

**PREDICTORS OF MAMMALIAN DIVERSITY AND COYOTE AND
FREE-RANGING CAT DISTRIBUTION IN THE NEW YORK
METROPOLITAN AREA**

by

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Abstract

Urbanization can have profound consequences for mammalian biodiversity and is thought to contribute to patterns of species richness and community composition. Large cities can be particularly challenging environments for mammals because these habitats are often impacted by anthropogenic perturbations, including high human population density, fragmented habitats, and extensive human development. In this study, I investigated mammalian species richness, Shannon-Wiener diversity, and evenness in the most densely populated region in the United States: the New York metropolitan area. Specifically, camera traps were deployed from 2015-2019 to investigate the impact of six drivers of mammalian diversity across 31 greenspaces: (1) human population density, (2) patch size, (3) habitat type, (4) surrounding land cover, (5) geographical barriers to dispersal, and (6) habitat heterogeneity. I found that mammal community composition is largely influenced by a multitude of anthropogenic factors. Specifically, mammal species richness was higher in greenspaces with larger patch sizes and lower in greenspaces surrounded by more development. Moreover, Shannon-Wiener diversity and evenness were higher in urban natural landscapes than human-altered landscapes. In a subset of data that only included carnivores, I found that carnivore Shannon-Wiener diversity was higher in urban natural habitats and in sites with lower human population densities. Finally, I found that geographical barriers contributed to both patterns of mammalian diversity and patterns of carnivore diversity: mammal taxa richness, Shannon-Wiener diversity, and evenness were all significantly higher on the continent (Bronx/Westchester) than on Long Island. These results suggest that preserving urban greenspaces is important for maintaining both mammalian and carnivore biodiversity and that management of mammals in cities should concentrate on maintaining large, connected, natural greenspaces.

Introduction

As urbanization continues to spread throughout the world, its consequences, including increased human population growth, habitat fragmentation, and deforestation, are becoming increasingly important to examine and understand, especially in terms of biodiversity (McKinney, 2002; McDonald et al., 2008). Urbanization has had profound impacts on ecosystem function and is thought to be a major driver of biodiversity loss (Czech et al., 2000; Ray, 2000; Sala et al., 2000; Dobson et al., 2006; McCleery, 2010; Seto et al., 2012; Lewis et al., 2015). Mammals are sensitive to urbanization because their habitats within cities are often fragmented or replaced by human developments (Fernández and Simonetti, 2013; Łopucki and Kitowski, 2017). Carnivores are especially impacted by increased urbanization due to their large home ranges, human intolerance, limited diets, and low densities (Ordeñana et al., 2010; Stark, 2020). However, while urbanization is often associated with a lack of wildlife, recent studies have shown that species diversity, richness, and abundance are actually high in some urban greenspaces (Gehrt et al., 2009; Gallo et al., 2017; Matthies et al., 2017; Parsons et al., 2018). Indeed, some mammals, including coyotes (*Canis latrans*), raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and foxes (e.g., *Vulpes vulpes*), are known as “urban adapters”, and have benefitted from being in close proximity to developed areas reaping the benefits of increased food sources, decreased competition, and increased protection from large predators (McKinney, 2002; Adams and Lindsey, 2010; Gehrt et al., 2013; Lombardi et al., 2017). Understanding what factors influence patterns of mammalian community composition are important considerations in maintaining and protecting biodiversity in urban habitats. In this study, I used camera traps to investigate the impact of six drivers of mammalian diversity across greenspaces in the New York metropolitan area: (1) human population density (Magura et al., 2021), (2) patch size (Arrhenius,

1921), (3) habitat type (McDonnell and Pickett, 1990), (4) surrounding land cover (Cavia et al., 2009), (5) geographical barriers to dispersal (MacArthur and Wilson, 1967), and (6) habitat heterogeneity (Cornelis and Hermy, 2004).

At first glance it would seem human population density would negatively affect wildlife diversity, and indeed this is the case for many species and circumstances (Olifiers et al., 2005; Schipper et al., 2008, Stark et al., 2020). However, the impact of human population density on biodiversity is species-specific and scale-dependent (e.g., Prange et al., 2004; McCleery, 2010; Gehrt et al., 2013; Lombardi et al., 2017). On a global scale, as the human population increases, more natural habitats are destroyed for residential, commercial, and agricultural use; mammals are forced from their habitats, and many do not survive (Lopes and Ferrari, 2000; Kasso and Bekele, 2014). Accordingly, several studies have reported a negative correlation between human population density and species richness (e.g., Gehrt and McGraw, 2007; Parsons et al., 2018; Stark et al., 2020). Another consequence of increased human population density is the occurrence of more hunting and culling in habitats once dominated by animals (Cullen et al., 2000). This is especially the case for large mammals that humans perceive as threats, such as coyotes (Nagy et al., 2017). Finally, although not as well-studied, vehicles have a major impact on mammalian diversity, in some years even greater than that of hunting (Forman and Alexander, 1998). Due to the abundance of roads located near forested areas, vehicular killings have contributed to overall mammal diversity loss in recent decades (Bashore et al., 1985; Forman and Alexander, 1998; Seiler, 2000; Shilling, 2021). While an inverse relationship between biodiversity and human population density has been documented in many circumstances, on a local scale, species richness and abundance of certain taxa, such as free-ranging cats (*Felis catus*), raccoons (*P. lotor*), and certain rodents, are actually higher in areas of

high human population density (Luck 2007; Gehrt et al., 2013; Lombardi et al., 2017). This may be largely attributed to the high availability of anthropogenic food sources in areas with high human population densities (Prange et al., 2004; Contesse et al., 2004; McCleery, 2010; Magura et al., 2021). Furthermore, close proximity to humans in urban landscapes has been shown to reduce predation pressures for small and medium size mammal species (Ditchkoff et al., 2006; McCleery, 2010). This is predominantly due to the displacement of large predators as a result of high human presence and activity in centrally populated areas (Muhly et al., 2011). When taking all these factors into consideration, densely populated cities typically have a net negative effect on mammalian species richness and especially pose a threat for larger mammals (Gehrt and McGraw, 2007; Parsons et al., 2018; Stark et al., 2020).

Patch size, defined as the arrangement and size of usable land area, have a major influence on patterns of mammalian diversity (Lombardi et al., 2017). In highly developed areas, increased urbanization often results in habitat fragmentation or isolation effects, which reduces the amount of available living space (Fahrig et al., 2003; Cavia et al., 2009; Nielsen et al., 2014) and separates larger populations into smaller subpopulations that, individually, are less viable. Some species of mammals are less likely to tolerate isolated patches of habitats that result from increased urbanization because they require more space to acquire vital resources (Etter et al., 2002; Prange et al., 2004; Moll et al., 2020). Accordingly, several studies have reported a positive association between patch size and species diversity (Saunders et al., 1991; Iida and Nakashizuka, 1995; Fahrig, 2002). Nielsen et al. (2014) found that a minimum of 10 hectares of patch size is necessary to ensure high species richness in urban greenspaces. However, some mammals, such as large carnivores, require an even greater amount of greenspace sometimes extending five square kilometers and beyond (Stark et al., 2020). Thus, mammalian diversity is

largely defined by species-area effects whereby species richness is a function of patch size (MacArthur and Wilson, 1967; Hodgkinson et al., 2007; Matthies et al., 2017).

The type of habitat might also affect patterns of mammalian diversity (Gallo et al., 2017). In urban areas, some greenspaces are dominated by *human-altered habitats* while other greenspaces are mainly comprised of *urban natural habitats*. Human-altered habitats include parks, which are characterized by manicured vegetation and high human activity (Nielsen et al., 2014); golf courses, which are comprised of large, semi-artificial greenspaces where human activity varies temporally (Boone et al., 2008); and cemeteries (Gallo et al., 2017). Some species can flourish in human-altered habitats (urban adapters), while other species cannot (urban avoiders) (McKinney, 2002, 2006). In contrast to human-altered habitats, urban natural habitats are typically composed of undeveloped woodlands with secondary growth forest (Vernon et al., 2014) situated within an urban or human-altered matrix. Natural areas within urban environments remain crucial in supporting mammal populations (Baker and Harris, 2007). Several studies have found that the presence of natural habitats within urban greenspaces allows for greater movement of multiple species (Radeloff et al., 2005; Gehrt, 2011; Bateman and Fleming, 2012; Scott et al., 2014).

The amount of developed land cover surrounding a habitat is another factor thought to be associated with mammalian diversity (Bierwagen, 2006; Cavia et al., 2009). Urban habitats often have decreased structural and functional connectivity between the highly developed cityscape and the less developed natural habitats within (LaPoint et al., 2015; Beninde et al., 2016). This reduced connectivity resulting from urbanization often leads to decreased distribution of smaller species (Zollner, 2000). Highly developed areas also have a high percent of impervious surface cover (i.e., roads, buildings, landscaping), and often have lower biodiversity than less developed

areas (McKinney, 2008; Gallo et al., 2017). High impervious surface cover surrounding natural habitats like roads, buildings, and parking lots restrict home ranges and can lead to increased death by vehicle collision (Trombulak and Frissell, 2000; Seiler, 2001; Gehrt et al., 2013). These barriers to dispersal reduce gene flow and population viability relative to a connected metapopulation and can lead to decreased species richness (Bateman and Fleming, 2012). Mammals situated in habitats surrounded by highly developed land cover also experience high rates of habitat and resource disturbance (Blair and Launer, 1997) and the loss of natural vegetation to development (McKinney, 2008; McCleery, 2010). Together, these changes to habitats that encompass greenspaces place limitations on the species within the greenspace itself. Therefore, in order to maintain mammalian diversity, it is important to have patches of natural habitat and vegetation as well as increased connectivity between greenspaces and highly developed surrounding areas (Beninde et al., 2016; Gallo et al., 2017; Fidino et al., 2020).

