this positive association weakened as the percentage of urban land cover increased, signaling a sensitivity to within-city metrics of anthropogenic pressure (Ordeñana et al., 2010). Evidently, urban systems produce a suite of complex and synergistic changes to processes at multiple ecological scales.

Despite evidence that human activity induces complex responses in urban wildlife, there is a dearth of studies that to quantify these effects at multiple scales of ecological organization, particularly for terrestrial carnivores. Further, the field of urban ecology is relatively new and the majority of approaches to characterizing effects on wildlife have been dominated by the use landscape-level metrics of the built environment as proxies for human activity (Wu, 2014). A meta-analysis of urban ecology studies found that only 10.2% of 244 studies quantified large mammal responses to urbanization and only 6% of all urbanization metrics employed in these studies explicitly considered humans (Moll et al., 2019). Worldwide population declines and range contraction in carnivores highlight the urgency to assess how spaces dominated by humans alter ecological interactions at community, population, and individual levels (Ceballos, & Ehrlich, 2002; Ripple et al., 2014a).

We leveraged a North American native carnivore guild comprised of coyotes, raccoons, red foxes, gray foxes (*Urocyon cinereoargenteus)*, and striped skunks to investigate how human occupancy influences spatial ecology at the individual, pairwise, and community level. Specifically, we implemented the first camera survey of city parks in Detroit, Michigan from 2017-2020 to study the city's carnivores. By directly measuring human activity and not proxies of human pressure such as housing density, we explicitly disentangled the effects of humans on wildlife from those related to the built environment.

In characterizing human effects on the carnivore community, two theoretical frameworks emerge with distinct expectations for mammalian community response to fine-scale human activity (Figure 1). The humans as shields hypothesis (HSH) argues that humans differentially exert top-down pressure on the apex predator in the system, indirectly benefitting the subordinate competitors and facilitating greater spatial overlap between humans and subordinate species (Moll et al., 2018; Shannon et al., 2014). A contrasting approach frames humans as competitors (HCH), asserting that anthropogenic pressure affects multiple species irrespective of their trophic level or dominance hierarchy (Chapron, & López-Bao, 2016; Farris et al., 2017). The HCH asserts that human presence is functionally similar to antagonism from another competitor in the guild, resulting in increased vigilance, competitive exclusion, and spatial avoidance across the entire community (Gallo et al., 2019).

Here, we addressed the following questions to test whether effects from anthropogenic pressures on native urban carnivores align with expectations of the HSH and HCH at different levels of ecological organization: 1) how does human activity in city parks affect the community structure? 2) how are pairwise interactions affected by human activity within a competing carnivore guild? 3) how do individual species of carnivores respond to areas of high human

activity? We evaluate the ecological role of humans in urban carnivore communities according to these two contrasting frameworks:

Humans as shields hypothesis (HSH)

With HSH, subordinate mesopredators will exploit the spatial refugia created by human top-down pressures on apex predators and spatially overlap with humans at the park scale (Geffroy et al., 2015; Moll et al., 2018). 1) At the community level, we expected spatial avoidance (i.e. low co-occurrence among carnivores) at low human activity versus spatial aggregation (i.e. increased spatial co-occurrence) at high human activity owing to multiple subordinate species exploiting spatial refugia (Amarasekare, 2003; Gehrt et al., 2013). 2) Within pairwise interactions, we expected increased apex carnivore activity and reduced subordinate carnivore activity at parks with low human activity versus reduced apex activity and increased subordinate activity at parks with high human activity (Smith et al., 2018). 3) At the individual level, we expected less spatial overlap between human and dominant carnivore hotspots as well as greater overlap between human and subordinate carnivore hotspots (Berger, 2007; Muhly et al., 2011).

Humans as competitors hypothesis (HCH)

Conversely, humans will function like a superior competitor, reduce the niche space and thus spatially displace carnivores regardless of whether they are apex or subordinate with HCH (Everatt et al., 2019). 1) At the community level, we expect greater co-occurrence and spatial aggregation of carnivores at low human activity versus low co-occurrence and spatial avoidance at parks with high human activity (Schuette et al., 2013). 2) Within pairwise interactions, we

expect increased activity and greater co-occurrence for all carnivore species in parks with low human activity versus reduced activity and low co-occurrence for all carnivore species in parks with increased human activity. 3) At the individual level, we expect separate, non-overlapping hotspots for humans and all other carnivore species (George, & Crooks, 2006).

MATERIALS & METHODS

Study Area

We surveyed the carnivore community at 24 urban parks throughout Detroit, a ~ 370 km² city in southeastern Michigan, USA using remotely triggered cameras (Figure 2). Parks sampled as part of our study represent 51% of the total area of the green space in city parks (City of Detroit, 2015). The Detroit River runs along the city's southern boundary and the Rouge River runs through the southwestern districts including an automotive manufacturing plant. Over the last 70 years, Detroit has experienced a substantial population decline, dropping from 1.8 million residents at the height of its industrial era in 1950 to approximately 673,000 residents in 2016 (U.S. Census Bureau, 2016). Current human population density is 1,819/km compared to 2,374/ km found in the smaller mid-western city of Milwaukee, Wisconsin. The number of empty lots peaked at roughly 120,000 vacant lots (33% of total parcels) and 48,000 abandoned buildings (13% of parcels) in 2010 (Detroit Residential Parcel Survey, 2010; Raleigh, & Galster, 2015). Over time, many empty lots have progressed through early successional stages and have even developed enough vegetative cover to support small mammal populations, a key prey source for urban carnivores (Bateman, & Fleming, 2012).