Another factor that contributes to patterns of mammalian diversity is habitat heterogeneity. The habitat heterogeneity hypothesis proposes that the species diversity of an area will increase as the number of habitats increases (MacArthur and MacArthur, 1961). Hence, it is predicted that a greater number of habitats can offer more resources to a wider range of animals (Garden et al., 2007; Hodgkinson et al., 2007; Matthies et al., 2017). In more heterogeneous habitats, there tend to be more habitat edges, creating more resources for supporting a greater number of mammals (Racey and Euler, 1982; Cramer and Willig, 2005). Accordingly, several studies of mammals have reported a positive association between habitat heterogeneity and species richness (Jepsen and Topping, 2004; Arques et al., 2014; Presley et al., 2019). Thus, urban greenspaces that have a variety of habitats are thought to be vital to mammalian diversity (Hodgkinson et al., 2007).

Lastly, geographical barriers can also influence patterns of mammalian diversity. Specifically, islands that are bounded by water create barriers to dispersal for many species (Weckel et al., 2015). Hice and Schmidly (2002) found that continental regions exhibit higher species diversity than island regions mainly because they do not require the crossing of harsh waterways or busy bridges for colonization. Some mammals, like coyotes (Harrison, 1992) and raccoons (Prange, 2004), can cross these barriers somewhat to move between the mainland and the island, which has been seen in major cities like New York (Weckel et al., 2015; Henger et al., 2020) and San Francisco (Sacks et al., 2006). Nonetheless, the intersection of urbanization and geographical barriers to dispersal are thought to lead to reduced mammal richness and evenness among urban habitats (Ekernas and Mertes, 2006; Weckel et al., 2015).

My goal was to determine predictors of mammalian diversity in various greenspaces across the New York metropolitan Area. To do so, I deployed camera traps across 31 study sites (Fig. 1.1; Table 1.1). I hypothesized that mammal community composition is influenced by a multitude of anthropogenic factors including human population density (Magura et al., 2021), patch size (Arrhenius, 1921), habitat type (McDonnell and Pickett 1990), surrounding land cover (Cavia et al., 2009), geographical barriers to dispersal (MacArthur and Wilson, 1967), and habitat heterogeneity (Cornelis and Hermy, 2004). Specifically, I predicted that mammalian diversity would be higher in study sites where there were lower human population densities, larger patch sizes, urban natural habitats, less developed land cover surrounding the core habitat, and more heterogenous habitats. Because bodies of water are important geographical barriers to dispersal, I also predicted that mammal diversity would be greater in the mainland (Bronx/Westchester) than in Long Island, Manhattan, and Randall's Island. Identifying and

understanding what factors influence patterns of mammalian diversity is critical to maintaining both mammalian populations and overall biodiversity.

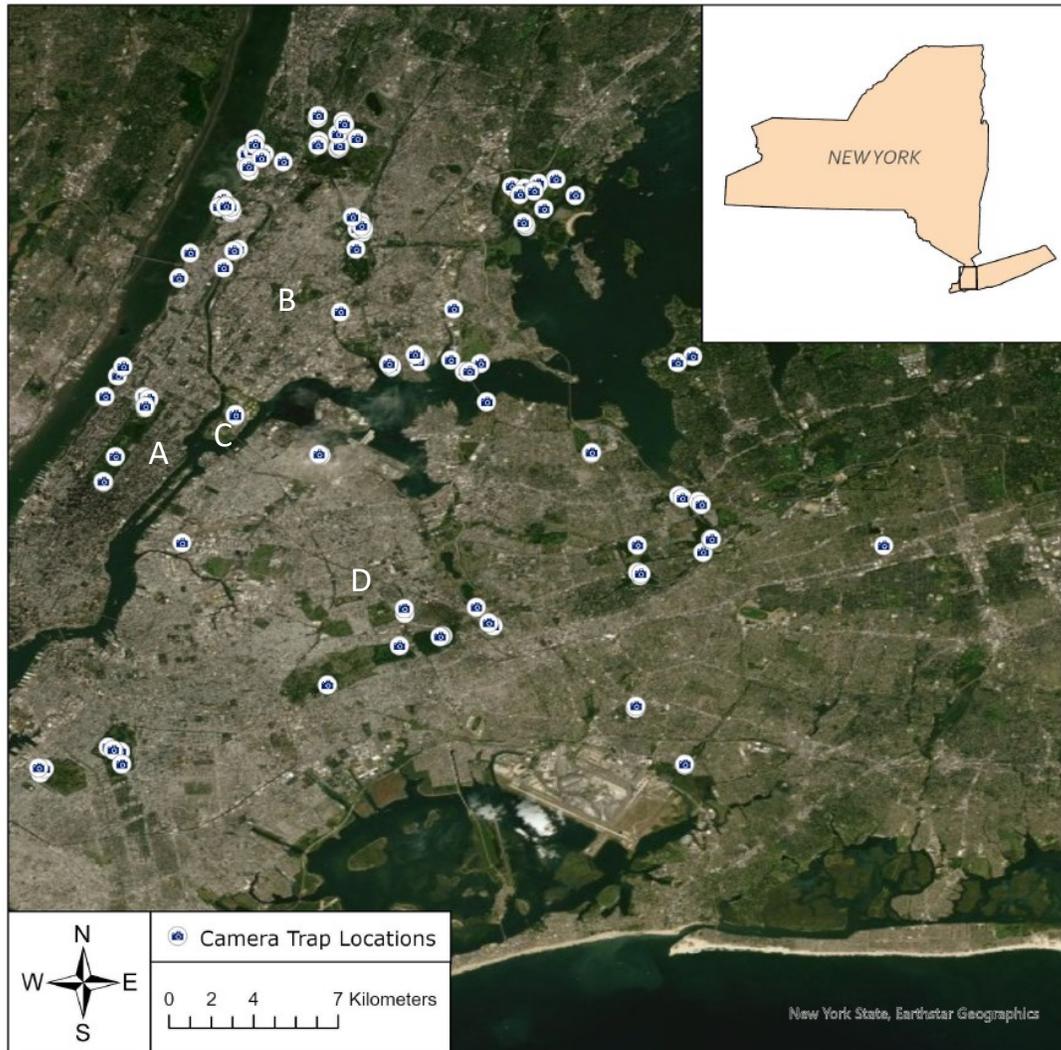


Figure 1.1. Map of camera locations across 31 greenspaces in which mammals were surveyed in the New York metropolitan area, 2015-2019. A = Manhattan; B = Mainland (Bronx/Westchester); C = Randall's Island; D = Long Island

Table 1.1. Dates, location, and characteristics of study sites surveyed 2015-2019

Study Site	Survey Dates	Latitude, Longitude ^A	Human Population Density people/km ² ^B	Patch Size (km ²)	Habitat Type	Percent Developed Land cover (500 m)	Percent Developed Land cover (1000 m)	Habitat Heterogeneity (500 m)	Habitat Heterogeneity (1000 m)	Region	Number of Cameras/km ²	Number of Cameras Deployed
Alley Pond	2/1/16 – 5/7/19	40.75742, -73.74266	28,552.03	2.82	Urban Natural Habitat	71.58	82.86	7	10	Long Island	2.48	7
Bronx Park	1/30/16 – 6/13/19	40.86273, -73.87398	139,345.89	2.95	Urban Natural Habitat	44.33	85.71	10	13	Mainland	3.39	10
Central Park	2/17/16 – 7/24/17	40.76635, -73.97463	271,920.26	3.43	Human-Altered Habitat	30.89	30.56	8	12	Manhattan	2.62	9
Clearview Golf Course	2/1/16 – 3/29/19	40.77767, -73.78519	34,319.93	0.48	Human-Altered Habitat	53.32	0	4	7	Long Island	6.25	3
Cunningham	2/3/16 – 5/7/19	40.74176, -73.76742	37,726.40	2.25	Urban Natural Habitat	41.83	33.33	7	8	Long Island	2.67	6
Elmjack Ingrams Field	5/27/16 – 5/10/19	40.77693, -73.89096	65,241.80	0.058	Human-Altered Habitat	69.89	51.43	7	7	Long Island	51.72	3
Ferry Point	2/1/16 – 5/16/19	40.81174, -73.82832	31,890.52	1.32	Human-Altered Habitat	44.46	50	13	13	Mainland	3.03	4
Forest Park	6/13/16 – 5/10/19	40.70644, -73.84295	68,951.44	1.30	Urban Natural Habitat	16.38	0	6	6	Long Island	3.08	4
Fort Washington	2/18/16 – 9/1/16	40.84486, -73.94538	160,249.04	0.51	Urban Natural Habitat	48.8	28.13	6	10	Manhattan	5.88	3
Francis Lewis	2/3/16 – 2/8/19	40.79685, -73.82587	36,189.90	0.039	Human-Altered Habitat	59.56	43.75	7	7	Long Island	25.64	1
Green-wood Cemetery	1/26/17 – 5/13/19	40.65319, -73.99909	75,492.97	1.90	Human-Altered Habitat	62.04	54.29	3	4	Long Island	1.58	3
Highbridge Park	7/9/17 – 7/28/17	40.84889, -73.92803	184,104.12	0.262	Urban Natural Habitat	66.71	19.44	9	12	Manhattan	7.63	2
Hutchinson	3/7/16 – 5/8/19	40.833, -73.83879	31,890.52	0.031	Urban Natural Habitat	85.01	83.33	4	5	Mainland	32.26	1
Idlewild Park	2/10/16 – 3/23/19	40.6564, -73.74908	32,512.12	1.65	Urban Natural Habitat	22.67	0	9	11	Long Island	1.21	2
Inwood Hill Park	12/26/15 – 5/10/19	40.87247, -73.92971	89,468.55	0.789	Urban Natural Habitat	19.11	0	10	11	Manhattan	10.14	8
Kings Point Park	6/29/16 – 9/1/16	40.81459, -73.74606	5,881.86	0.70	Urban Natural Habitat	9.3	0	7	10	Long Island	2.86	2
Maple Grove Cemetery	3/7/16 – 5/10/19	40.71028, -73.82334	88,168.38	0.272	Human-Altered Habitat	88.89	80	4	4	Long Island	7.35	2
Pelham Bay Park	2/2/16 – 5/11/19	40.86636, -73.81177	31,890.52	2.23	Human-Altered Habitat	7.91	2.86	7	13	Mainland	6.73	15
Prospect Park	7/7/17 – 5/13/19	40.65661, -73.96745	139,567.73	2.46	Urban Natural Habitat	8.29	5.41	12	14	Long Island	1.63	4
Pugsley Creek	2/18/16 – 5/7/19	40.81244, -73.85221	69,530.82	2.40	Urban Natural Habitat	72.66	20	9	12	Mainland	1.67	4
Queensline	2/10/16 – 5/10/19	40.71709, -73.85794	95,769.99	0.198	Urban Natural Habitat	94.85	89.19	4	4	Long Island	15.15	3
Railroad	2/10/16 – 5/10/19	40.67924, -73.76794	47,282.82	0.152	Urban Natural Habitat	90.16	16.67	4	4	Long Island	13.16	2
Randall's Island	2/3/16 – 5/4/19	40.79188, -73.9234	63,011.82	.092	Human-Altered Habitat	86.74	87.88	9	11	Randall's Island	21.74	2
Ridgewood Highland	1/26/18 – 5/16/18	40.68739, -73.8877	70,792.15	1.71	Human-Altered Habitat	40.96	8.33	11	11	Long Island	0.58	1
Riverdale	1/31/16 – 5/12/19	40.89881, -73.91566	72,364.27	0.51	Urban Natural Habitat	11.71	8.82	12	14	Mainland	21.57	11
Riverside Park	2/17/16 – 4/16/19	40.81059, -73.96693	208,386.12	0.35	Human-Altered Habitat	47.36	22.86	8	8	Manhattan	11.43	4
Smiling Hogshead Ranch	1/27/17 – 4/29/18	40.74252, -73.94411	25,236.84	0.008	Human-Altered Habitat	99.66	100	5	5	Long Island	125	1
Soundview	7/3/16 – 5/7/19	40.81164, -73.86387	69,530.82	0.719	Urban Natural Habitat	57.88	0	9	9	Mainland	4.17	3
Starlight Park	2/18/16 – 5/12/16	40.83183, -73.88263	131,408.23	0.011	Urban Natural Habitat	97.59	75.76	4	4	Mainland	90.91	1
Van Cortlandt	1/27/16 – 5/16/19	40.90697, -73.89154	51,011.11	4.65	Urban Natural Habitat	12.39	0	7	7	Mainland	3.44	16
Willow Lake	2/10/16 – 1/9/17	40.71763, -73.82987	67,286.60	0.665	Urban Natural Habitat	53.54	0	9	9	Long Island	1.5	1

^A For sites containing multiple camera sites, the latitude and longitude was recorded based on the location at which there were the most photo captures.

^B The human population density was calculated by averaging the population density of all of the zip codes surrounding each site.

Methods

Field Sites

This research focused on mammalian diversity across various greenspaces in the New York metropolitan Area. My study sites included 31 greenspaces throughout four geographical regions: (1) Long Island; (2) mainland (Bronx and Westchester); (3) Manhattan; and (4) Randall's Island (Table 1.2). Of the 31 sites, 16 were located in Long Island, nine in the mainland, five in Manhattan, and one in Randall's Island. Within each of these regions, there were various types of greenspaces. Of the 16 sites on Long Island, one was a baseball field, one was a golf course, one was a ranch/farm, two were cemeteries, and the remaining eleven sites were urban parks. Of the nine mainland sites, all contained natural vegetation with one site also containing multiple recreational and tourist facilities. In Manhattan, four of the five sites were parks consisting mainly of natural vegetation, while the fifth site was a more developed urban park containing a mixture of natural vegetation and human altered habitats. The Randall's Island site was comprised of a combination of open areas, natural vegetation, and human made recreational facilities. Each of the greenspaces contained one or more cameras to monitor wildlife and predict patterns of mammalian diversity.

Table 1.2. Field site descriptions and features

Study Site	Site Description and Features
Alley Pond Park	greenspace characterized by woodlands and hilly terrain with sandy ridges, meadows, ponds, and surrounding wetlands ¹ .
Bronx Park	an urban park characterized by a natural streamside terrain with a mixture of red maple hardwood and floodplain forests along the banks of the Bronx River ² .
Central Park	an urban park dominated by large American elms and containing a multitude of athletic and recreational facilities ³ (Atha et al., 2020).
Clearview Golf Course	human-altered habitat consisting of a hilly terrain with a combination of open and tree lined fairways; in addition to natural forests, this location also contains artificial ponds ⁴ .
Cunningham Park	greenspace characterized by hilly terrain with many hiking trails, sports facilities, and developed greenways; this park contains a section of relatively untouched woodland containing mostly of oak-hickory trees ⁵ .
Elmjack Ingrams Field	athletic field lined by small, forested area on three sides and an empty lot on the fourth side; due to its recreational purposes, it has a manicured field with multiple patches of dirt.
Ferry Point Park	an urban park containing golf courses as well as sports fields and recreational pathways; due to its location and proximity to multiple parkways, it serves as a connection to multiple parks ⁶ .
Forest Park	greenspace made up of a combination of natural areas and manicured habitats; on the hilly terrain of the eastern side, it contains natural forests of great oaks, while on the western side it contains athletic fields and golf courses ⁷ (Glaeser, 2006).
Fort Washington Park	an urban park serving as a connection between parklands along a large portion of the Hudson River; home to many native trees and shrubs; filled with meadow grasses ⁸ .
Francis Lewis Park	greenspace where the majority of its area is above water while the remaining area is submerged under water; this park also allows for beach access unlike many other parks in New York City ⁹ .
Green-wood Cemetery	cemetery known as one of the largest urban grasslands in New York City; comprised of a rolling landscape with diverse flora, this cemetery provides an “urban oasis” when compared to its dense, urban surroundings (Charap et al., 2020).
Highbridge Park	an urban park that is set atop a rocky cliff and contains a variety of trees creating woodlands and glens ¹⁰ .
Hutchinson	patch of greenspace comprised of patchy forested areas, manicured lawns, and is flanked by a nearby parking lot.
Idlewild Park	urban greenspace characterized by a diverse array of habitats including woodlands, meadowlands, tidal wetlands, freshwater wetlands, and grasslands ¹¹ .
Inwood Hill Park	greenspace characterized by four plant communities: 1) salt marsh 2) forest 3) lawn 4) successional field, as well as seven types of vegetation; this park