Camera Survey

We conducted a 3-year, non-invasive survey by installing motion-triggered trail cameras (Reconyx© PC 850, 850C, 900, 900C) throughout city parks during the fall-winter season in Detroit (November 2017-March 2018, November 2018-February 2019, November 2019 – March 2020). We deployed 39 stations across 23 city parks in 2017, 41 stations across 24 parks in 2018, and 36 stations at 23 parks in 2019; the first such camera survey in Detroit. We selected parks to ensure representation of ecological and anthropogenic features such as park size, vegetation cover, distance to water, trails, and built infrastructure such as visitor pavilions and playgrounds. To improve the detection probability of mammals, camera placement was informed animal sign such as tracks, scat, or natural trails. Unbaited cameras were placed approximately 0.5 m from the ground on trees >10 cm in diameter, following standard protocol for mesocarnivore camera trap studies (Cove et al., 2012). Camera settings were set to high sensitivity, with three images captured per trigger at 1s intervals, and 15s delay between triggers. For parks with > 1 camera station, the average distance between cameras was 1,416 m, while the average distance between parks was 3,200 m.

After camera retrieval, at least two members of the [redacted for peer review] classified images to species and confirmed accuracy. Any unresolved photos were classified as "unknown" and removed from the analysis. We implemented a 30-minute quiet period to account for pseudoreplication and improve independence for analysis, given some animals tend to remain in front of the camera and trigger it multiple times. We categorized skunks, raccoons, red foxes, and gray foxes as subordinate, based on both their relatively smaller body sizes (< 10 kg) and a shared history of intraguild killing and antagonistic interactions with the dominant carnivore in this system, the coyote (Fedriani et al., 2000). Domestic dogs and cats were excluded from the analysis as we could not differentiate between feral animals who form part of the local carnivore

community and those which were temporarily off-leash or roaming from their owners. Focal species in this study are relatively common in the eastern United States and comprise a guild that is hierarchically structured, ideal for investigating the effects of human presence on the space use of a carnivore community in urban environments.

Modeling Human Occupancy

To quantify human activity at each park, we constructed single-species, single-season occupancy models with year as a covariate (MacKenzie et al., 2003; Mackenzie, & Royle, 2005). We generated weekly detection histories (i.e. presence '1' or absence '0' of humans at each camera location) using the R package 'camtrapR' (Niedballa, 2016). The occupancy modeling framework considers the maximum likelihood of both the process of detection (p) and the state of occupancy (φ) given the data, each with covariates which might potentially explain heterogeneity (MacKenzie et al., 2003). To build the detection model while holding occupancy constant, we first included covariates such as year (YR), understory vegetation at camera (VEG), number of trap nights (TN). We then used the top detection model to build the occupancy model, with distance to nearest school (DSCH), and park size (AREA) as covariates explaining occupancy (Table S1). Top models were selected using an information theoretic approach using Akaike's Information Criterion (AIC) to identify the model with the lowest ΔAIC and greatest weight (w). Model goodness-of-fit was assessed using a chi-squared discrepancy method (MacKenzie, & Bailey, 2004).

Human occupancy estimates were then calculated at the camera level; for parks containing >1 camera station, we averaged occupancy model estimates for all cameras within the park. We calculated the global average of human occupancy for all the parks in the study to

205 produce the threshold value for categorizing parks as having either "high" (above average
206 occupancy) versus "low" (below average occupancy) human activity.
207

208 **Community-Level Response to Human Activity**

209 To compare the carnivore community structure at varying levels of human occupancy, we
210 first pooled detections at camera stations according to park and subsequently created a species'
211 detections per park matrix, allowing for park-level analyses of community composition and
212 spatial structure. We then used the R package 'EcoSimR' to test for significant spatial
213 aggregation or segregation in community assemblages. *EcoSimR* uses a null-model approach and
214 generates random matrices (n=1000) using Markov chain Monte Carlo (MCMC) methods. The
215 null-model matrix approach assumed: 1) species rarity and species richness vary at each site; and
216 2) for each iteration, both the number of parks each species occurs at as well as the number of
217 species occurring at each park was held constant (Gotelli et al., 2015). We used "Simulation 10"
218 in the EcoSimR package where each species' occurrence at a park was weighted by its overall
219 prevalence throughout the study area, such that the presence of a rare species was not equivalent
220 to the presence of a common one (Gotelli et al., 2015).
221 We calculated c-scores for parks at low vs high human occupancy, which were then
222 compared to the aggregated c-score for the randomly generated null model matrices (Stone, &
223 Roberts, 1990). Negative c-scores or values close to zero indicate clustering or greater co-
224 occurrence among all species in the community than expected by random chance. In contrast,
225 large observed c-scores indicate spatial avoidance or lower co-occurrence than expected. If the
226 community structure was clustered significantly at high human occupancy and segregated at low
227 occupancy, our interpretation was that humans were facilitating positive spatial co-occurrence

among subordinate species consistent with the HSH (Berger, 2007). Alternatively, we interpreted segregation of the community structure at a high human activity and aggregation at low activity as evidence of spatial partitioning and competition avoidance, following the HCH (de Satgé et al., 2017).

Two additional scenarios exist: segregation at both low and high human occupancy, indicating spatial avoidance between competing carnivores irrespective of human activity as well as aggregation at both low and high human occupancy, indicating that carnivores are spatially clustered within city parks regardless of human activity. Both of these latter scenarios would suggest that the spatial structure of the carnivore community is determined not by the degree of human activity, but by other park and landscape attributes such as park size, vegetation, access to water, or food availability (Gompper et al., 2016).