	also contains wooded forests as well as the last salt marsh in Manhattan ¹² (Loeb, 1986).
Kings Point Park	urban park that is located near the Long Island Sound and contains swamps consisting of red maples, sweetgum, sour gum, sassafras, as well as black birch; within the park, there are multiple manicured athletic fields as well as numerous hiking trails ¹³ (Greller et al., 2006).
Maple Grove Cemetery	cemetery situated at one of the highest elevations in Queens atop rocky hills and surrounded by railroads; this site contains a natural dense forest with manmade lakes ¹⁴ .
Pelham Bay Park	urban park situated between two bodies of water and comprised of a mixture of meadows, rocky shores, dense woodlands, and saltwater marshes; transitioning into a secondary forest from a wooded savannah, this park is home to oaks and low grassy vegetation, as well as golf courses, athletic fields, and hiking trails ¹⁵ (Ekernas and Mertes, 2006).
Prospect Park	urban park known for containing one of Brooklyn's last remaining and richest forests filled with the pin oaks, Norway maples, and sycamore maples; this site contains woodlands, wetlands, meadows, and the only lake in Brooklyn ^{16,17,18} .
Pugsley Creek Park	greenspace bordered by both two creeks from which the East River flows into; Pugsley Creek Park is one of the few parks that have remained mostly undeveloped with pristine freshwater wetlands ¹⁹ .
Queensline	greenspace characterized by a unique thin line of forested area lying on the border between Forest Hills and Rego Park, Queens; this patch of forest is perpendicular to the Long Island Railroad and is in close proximity to other greenspaces including parks, cemeteries, and athletic fields.
Railroad Park	greenspace located next to a railroad and known as a woodland preserve; this site is mostly fenced off and is mainly comprised of natural flora with some landscaping ²⁰ .
Randall's Island	large greenspace home to several different natural habitats including an urban forest, freshwater wetlands, a tidal marsh, meadows, coastal areas, as well as an urban farm; the park is dominated by wild grasses and herbaceous plants and is also home to white ash, common hackberry, and eastern cottonwood trees ^{21,22} .
Ridgewood Highland	urban park located within the Ridgewood Reservoir and home to a lush, dense forest as well as a freshwater pond; there are also playgrounds and athletic fields located within the park ²³ .
Riverdale Park	this urban park runs along a railroad beside the Hudson River in the Bronx and is home to a large oak hickory forest as well as a successional forest as a result of glacial activity ²⁴ .
Riverside Park	situated above the Hudson River, this park is characterized by hilly terrain and a combination of natural areas and fields, courts, and slopes for athletic purposes ²⁵ .
Smiling Hogshead Ranch	urban farm formed atop abandoned railroad tracks and containing both agricultural farm area and gardens ²⁶ .
Soundview Park	greenspace characterized by vast marshlands located in close proximity to the point in which the Bronx River changes from saltwater to the only freshwater

	river in New York; initially built atop a landfill, this park now contains athletic fields including courts, fields, and tracks ^{27,28} .
Starlight Park	urban park containing numerous athletic fields, playgrounds, picnic areas, and a dock for kayaking; my study site location was set in the Bronx River greenway, a small, forested area across from the Bronx River and parallel to Starlight Park ²⁹ .
Van Cortlandt Park	urban park known as the third-largest park in New York City with a secondary forest composed of a mixed hardwood forest of white ash, oaks, and tulip poplars; along with natural wetlands and woodlands, this park also contains multiple athletic spaces including a stadium, golf courses, and hiking trails (McDonnell et al.,1990).
Willow Lake	greenspace containing one of the largest bodies of water in Queens, surrounded by the parkland of Flushing Meadows Corona Park; this site contains thick reeds across the freshwater wetlands as well as a multitude of willows and other flower species ³⁰ .

Camera Surveys

For camera surveys, I adopted previous methodologies as described in Nagy et al., (2016). Camera traps were deployed across 31 sites in the New York metropolitan area from December 2015 to June 2019. Except for small rodents, which I classified at the family level (family Muridae), I identified all mammals to the species level using photographs captured by each camera trap. Throughout the five-year course of this study, three types of Reconyx cameras were used: RC55, PC800, and HC500 motion- and heat-activated camera traps (Reconyx, Inc., Holmen, WI). Each of these cameras had 0.2s trigger speed, 1080p resolution, and comparable infrared flash ranges (RC55 and HC500: 15m, PC800: 21m). There were two models of the RC55 used, with the older one having a 5.0 x 7.6 cm red/infrared flash primarily for night pictures, and the newer one with a single LED bulb for a “semi-covert” infrared flash. Using ArcGIS 9 and ArcGIS10 (ESRI, Redlands, California), random locations were selected for camera deployment in the different greenspaces with at least 500 m distance between each camera. At each location, cameras were deployed in a substantial patch of forest or undeveloped area. Because I had a limited number of camera traps, in cases in which a study area consistently

surveyed the same mammals, I shifted camera traps to new locations within a greenspace to increase coverage. Many of the cameras required relocation due to theft, legal ramifications, or necessity for a better-suited placement. Each of these relocations were at least within ~50 m of the originally planned locations. The actual number of cameras per greenspace varied, however, the density of cameras in most cases was at least one camera per 0.5 km² in each of the greenspaces (Table 1.1). Across the five years of the study, the cameras were typically placed in the same general areas unless there were natural disasters or theft that previously influenced the camera placement.

Predictors of Mammalian Diversity

In this study, I was interested in determining predictors of mammalian diversity in various greenspaces across the New York metropolitan Area. To gain better insight into what predicts mammalian diversity across an urban landscape, I modeled three response variables: (1) richness, defined as the number of different mammal taxa present in a given greenspace or region (Dorji et al., 2019); (2) evenness, defined as the abundance equality of mammal taxa in a specific greenspace or region (Dorji et al., 2019); and (3) Shannon-Wiener diversity, defined as the proportional abundance of each mammal taxon from the total sample of individuals within the given surveyed community (Ekernas and Mertes, 2006). I conducted two analyses, one that included all mammal taxa identified in my camera trap surveys, and another that excluded humans and domestic dogs. In cases in which both analyses yielded the same best supported model, I report the results including all mammal taxa. In cases in which the best supported model differed between analyses, I report two sets of results, one including all mammal taxa and another excluding humans and domestic dogs. I included free-ranging cats in both analyses

because these can include feral cats as well as free-roaming cats possibly subsidized by human foods (Elizondo and Loss 2016).

For my analysis of interest—predictors of mammalian diversity in the greenspaces of the New York metropolitan area—I modeled six predictor variables (Table 1.3): (1) human population density; (2) patch area; (3) habitat heterogeneity; (4) type of habitat; (5) percent developed land cover; and (6) region. I also included cameras per square kilometer in my models to control for variation in camera deployment. The number of cameras deployed at each site ranged from one to sixteen with a mean of 4.452 cameras per site ($SD \pm 4.006$). Sampling effort ranged from 50 camera trap days to 2279 camera trap days ($SD \pm 478$).

(1) **Human population density.** To measure human population density, I used United States Zip Code data³¹ to ascertain the number of individuals per square mile in the zip code in which the study site was located and then I converted these data to the number of individuals per square kilometer. In cases in which study sites were situated in more than one zip code, I calculated the mean human population density of the zip codes surrounding the study site.

(2) **Patch size.** I calculated patch size using the “measure distance” tool on Google Maps³².

(3) **Habitat type.** I classified study sites into two main categories based on habitat type. If a greenspace was comprised of greater than 50 percent secondary growth forest, I classified this habitat as *urban natural* (Gallo et al., 2017). On the other hand, if a greenspace was comprised of greater than 50 percent manicured lawns, athletic fields,

playgrounds, and golf courses, I classified this habitat as *human-altered* (Gallo et al., 2017).

(4) Percent developed land cover. ArcGIS Pro 2.6 and the National Land Cover

Database (NLCD 2019)³³ were used to calculate percent developed land cover at each of the 31 greenspaces. I constructed buffers of 500 m to assess whether developed land cover in the immediate habitat impacted mammalian diversity (e.g., Gallo et al., 2017) and buffers of 1000 m to assess whether land use surrounding a greenspace impacted mammalian diversity (e.g., Gomes et al., 2011). In cases in which the best supported model yielded the same results regardless of spatial scale, I report and discuss the model results based on land cover within 500 m (Gallo et al., 2017).

Following Callaghan et al. (2019), Stark et al. (2020), and Goldstein et al. (2022), I combined the percent land cover of three different NLCD classes (“developed, low intensity”; “developed, medium intensity”; and “developed, high intensity”) into a superclass called “developed land cover”. Developed land cover included areas with a mixture of both constructed materials and vegetation, and where impervious surface cover accounted for at least 20 percent of the land cover (NLCD 2019).

(5) Habitat heterogeneity. To calculate habitat heterogeneity, I counted the number of different habitat types based on 15 categories provided by the National Land Cover Database (NLCD 2019) (Table 1.4). I calculated habitat heterogeneity at two spatial scales: buffers of 500 m and 1000 m surrounding each of the 31 greenspaces. As with percent developed land cover, in cases in which the best supported model yielded the same results regardless of spatial scale, I report and discuss the model results based on land cover within 500 m (Gallo et al., 2017).

(6) **Region.** I classified region into four categories: (1) Long Island; (2) Manhattan; (3) mainland (Bronx and Westchester); and (4) Randall’s Island.