Pairwise Interspecific-Level Response to Human Activity

To understand how human activity affects paired interspecific spatial relationships, we compared independent detections for four species (coyote, raccoon, red fox, skunk) at parks designated as high human occupancy versus low. Grey foxes were only detected at 1 park and were thus excluded from this component of our analysis. Using the species detections matrix from the community-level analysis where each park is a spatial replicate, we calculated Spearman's *R* correlation coefficients for each species pair to test for significant positive or negative associations. In support of the HSH, we expected humans and subordinate carnivores to be positively correlated while for humans and coyotes to be negatively correlated at parks where human occupancy was high. Additionally, we expected the subordinate species to be negatively correlated with coyotes at low human occupancy, indicating competitive spatial partitioning in

the absence of the "shield", though we expected the raccoon and skunk response to be weaker (Gehrt, & Prange, 2006; Gosselink et al., 2003; Prange, & Gehrt, 2007; Prugh et al., 2009). Conversely, we expected humans and all carnivore species to be negatively correlated at parks with high human occupancy, with a weaker negative or non-significant correlation at parks where human occupancy was low in support of the HCH. If humans are negatively correlated with species across the community, it would indicate that humans do not simply exert top-down pressure on the apex carnivore, but that these finer patch-scale effects are felt for other species as well (George, & Crooks, 2006).

To test for changes in associations between species pairs in response to human activity, we transformed the Spearman's *R* correlation coefficient to Fisher's Z-statistic and compared "high" vs "low" groups at α=0.05 significance (Myers, & Sirois, 2014).

Species-Level Response to Human Activity

Finally, we quantified individual species-level response to human occupancy, by generating activity heatmaps for human, coyote, red fox, skunk, and raccoon occurrence in Detroit city parks with kernel density estimation (KDE) in ArcMap software (v 10.6.1, ESRI 2010). KDE heatmaps measured the frequency of activity in an area scaled by total activity (min: 0, max: 1), where 1 indicates the highest activity for a species at a site. We then used the kernel density values at each park to calculate a Getis-Ord Gi* statistic (Z-score) and test for areas of significant activity for each species (i.e. "hotspots"). Determining which sites were hotspots for each carnivore species and comparing them to where hotspots of human activity occurred enabled a spatially explicit analysis of each individual carnivore species' use of urban parks.

Given that Detroit is classified as a major metropolitan area and that > 50% of its 309 city parks are designated as "mini" (i.e. < 3 acres) and embedded within neighborhoods with high foot traffic, we anticipated that the majority of city parks would be hotspots of high human activity (U.S. Census Bureau, 2016). With respect to the HSH versus HCH hypothetical framework, we expected hotspots of human and subordinate species (i.e. red fox, skunk and raccoon) to occur at the same parks in support of the HSH. Alternatively, if the data supported the HCH, we expected the parks where human and carnivore hotspots occurred to be distinct.

RESULTS

Our 12,106-trap night survey yielded detections of coyotes (n=220), raccoons (n=1,496), red (n=88) and grey (n=11) foxes, and striped skunks (n=38) in a highly urbanized landscape from 2017-2020. The proportion of sites occupied (uncorrected for imperfect detection) varied by species and year (Table 1). Contrary to our expectations, sites of significant densities of human detections were localized to a small proportion of parks.

Human Occupancy Estimation

We recorded 1,103 human detections at 25 parks (naïve occupancy 0.64 for combined 2017-2020 data). The top model (lowest ΔAIC and highest *w*) revealed that the number of trap nights (TN, β=0.01, p=0.03), understory vegetation (VEG, β=-0.62, p<0.01), camera type (CAM, β=-0.57, p<0.01), and park size (AREA, β=-0.0009, p<0.01) best explained human detection. Housing density within 500 meters (HOUSE, β=0.001, p=0.03) best explained human occupancy (Table 2). Using the top performing model, we found the average occupancy across

all sites was φ=0.68. Neither the distance to the nearest school nor year covariates appeared in any of the top candidate models, and thus did not influence human occupancy.

Community-Level Response to Human Activity

Using the threshold value of "high" and "low" from the top human occupancy model, we found significant clustering at both levels of human presence: (Observed C-Score$_{Low}$: 0.0714, p=0.026, Observed C-Score$_{High}$: 0.396, p=0.008). Therefore, the emergent trend was that the carnivores' spatial structure was aggregated at both high and low human occupancy, supporting the alternate scenario where habitat-related resources such as vegetation cover, prey availability, or water drive significant spatial overlap in the limited city green space (Gompper et al., 2016). Though we found spatial aggregation across levels of human occupancy, the degree of observed clustering was higher at parks with high human occupancy.

Pairwise Interspecific Level Response to Human Activity

At both levels of human occupancy, all species dyads had non-significant Spearman's correlation coefficients (Figure 3). We did not find any significant differences between correlation coefficients going from low to high human occupancy for any species pair, though several dyads changed the direction of their association in response to human activity. Coyote-skunk (R=0.16, R=-0.33), raccoon-fox (R=0.32, R=-0.44), and skunk-fox (R=0.48, R=-0.02) correlated positively at low human Ψ and negatively at high human Ψ.