Table 1.3. Response and predictor variables for mammalian diversity among 31 greenspaces in the New York metropolitan area

<i>Response Variables</i>	
Richness	the number of different taxa present per study site
Shannon-Wiener diversity	the proportional abundance of each taxon from the total sample of individuals within the given surveyed community
Evenness	the abundance equality of a given species in a specific study site
<i>Predictor Variables</i>	
Human population density	the number of individuals per square kilometer in the zip code in which the study site was located
Patch size	the area in kilometers of each of the study sites
Habitat type	the type of greenspace that makes up greater than 50% of the patch size of the study site (coded as either <i>urban natural habitat</i> or <i>human-altered habitat</i>)
Percent developed land cover	the percentage of land cover type within a 500 m or 1000 m buffer comprised of a mixture of constructed materials and vegetation and where impervious surface cover accounts for at least 20 percent of the land cover
Habitat heterogeneity	the number of different greenspace types based on 15 classifications from the National Land Cover Database (2019) constituting each study site (Table 1.4)
Region	geographical location of camera traps defined as: 1) mainland (Bronx/Westchester); 2) Manhattan; 3) Long Island; 4) Randall’s Island
Cameras per km ²	number of cameras sites per study site divided by patch size of study site

Table 1.4. National Land Cover Database classes

Class	Classification Description
Open water	sites consisting of open water with less than 25% soil or vegetation
Developed: Open space	sites with a combination of lawn grasses and built materials with less than 20% impervious surfaces (i.e., parks, manicured lawns, golf courses, housing developments)
Developed: Low intensity	sites containing a combination of natural vegetation and built materials with 20-49% impervious surfaces
Developed: Medium intensity	sites with both natural vegetation and built materials with impervious surfaces accounting for 50-79% of the land cover
Developed: High intensity	sites where impervious surfaces make up 80-100% of the land cover due to high development resulting from commercial and industrial activities
Barren land	sites consisting mainly of natural earthy material with less than 15% of the land cover being vegetation
Deciduous forest	sites that consist of more than 20% vegetation cover; predominantly comprised of trees over five meters tall with over 75% of the trees shedding leaves seasonally
Evergreen forest	sites with vegetation encompassing more than 20% of total land cover and trees that maintain their green color and do not shed leaves seasonally
Mixed forest	sites with more than 20% of their land cover consisting of vegetation with neither deciduous nor evergreens comprising more than 75% of the tree cover
Shrub/scrub	sites that have more than 20% of their land cover consisting of shrubs less than five meters tall
Grassland/herbaceous	sites that have 80% or more of total land cover as grass-like vegetation
Pasture/hay	sites that have more than 20% of their land cover as some form of grasses or legumes for animals to graze on or to produce hay
Crops	sites where crop vegetation accounts for over 20% of the total land cover and the area is continuously tilled and used for producing annual crops
Woody/wetlands	sites in which shrubland or forests comprise more than 20% of the total land cover, and the soil is intermittently soaked with water
Emergent herbaceous wetlands	sites that consist of more than 80% perennial herbaceous vegetation and the soil is intermittently soaked with water

Statistical Analyses

All statistical analyses were completed using the R Project for Statistical Computing³⁴.

To calculate measures of biodiversity, I used the R package *vegan*³⁵. First, I created a species accumulation curve of the 31 sampling sites to ensure adequate sampling effort (Fig. 1.2).

Second, I calculated alpha diversity (mammal taxa richness) of each study site and gamma

diversity (total mammal taxa richness) across all study sites. Third, I used capture frequencies of each mammalian taxon as a proxy for relative abundance (Pardo et al., 2018; Knowlton et al., 2019). To calculate relative abundance, I used the following calculation: number of independent photographs \div sampling effort x 100. Sampling effort was calculated as the sum of the number of active camera days. Independent photographs were calculated by counting the maximum number of individuals from the same taxon in the same photograph during hourly intervals. Only detections of the same taxon taken at durations greater than 60 minutes were considered as independent (Cusack et al., 2015; Lewis et al., 2015; Stark et al., 2020). Lastly, I calculated Shannon-Wiener diversity and evenness using the diversity function in *vegan*.

I performed multiple linear regressions to test for predictors of mammal taxa richness, Shannon-Wiener diversity, and evenness. Because carnivores might be more sensitive to the impacts of urbanization (Woodroffe, 2000; Crooks, 2002; Šálek et al., 2014), I also performed multiple linear regressions to detect patterns of species richness, Shannon-Wiener diversity, and evenness with a subset of the data that only included carnivores. For these analyses, I classified carnivores as a functional feeding group (Stark et al., 2020). Therefore, carnivores included all species from the order Carnivora as well as the Virginia opossum (*D. virginiana*), a marsupial that behaves functionally as a carnivore (Stark et al., 2020).

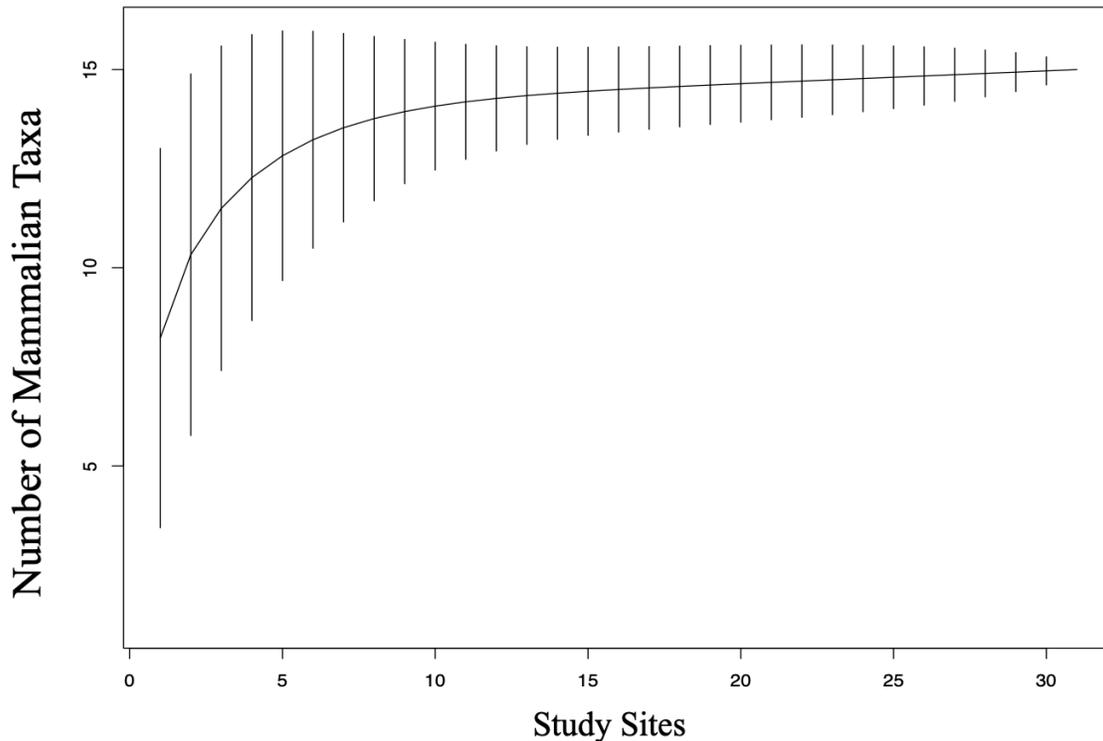
To perform all multiple linear regression models, I used the *stats* package in R. All predictor variables and response variables are described in Table 1.3. Because measures of richness incorporated count data, I modeled these response variables using the *glm* function with Poisson error distribution. Because Shannon diversity indices are strictly positive and continuous, I modeled Shannon diversity using the *glm* function with Gamma error distribution. Finally, I modeled evenness using the *lm* function and tested for model assumptions using the

gvlma package (Peña and Slate, 2019). I found no violations of any of the model assumptions of linear models.

For all analyses, I performed multiple comparison tests of all possible parameter combinations using the *MuMIn* package³⁶, and I used Akaike information criterion (AIC) to select the best fitting models (Burnham and Anderson, 2004). In cases in which more than one model yielded an AICc difference of <2 , I performed model averaging using the summed weight method (Burnham and Anderson, 2004; Grueber et al., 2011). The model-averaged coefficients were calculated using conditional R^2 (Nakagawa and Schielzeth, 2013).

Lastly, to detect for multicollinearity, I calculated generalized variance inflation factors (GVIFs) for model predictor variables using the package *car* (Fox and Weisberg, 2011). I found no evidence of problematic multicollinearity as all GVIFs were <2.5 (Fox, 2015).

Figure 1.2. Species accumulation curve representing the number of mammalian taxa present across the 31 study sites



Results

Mammalian taxa richness, diversity, and evenness

Across the 31 study sites that were sampled, I observed a total of 15 mammal taxa including 8 carnivore species (Table 1.5). A species accumulation curve indicated that there was adequate sampling effort (Soberón and Llorente, 1993; Fig. 1.2). Measures of diversity (mean \pm SD) varied across study sites. Across all mammals, taxa richness ranged from five taxa at both Starlight Park and Willow Lake to a maximum of 13 taxa at Riverdale Park (8.23 ± 2.43 ; Table 1.6). Shannon-Wiener diversity ranged from 0.703 at Ridgewood Highland to 1.788 at Van Cortlandt Park (1.26 ± 0.289 ; Table 1.6). Evenness ranged from 0.392 at Ridgewood Highland to 0.856 at Railroad Park (0.61 ± 0.12 ; Table 1.6). The three most common mammal taxa were free-ranging cats (*Felis catus*), gray squirrels (*Sciurus carolinensis*), and raccoons (*P. lotor*); these were found at all 31 study sites. The most common carnivores were free-ranging cats (100% of study sites), raccoons (100% of study sites), and opossums (*D. virginiana*; 87% of study sites) (Table 1.7). The three rarest taxa were mink (*Mustela vison*; 3% of study sites; n = 1 study site), groundhogs (*Marmota monax*; 19% of study sites; n = 6 study sites), and white-tailed deer (*Odocoileus virginianus*; 19% of study sites; n = 6 study sites). Carnivore species richness ranged from three species at Highbridge Park, Ridgewood Park, and Starlight Park to seven species at Inwood Hill Park, Pelham Bay Park, and Riverdale Park (4.58 ± 2.12). Carnivore Shannon-Wiener diversity ranged from 0.14 at Central Park to 1.32 at Ferry Point Park (0.71 ± 0.26). Carnivore evenness ranged from 0.13 at Central Park to 0.81 at Railroad Park (0.47 ± 0.02). The parks with the lowest diversity were mainly comprised of free-ranging cats, gray squirrels, humans, raccoons, small rodents (Family Muridae), and opossums (Table 1.7).