Species-Level Response to Human Activity

We found distinct areas of high kernel density activity for humans, coyotes, raccoons,

striped skunk, and red foxes across urban parks in Detroit (Figure 4). Of the 24 city parks sampled, 4 (17.39%) were significant hotspots based on intensity of use by humans. However, none of the carnivore species' hotspots significantly overlapped with human hotspots, indicating spatial avoidance of human activity in support of the HCH. Surprising for an urban environment, humans were the only species in the system to have a "coldspot" (Getis-Ord Gi* z-score < 0) meaning activity was significantly lower than the expected value. One park contained significant hotspots for coyote, red fox, and skunk, the only such location with > 2 species hotspots. Two parks were hotspots for two carnivores pairs: coyote-raccoon and raccoon-red fox.

DISCUSSION

Our study provides necessary insights into carnivore spatial responses to human occupancy in parks at multiple levels of ecological organization. Common proxies for human activity derived from landscape-level metrics of urbanization such as housing density, percent impervious surfaces, or road density may not capture the resolution necessary to determine fine-scale consequences for wildlife (Tablado, & Jenni, 2017). The inclusion of indices of direct human activity is therefore needed in future urban ecology studies to disentangle the effects of humans from the built environment (Nickel et al., 2020). Further, the design of parks and urban green spaces should include considerations of how human presence shapes animal communities to adequately balance the needs of people and wildlife.

Support for either the HSH or HCH frameworks depended upon the scale of ecological complexity. At the community level, carnivores were spatially aggregated and co-occurred significantly at parks with low human activity and high human activity, indicating that factors

other than humans were driving space-use in the parks. Key resources such as den sites and prey availability may be intrinsically concentrated in urban green spaces, given that they are essentially habitat fragments embedded in an urban matrix (Marzluff, 2005). Carnivores in our study being aggregated, even at parks with significant human activity, highlights the importance of city parks for both people and wildlife. Measures to both improve habitat quality and reduce human-wildlife conflict are of paramount importance for urban natural resource managers in order to ensure both the long-term persistence of wildlife and access to beneficial outdoor recreation opportunities for city dwellers.

Whether the species pair was apex-subordinate or subordinate-subordinate changed the interpretation of whether the results supported the HSH or HCH at the pairwise interspecific correlation level. Coyote-skunk and multiple subordinate-subordinate species pairs changed the direction of their association in response to human occupancy, though these changes were not statistically significant. It is unclear whether this is due to low site sample size and limited statistical power or a case where biological and statistical significance are incongruent (Martínez-Abraín, 2008). Both coyotes and skunks are particularly effective urban exploiters, given their generalist dietary breadth and ability to capitalize on anthropogenic food sources (Gehrt et al., 2011; Murray et al., 2015; Prange, & Gehrt, 2004). Because humans increase nocturnality in urban wildlife, the change from positive to negative association between coyotes and skunks in response to human activity may be evidence of spatial avoidance, given their increased temporal overlap (Gaynor et al., 2018).

Following results from pairwise species correlations, none of the four focal carnivore species shared hotspots of significant activity with humans at the individual level, lending support to the HCH. Raccoons, red foxes, and coyotes are emblematic of organisms who are

spatially associated with urbanization at a coarse scale, but our results illustrate that in spite of being embedded in a highly urbanized cityscape, these species are still finding pockets of spatial refugia away from people (Prange et al., 2004). Results from the paired interspecific spatial correlations appear to contradict those at the individual species level, which we believe is a result of methodological differences in our approach to quantifying each level's response. For paired species correlations, we categorically binned parks based on high versus low human occupancy, while the geospatial tool was informed by continuous relative activity data (i.e. the number of detections). A solution for future studies could be a before-after-controlled-impact (BACI) approach to experimentally manipulate human activity at each park and thus compare community aggregation, paired species associations, and individual hotspots at each location in response to a similarly measured variable of human activity.

Patterns in nature are coupled with the scale at which they are observed, thus scale is a critical component in ecological studies and we further corroborate this tenet for urban environments (Levin, 1992; Sayre, 2005). The effect of human activity did not scale with levels of ecological organization, suggesting that the causal mechanism through which human pressures illicit responses from wildlife is different for individuals, species pairs, and communities. For example, reduction of mortality through spatial avoidance of people could determine individual-level responses to human occupancy (Loveridge et al., 2017; Ordiz et al., 2011). In contrast, human activity might alter higher order interactions through changes in temporal activity in dominant carnivores, facilitating spatial overlap at the community-level (Billick, & Case, 1994; Dröge et al., 2017).

If humans function as shields and facilitate spatial overlap in the carnivore community, then urban areas could serve as key refugia in cities and increase co-existence in an otherwise

highly competitive guild. Paradoxically, the human shield hypothesis indicates that urbanization does not inherently result in biodiversity loss at the patch scale, given that subordinate species can exploit refugia (Lewis et al., 2019; Moll et al., 2018). However, biodiversity loss due to urbanization at both the landscape and global scale remains a concern for conservation efforts (Lewis et al., 2015; McDonald et al., 2013; McIntyre, 2014).

In addition to wild carnivores, domestic dogs and cats were commonly detected and often without human company. Human affiliates such as dogs and cats are widely recognized as having significant detrimental effects on wildlife (Lenth et al., 2008; Loss et al., 2013; Vanak, & Gompper, 2009). Despite this, the distinction between free roaming, feral, or simply temporarily off leash remains unresolved in our study system. As a result, we were unable to determine whether these human affiliates were true long-term members of the local carnivore assembly and thus were excluded from the analysis. Leashed dogs sometimes harass and injure wildlife, including some of the focal species for this study (Hughes, & Macdonald, 2013). However, how these antagonistic interactions determine the composition, structure, and distribution of carnivore communities in urban spaces are not well understood. Because dogs are one of the most widely distributed terrestrial carnivores, filling this knowledge gap should be a key consideration for future studies to better inform natural resource managers seeking to mitigate their effects on wildlife (Gehrt et al., 2010).

Our study provides a multilevel analysis of an urban carnivore community in a mid-sized city whose population has declined over the last 70 years. Notably, this emigration of people from the city of Detroit is complex and tied to various historical socioeconomic biases. Further, we recognize that how people are distributed in the city and who has access to green spaces is not equitable and a consequence of discriminatory housing policies (Watkins, & Gerrish, 2018).

This economic and racial segregation of neighborhoods introduces a bias to understanding human-wildlife interactions in cities, requiring further study to disentangle species coexistence patterns, resource availability, and socioeconomic factors.

Examples abound in the literature of generalizations about biodiversity loss and homogenization of community assemblages based primarily in large cities (Groffman et al., 2014; Pearse et al., 2018). Homogenization patterns in urban systems do not necessarily scale down to smaller cities. Moreover, the historical trajectory and relationship between of population decline, housing vacancy, and vegetation varies by city (Schwarz et al., 2018). We therefore anticipate that future multi-city comparisons will need to incorporate locations of varying combinations of urban area and human population density (Magle et al., 2019; Steele, & Wolz, 2019). As the world continues to develop and urbanize, our work informs how carnivore communities may respond to living in a human-dominated landscape.

Finally, our study could inform the way natural resource managers and city planners approach urban design. Given that urban carnivores seek spatial refuge from human activity hotspots, future park designs could incorporate wildlife zones where the use of walking trails diverts human foot traffic around rather than through important habitat. Urban planners are thus tasked with promoting access to natural areas for the public, while still conserving habitat for wildlife. City parks are an important resource for urbanites and provide recreational, cultural, psychological and physiological benefits to visitors (Soga, & Gaston, 2020). Therefore, finding a balance between the wellbeing of people and wildlife is a fundamental challenge of the 21st century (Chawla, 2015; Liu et al., 2017; Rigolon, 2016).

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Table 1 Summary of 2017-2020 DMP camera survey including trap nights, number of sampling sites, detections for all species, and number and proportion of sites occupied at parks with low versus high human occupancy.

	Low Human Ψ	High Human Ψ	Total
Trap Nights	5,572	6,534	12,106
Sites	8	18	26
	Summary of DMP 2017-2020 Camera Detections		
Human	99	1,004	1,103
Coyote	122	98	220
Red Fox	72	16	88
Grey Fox	9	2	11
Raccoon	1,044	452	1,496
Skunk	19	19	38
Domestic Dog	245	355	600
Domestic Cat	139	300	439
	Number (Proportion) Sites Occupied		
Human	7 (0.86)	18 (1)	25 (0.96)
Coyote	7 (0.86)	9 (0.50)	16 (0.62)
Red Fox	3 (0.38)	4 (0.22)	7 (0.27)
Grey Fox	1 (0.13)	1 (0.06)	2 (0.08)
Raccoon	7 (0.86)	12 (0.67)	19 (0.73)
Skunk	3 (0.38)	3 (0.17)	6 (0.23)
Domestic Dog	8 (1)	16 (0.89)	24 (0.92)
Domestic Cat	7 (0.86)	16 (0.89)	23 (0.88)

Table 2 Summary of candidate human occupancy models with covariates including trap nights (TN), distance to nearest school (DSCH), understory vegetation at camera (VEG), park size (AREA), and year (YR). Dot models (.) denote null (i.e. random) occupancy or detection. Akaike's Information Criterion (AIC), delta AIC, AIC model weight, model goodness of fit (X^2), and overdispersion ($\hat{c}$) are listed.

Model	**AIC**	**ΔAIC**	**AIC Weight**	**Goodness of Fit (X^2)**	$\hat{c}$
ρ(TN+AREA+VEG +CAM) Ψ (HOUSE)	1509.94	0.00	0.351	*p*=0.756	0.985
ρ(TN+AREA+VEG+CAM) Ψ (AREA)	1511.18	1.24	0.189	*p*=0.451	1.000
ρ(TN+AREA+VEG+CAM) Ψ (HOUSE + AREA)	1511.27	1.33	0.181	*p*=0.215	1.015
ρ(TN+AREA+VEG+ CAM) Ψ (.)	1511.36	1.42	0.173	*p*=0.474	1.002
ρ (AREA+VEG+ CAM) Ψ (HOUSE)	1513.23	3.28	0.068	*p*=0.085	0.975
ρ (AREA+VEG+ CAM) Ψ (AREA)	1514.33	4.38	0.039	*p*=0.089	1.009