Table 1.5. Mammal taxa identified across the 31 study sites by region and number of sites

Taxa	Mainland	Manhattan	Long Island	Randall's Island	Number of Sites
Chipmunk (<i>Tamias striatus</i>)	X	X	X		7
Cottontail (<i>Sylvilagus floridanus</i>)	X	X	X		15
Coyote (<i>Canis latrans</i>) *	X	X	X		11
Free-Ranging Cat (<i>Felis catus</i>) *	X	X	X	X	31
Domestic Dog (<i>Canis familiaris</i>) *	X	X	X	X	23
Gray Squirrel (<i>Sciurus carolinensis</i>)	X	X	X	X	31
Groundhog (<i>Marmota monax</i>)	X	X	X		6
Human (<i>Homo sapiens</i>)	X	X	X	X	27
Mink (<i>Mustela vison</i>) *		X			1
Raccoon (<i>Procyon lotor</i>) *	X	X	X	X	31
Red Fox (<i>Vulpes vulpes</i>) *	X	X	X		7
Small Rodent (Family Muridae)	X	X	X	X	21
Striped Skunk (<i>Mephitis mephitis</i>) *	X	X	X		11
Virginia Opossum (<i>Didelphis virginiana</i>) *	X	X	X	X	27
White-Tailed Deer (<i>Odocoileus virginianus</i>)	X		X		6

* denotes species included in carnivore analysis

Table 1.6. Average mammal taxa richness, Shannon-Wiener diversity, and evenness for each of the 31 study sites

Study Site	Richness	Shannon-Wiener	Evenness
Alley Pond Park	11	1.484	0.619
Bronx Park	11	1.425	0.594
Central Park	8	1.292	0.621
Clearview Golf Course	7	0.888	0.456
Cunningham Park	8	1.098	0.528
Elmjack Ingrams Field	7	0.768	0.395
Ferry Point Park	12	1.605	0.646
Forest Park	7	1.217	0.625
Fort Washington Park	10	1.599	0.695
Francis Lewis Park	5	1.331	0.827
Green-wood Cemetery	8	0.835	0.401
Highbridge Park	6	0.944	0.527
Hutchinson	8	1.339	0.644
Idlewild Park	7	1.241	0.638
Inwood Hill Park	10	1.632	0.709
Kings Point Park	8	1.212	0.583
Maple Grove Cemetery	6	1.151	0.642
Pelham Bay Park	13	1.437	0.560
Prospect Park	7	1.035	0.532
Pugsley Creek Park	11	1.194	0.498
Queensline	9	1.353	0.616
Railroad Park	7	1.534	0.856
Randall's Island	7	1.272	0.654
Ridgewood Highland	7	0.703	0.392
Riverdale Park	13	1.617	0.631
Riverside Park	6	0.940	0.525
Smiling Hogshead Ranch	6	1.016	0.567
Soundview Park	10	1.787	0.7761
Starlight Park	5	1.181	0.734
Van Cortlandt Park	12	1.788	0.720
Willow Lake	6	1.188	0.738
Mean (SD)	8.23 (2.43)	1.26 (0.289)	0.61 (0.12)

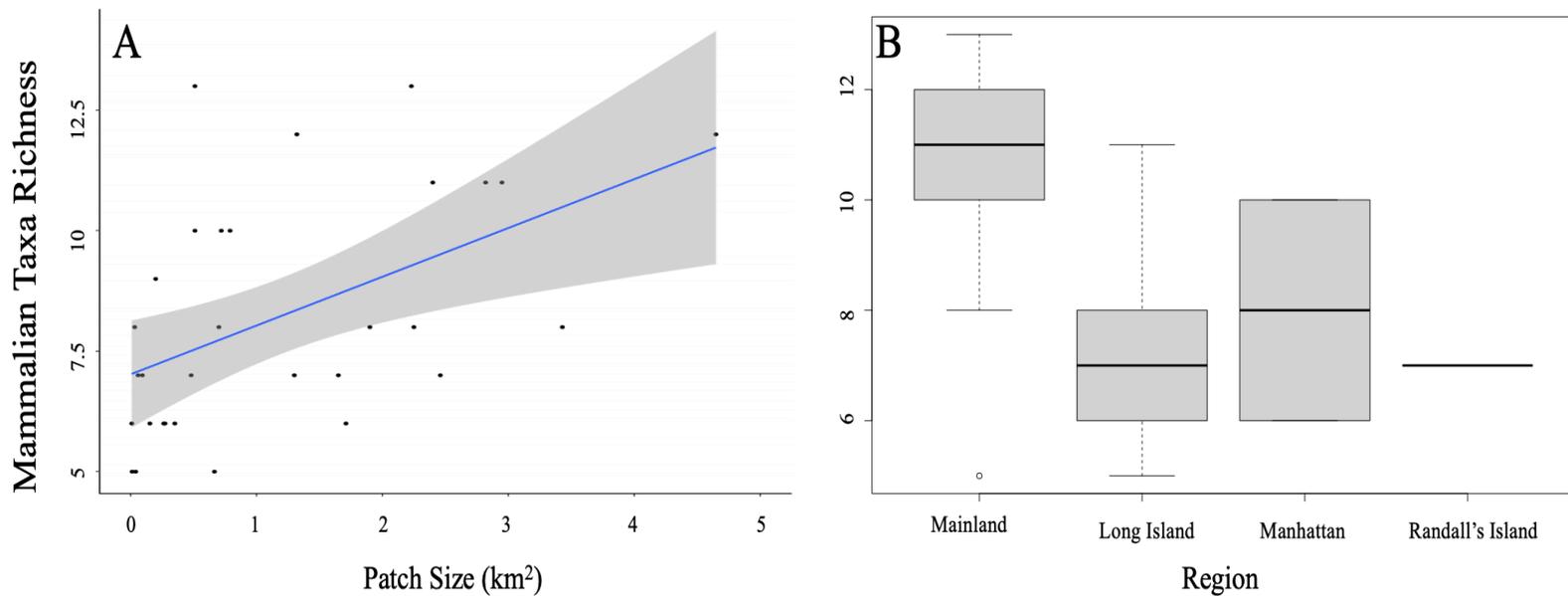
Table 1.7. Mammal taxa detection across the 31 study sites

Study Site	Chipmunk	Cottontail Rabbit	Coyote	Free-Ranging Cat*	Domestic Dog*	Gray Squirrel	Groundhog	Human	Mink	Raccoon	Red Fox	Small Rodent	Striped Skunk	Virginia Opossum	White-tailed Deer	Total Richness	Camera Trap Days
Alley Pond Park	X	X		X	X	X		X		X	X	X	X	X		11	1089
Bronx Park	X	X	X	X	X	X		X		X		X		X	X	11	835
Central Park	X			X	X	X	X	X		X		X				8	362
Clearview Golf Course		X		X	X	X		X		X				X		7	201
Cunningham Park				X	X	X		X		X	X	X		X		8	387
Elmjack Ingrams Field			X	X		X		X		X		X		X		7	132
Ferry Point Park	X	X	X	X	X	X		X		X		X	X	X	X	12	680
Forest Park				X	X	X		X		X		X		X		7	141
Fort Washington Park		X		X		X	X	X	X	X		X	X	X		10	159
Francis Lewis Park				X	X	X		X		X						5	224
Green-wood Cemetery		X		X		X	X	X		X			X	X		8	165
Highbridge Park				X		X	X	X		X		X				6	29
Hutchinson				X		X	X	X		X	X		X	X		8	177
Idlewild Park				X	X	X		X		X		X		X		7	246
Inwood Hill Park		X	X	X	X	X		X		X	X		X	X		10	564
Kings Point Park				X	X	X				X	X	X		X	X	8	91
Maple Grove Cemetery				X	X	X		X		X				X		6	404
Pelham Bay Park	X	X	X	X	X	X		X		X	X	X	X	X	X	13	1280
Prospect Park		X		X	X	X		X		X		X				7	223
Pugsley Creek Park		X	X	X	X	X		X		X		X	X	X	X	11	350
Queensline		X	X	X	X	X		X		X		X		X		9	176
Railroad Park			X	X	X	X				X				X		6	196
Randall's Island				X	X	X		X		X		X		X		7	283
Ridgewood Highland		X		X		X				X		X		X		6	54
Riverdale Park	X	X	X	X	X	X	X	X		X	X	X	X	X		13	2279
Riverside Park				X	X	X		X		X				X		6	223
Smiling Hogshead Ranch				X	X	X		X		X				X		6	195
Soundview Park		X	X	X	X	X		X		X		X	X	X		10	393
Starlight Park				X		X		X		X				X		5	65
Van Cortlandt Park	X	X	X	X	X	X		X		X		X	X	X	X	12	1176
Willow Lake				X		X				X		X		X		5	50
Proportion of sites occupied	0.23	0.48	0.35	1.00	0.74	1.00	0.19	0.87	0.03	1.00	0.23	0.68	0.35	0.87	0.19		
"X" denotes detection of taxa on at least one camera trap at the given study site * denotes domestic animal																	

Predictors of mammalian taxa richness

Based on model averages, I found that patch size and region were significant predictors of mammalian taxa richness at a scale of 500 m. Specifically, study sites with larger patch sizes harbored significantly more mammal taxa than study sites with smaller patch sizes ($\beta = 0.109$; 95% CI: 1.594 – 2.578; $p = 0.046$; Fig. 1.3A; Table 1.8). Moreover, mammal taxa richness was lower in Long Island than on the mainland (Bronx and Westchester) ($\beta = -0.408$; 95% CI: -6.938 – -1.213; $p = 0.005$; Fig. 1.3B; Table 1.8). However, at a scale of 1000 m, the effect of patch area and region on mammalian species richness was masked by the percent developed land cover surrounding urban greenspaces. Specifically, greenspaces surrounded by more developed land cover harbored significantly lower mammalian taxa richness than greenspaces surrounded by less developed land cover ($\beta = -0.006$; 95% CI: -0.012 – -0.0003; $p = 0.038$; Fig. 1.4; Table 1.8).