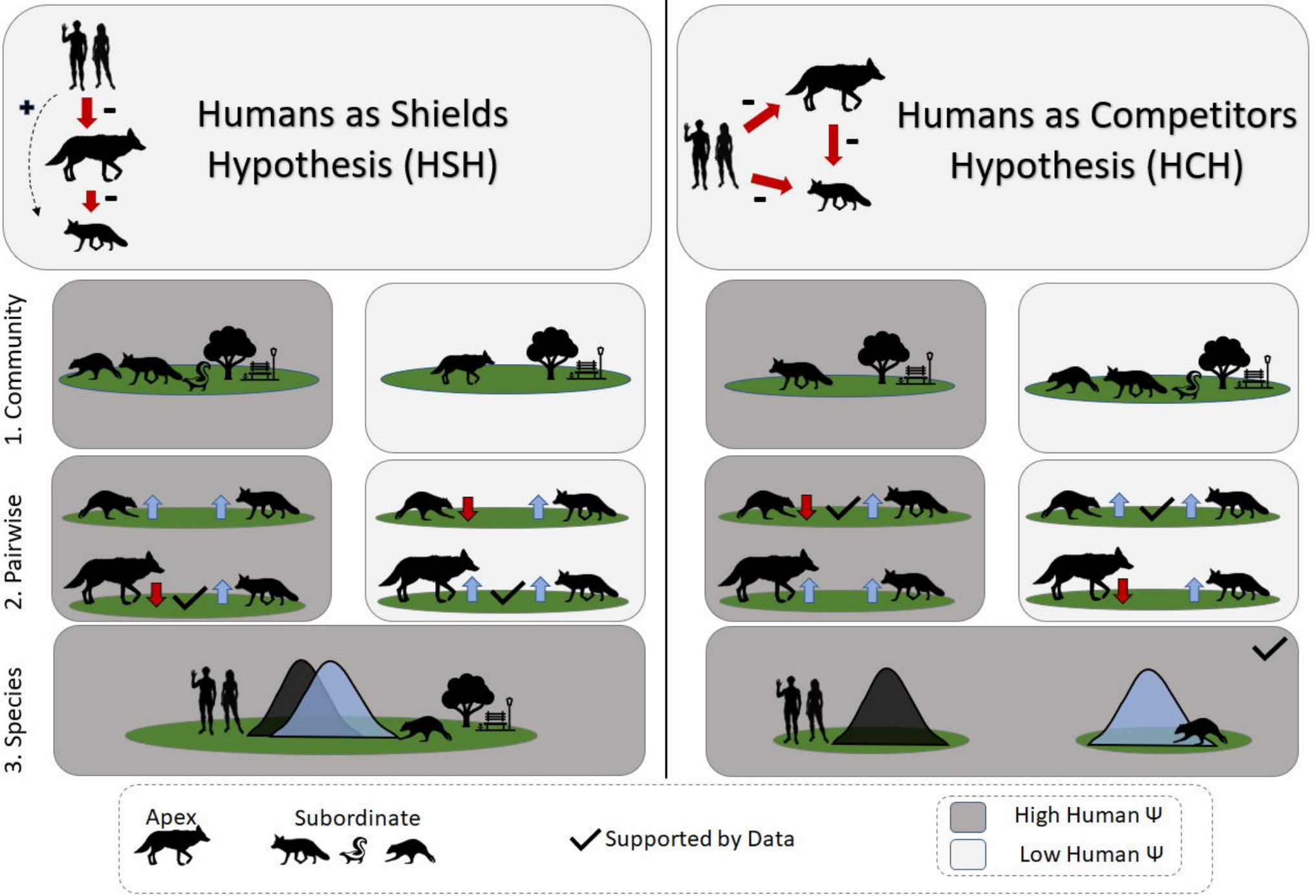
Figure Legends

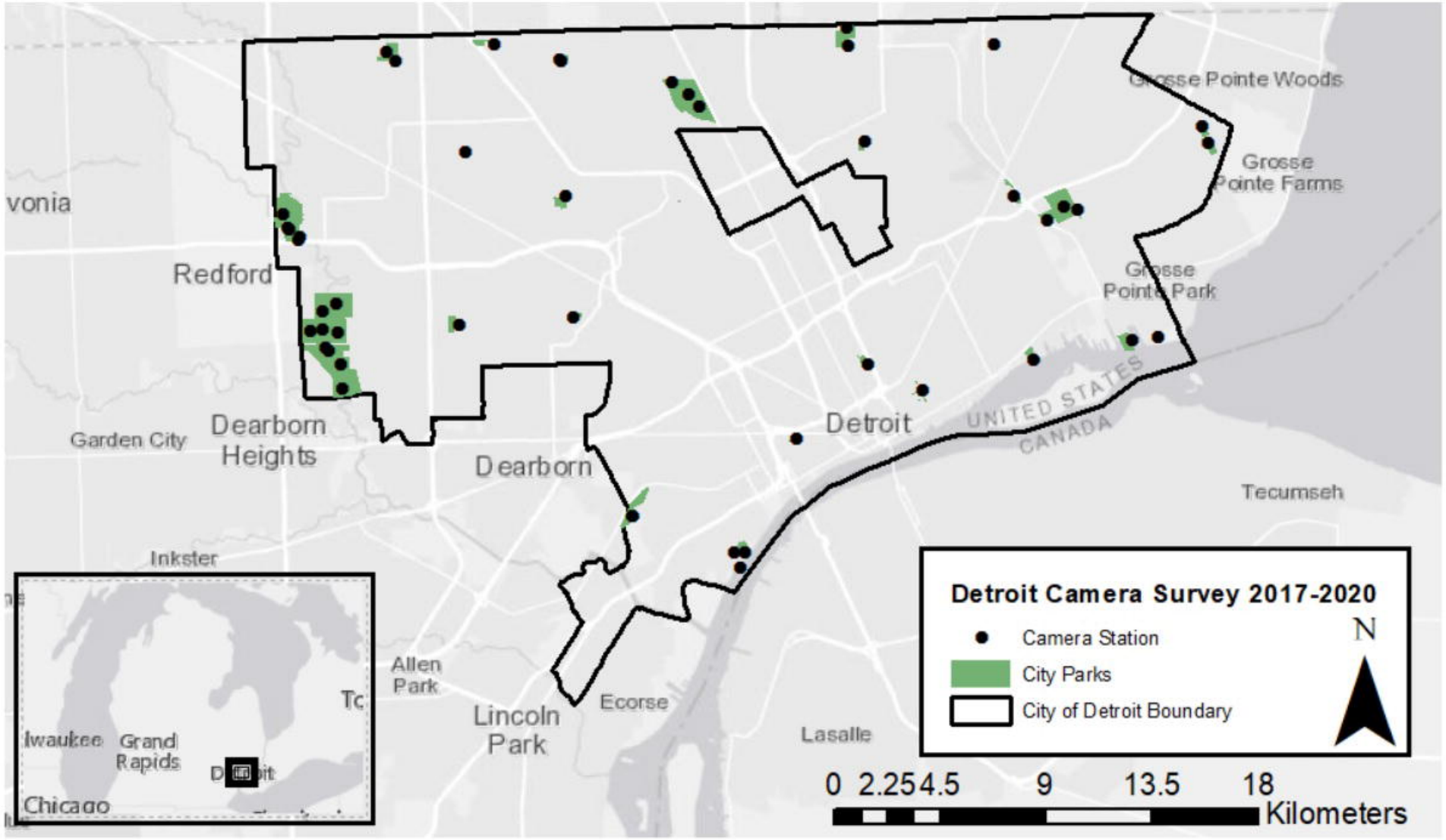
Figure 1. Conceptual framework for the effects of humans on carnivores at community (1), pairwise interspecific interactions (2), and species level (3) under two hypotheses: humans as shields (HSH) and humans as competitors (HCH). HSH1: Humans exert top-down pressure on dominant carnivore, facilitating spatial aggregation at high human occupancy (Ψ). HSH2: Positive association between subordinate carnivores at high human Ψ, negative association at low human Ψ, while apex-subordinate pairs negative at both. HSH3: Overlap between human and subordinate carnivore hotspots. HCH1: Increased activity from human competitors reduces available niche space for all carnivore species, community is spatially segregated at high human Ψ, aggregated at low human Ψ. HCH2: Negative association between subordinate carnivores at high human Ψ and positive association at low human Ψ, while apex-subordinate pairs negative at both. HCH3: No overlap between human and subordinate carnivore hotspots.

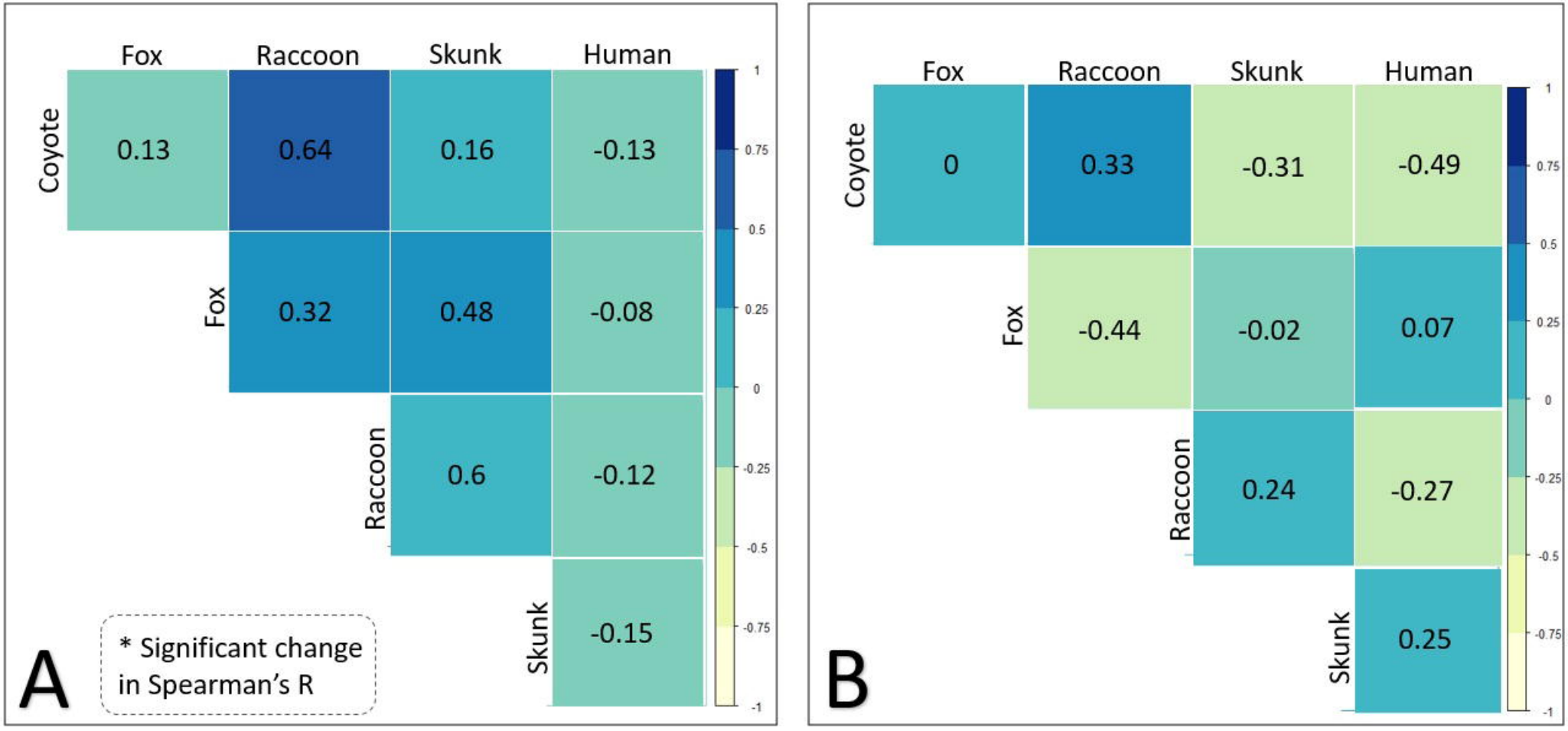
Figure 2. Study area – City of Detroit, Michigan. Shaded polygons represent the 24 city parks in the Detroit Metro Parks system included in the analysis while black dots denote camera stations in the study.