Figure 1.3. Patterns among mammalian taxa richness and (a) patch size (km²); and (b) region across the 31 study sites.



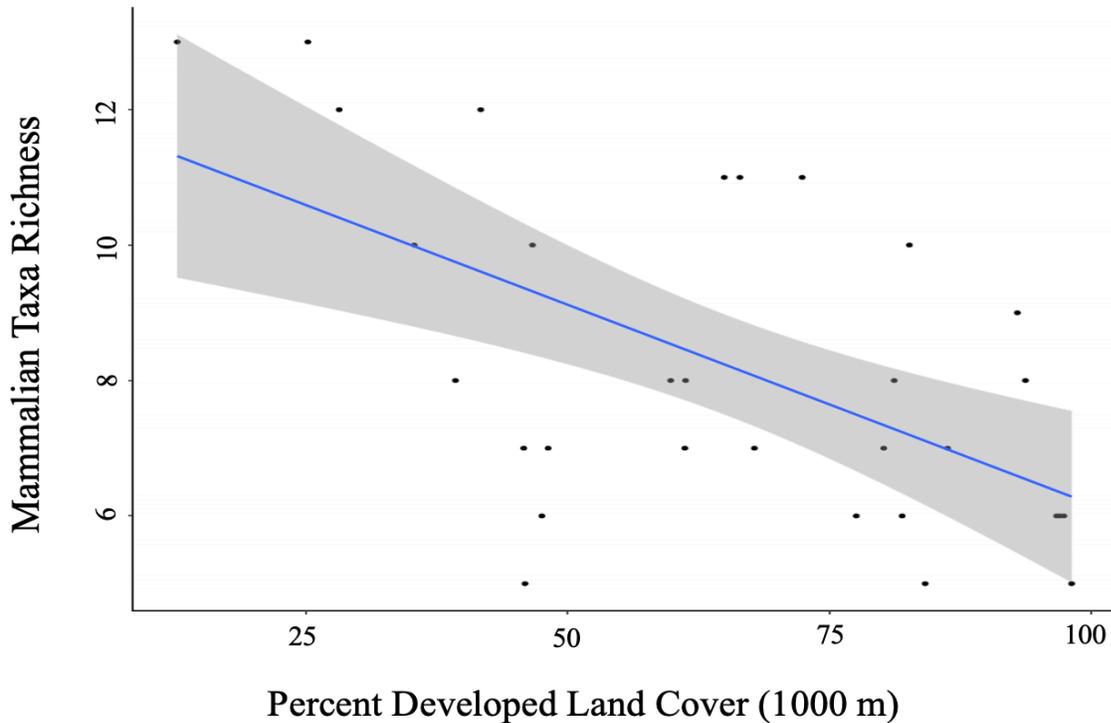


Figure 1.4. Patterns among mammalian taxa richness and percent developed land cover at a 1000 m scale surrounding the 31 study sites.

Predictors of mammalian Shannon-Wiener diversity

Across all mammal taxa, there were two model parameters that best predicted Shannon-Wiener Diversity at the scale of 500 m: habitat type and region. Specifically, Shannon-Wiener diversity was significantly higher in greenspaces where the dominant habitat type was an urban natural habitat rather than a human altered habitat ($\beta = -0.154$; 95% CI: $-2.860 - -2.138$; $p = 0.023$; Fig. 1.5A; Table 1.8). Also, Shannon-Wiener diversity was significantly higher on the mainland (Bronx and Westchester) than Long Island ($\beta = 0.192$; 95% CI: $6.546 - 3.193$; $p = 0.003$; Fig. 1.5B; Table 1.8). When I excluded humans and domestic dogs from my analysis, at a scale of 500 m, one additional model parameter best predicted Shannon-Wiener diversity: human population density. Specifically, Shannon-Wiener diversity was significantly higher in greenspaces with lower human population densities than in greenspaces with higher human

population densities ($\beta = 0.000002$; 95% CI: 0.0000002 – 0.000005; $p = 0.035$). At a scale of 1000 m, greenspaces surrounded by less developed land cover exhibited higher Shannon-Wiener diversity indices than greenspaces surrounded by more developed land cover ($\beta = 0.003$; 95% CI: 0.0003 – 0.005; $p = 0.030$; Fig. 1.6; Table 1.8).

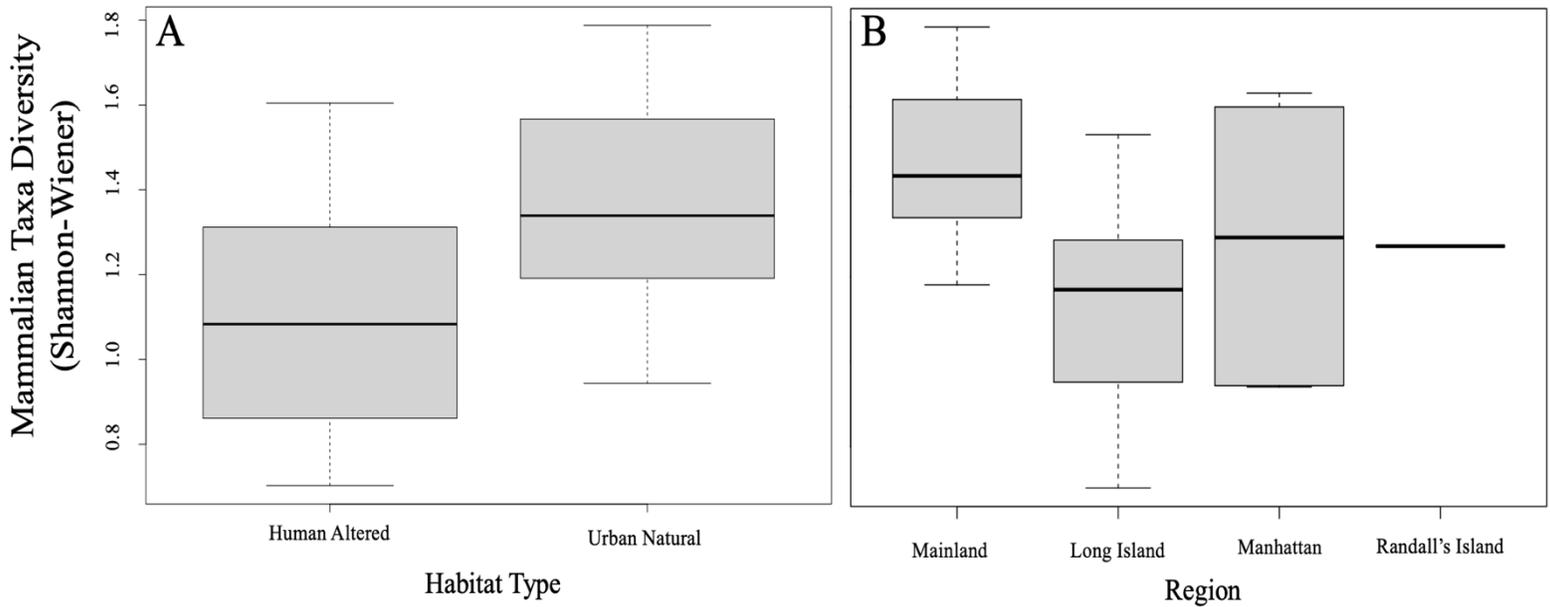


Figure 1.5. Patterns among mammalian taxa diversity (Shannon-Wiener index) and (a) type of habitat; and (b) region across the 31 study sites. Points and whiskers on the plot represent the mean and standard error.