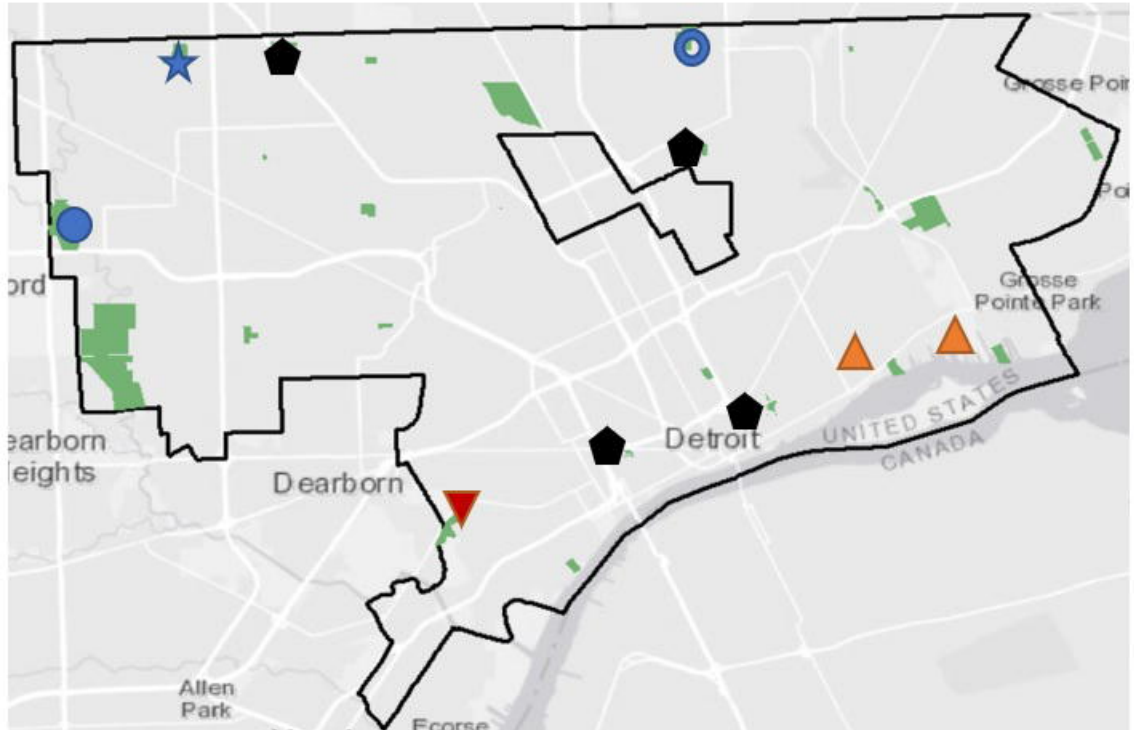
Figure 3. Correlogram of pairwise interspecific associations using Spearman's *R* at: A) low human occupancy versus B) high human occupancy. Values in white backgrounds denote non-significant correlation at 95% confidence while values in color tiles denote $p<0.05$. Asterisk indicates a significant change in Spearman's *R* from low to high human occupancy.

Figure 4. Hotspots (Getis-Ord Gi* at 95% confidence) of significant activity of carnivore species and humans in Detroit Metro Parks from camera survey, 2017-2020. Hotspots are denoted by unique symbols for each species and/or combination.


Humans as Shields Hypothesis (HSH)
Humans as Competitors Hypothesis (HCH)
1. Community
2. Pairwise
3. Species
Apex
Subordinate
Supported by Data
High Human Ψ
Low Human Ψ


Detroit Camera Survey 2017-2020
Camera Station
City Parks
City of Detroit Boundary
N
0 2.25 4.5 9 13.5 18
Kilometers
Redford
Garden City
Dearborn Heights
Dearborn
Detroit
Grosse Pointe Woods
Grosse Pointe Farms
Grosse Pointe Park
UNITED STATES
CANADA
Tecumseh
Inkster
Allen Park
Lincoln Park
Ecorse
Lasalle
Chicago
Grand Rapids


Fox
Raccoon
Skunk
Human
Coyote
0.13
0.64
0.16
-0.13
Fox
0.32
0.48
-0.08
Raccoon
0.6
-0.12
Skunk
-0.15
1
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
-1
A
* Significant change in Spearman's R
Fox
Raccoon
Skunk
Human
Coyote
0
0.33
-0.31
-0.49
Fox
-0.44
-0.02
0.07
Raccoon
0.24
-0.27
Skunk
0.25
1
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
-1
B

Species Hotspots
(Getis Ord-Gi*)

- Human
- Skunk
- Coyote
- Red Fox, Coyote
- Raccoon, Coyote
- Raccoon, Red Fox, Skunk