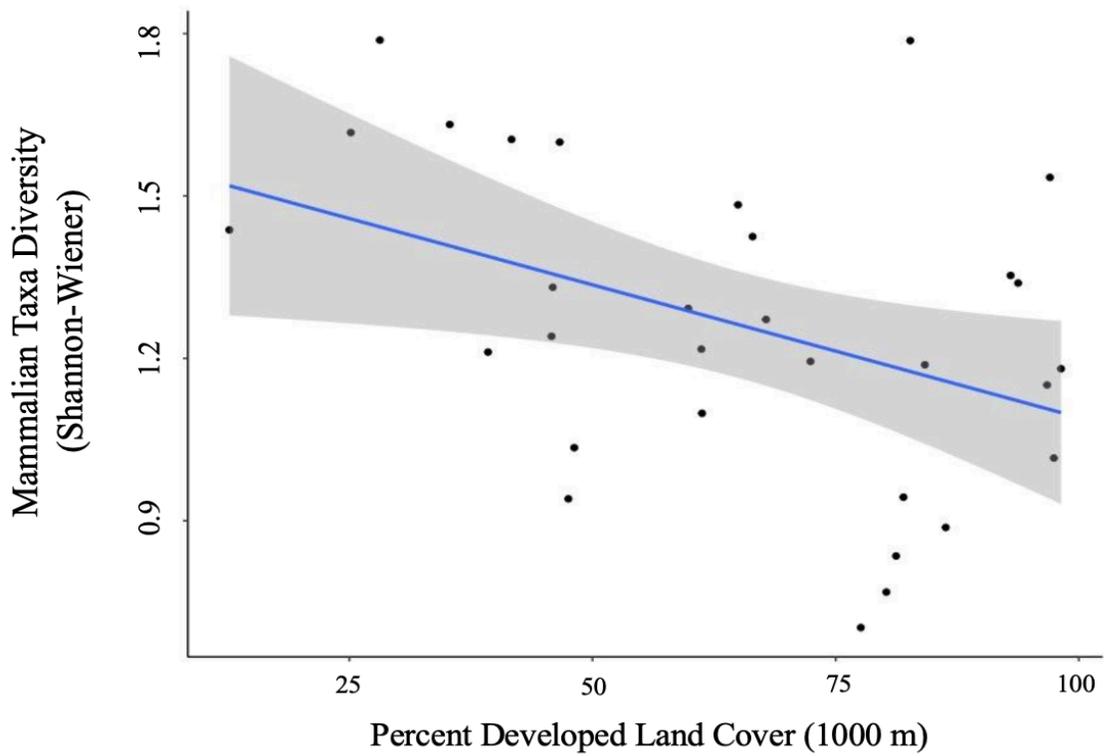


Figure 1.6. Patterns among mammalian taxa diversity (Shannon-Wiener index) and percent developed land cover at a 1000 m scale surrounding the 31 study sites.

Predictors of mammalian taxa evenness

Across all mammal taxa, the model parameter that best predicted evenness across the 31 study sites was habitat type. Specifically, evenness was significantly higher in study sites where the dominant habitat type was an urban natural habitat than study sites where the dominant habitat type was a human-altered habitat ($\beta = 0.091$; 95% CI: 0.008 – 0.175; $p = 0.032$; Fig. 1.7; Table 1.8). However, habitat type was not a significant predictor of evenness when I excluded domestic dogs and humans from the analysis.

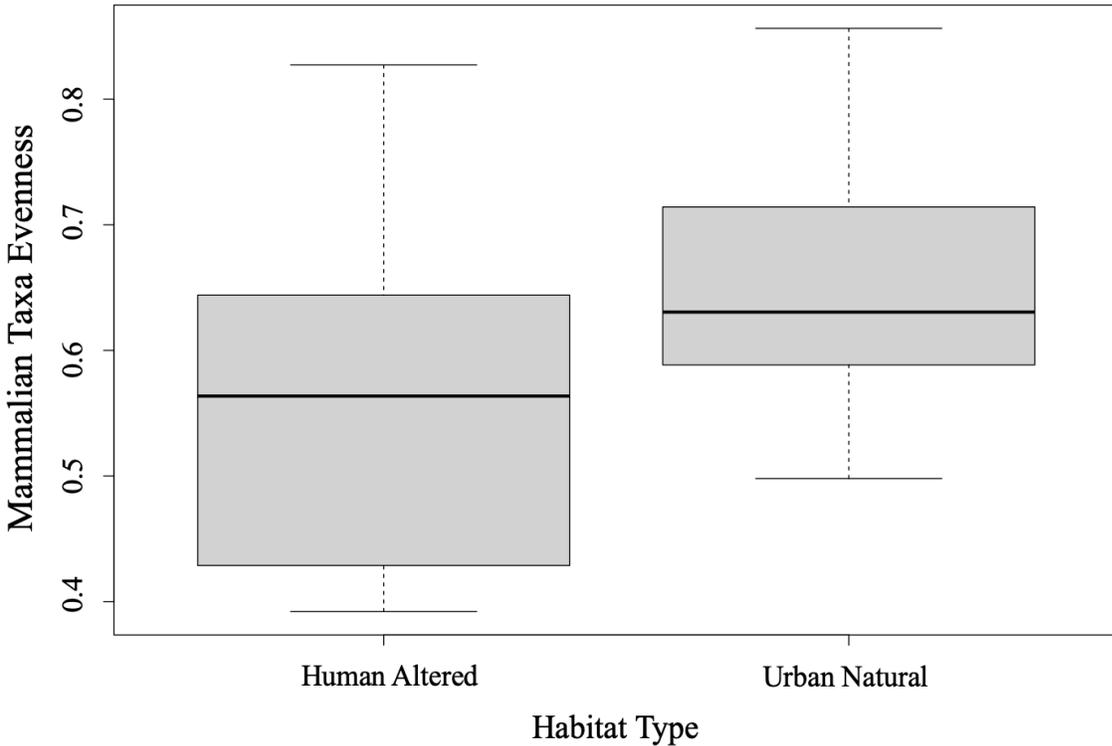


Figure 1.7. Patterns among mammalian taxa evenness and type of habitat across 31 study sites. Points and whiskers on the plot represent the mean and standard error.

Table 1.8. Best supported models for each response variable for mammalian diversity based on averaging of parameter estimates. Model-average coefficients (conditional average), standard error, adjusted SE, z-value, and *P* value of the averaged models are shown.

Response Variables	Fixed Effects	Estimate	Std. Error	Adjusted SE	z value	<i>P</i> value
Mammal taxa richness (500 m scale)	Patch size	0.109	0.052	0.054	1.995	0.046*
	Heterogeneity (fine scale)	0.025	0.025	0.026	0.979	0.327
	Percent developed	-0.003	0.003	0.003	1.232	0.218
	Human population density	0.000	0.000	0.000	0.886	0.376
	Cameras per km ²	-0.004	0.003	0.003	1.534	0.125
	Region – Long Island	-0.408	0.139	0.146	2.790	0.005**
	Region – Manhattan	-0.299	0.190	0.199	1.498	0.134
	Region – Randall’s Island	-0.400	0.392	0.411	0.974	0.330
	Habitat Type (natural)	0.091	0.132	0.138	0.659	0.510
Mammal taxa richness (1000 m scale)	Percent developed	-0.006	0.003	0.003	2.074	0.038*
	Patch size	0.070	0.054	0.057	1.243	0.214
	Habitat type (natural)	0.119	0.131	0.137	0.871	0.384
	Heterogeneity (fine scale)	0.036	0.028	0.029	1.248	0.212
Shannon-Wiener diversity (500 m scale)	Human population density	0.000001	0.000001	0.000001	1.746	0.081
	Habitat type (natural)	-0.154	0.065	0.068	2.277	0.023*
	Region – Long Island	0.192	0.062	0.065	2.971	0.003**
	Region – Manhattan	0.014	0.110	0.114	0.121	0.904
	Region – Randall’s Island	-0.001	0.163	0.172	0.007	0.995
Shannon-Wiener diversity (1000 m scale)	Habitat type (natural)	-0.164	0.061	0.064	2.555	0.011*
	Percent developed	0.003	0.001	0.001	2.172	0.030*
	Region – Long Island	0.152	0.062	0.065	2.349	0.019*
	Region – Manhattan	0.090	0.078	0.082	1.104	0.270
	Region – Randall’s Island	-0.038	0.162	0.170	0.224	0.823
Mammalian taxa evenness (500 m scale)	Habitat type (natural)	0.091	0.041	0.043	2.142	0.032*
	Patch size	-0.021	0.017	0.017	1.205	0.228
	Percent developed	0.001	0.001	0.001	0.881	0.378

* denotes significance of <0.05

** denotes significance of <0.01

Predictors of carnivore diversity

In analyses that specifically focused on carnivores, there were no significant predictors of carnivore species richness. Carnivore Shannon-Wiener diversity was higher in greenspaces with lower human population densities than in greenspaces with higher human population densities ($\beta = 0.00001$; 95% CI: $3.3 \text{ e-}06 - 1.6 \text{ e-}05$; $p = 0.007$; Fig. 1.8A; Table 1.9). Carnivore Shannon-Wiener diversity was also significantly higher on the mainland (Bronx and Westchester) than Long Island ($\beta = 0.777$; 95% CI: $3.438 - 1.225$; $p = 0.002$; Fig. 1.8B; Table 1.9). Further, Shannon-Wiener diversity of carnivores was higher in greenspaces where the dominant habitat

type was urban natural rather than human altered ($\beta = -0.528$; 95% CI: $-1.065 - -5.737$; $p = 0.049$; Fig. 1.8C; Table 1.9). Finally, the best model parameter for predicting carnivore evenness was region. Specifically, evenness was significantly lower in Long Island than on the mainland ($\beta = -0.203$; 95% CI: $-3.411 - -6.5678$; $p = 0.004$; Fig. 1.9; Table 1.10).

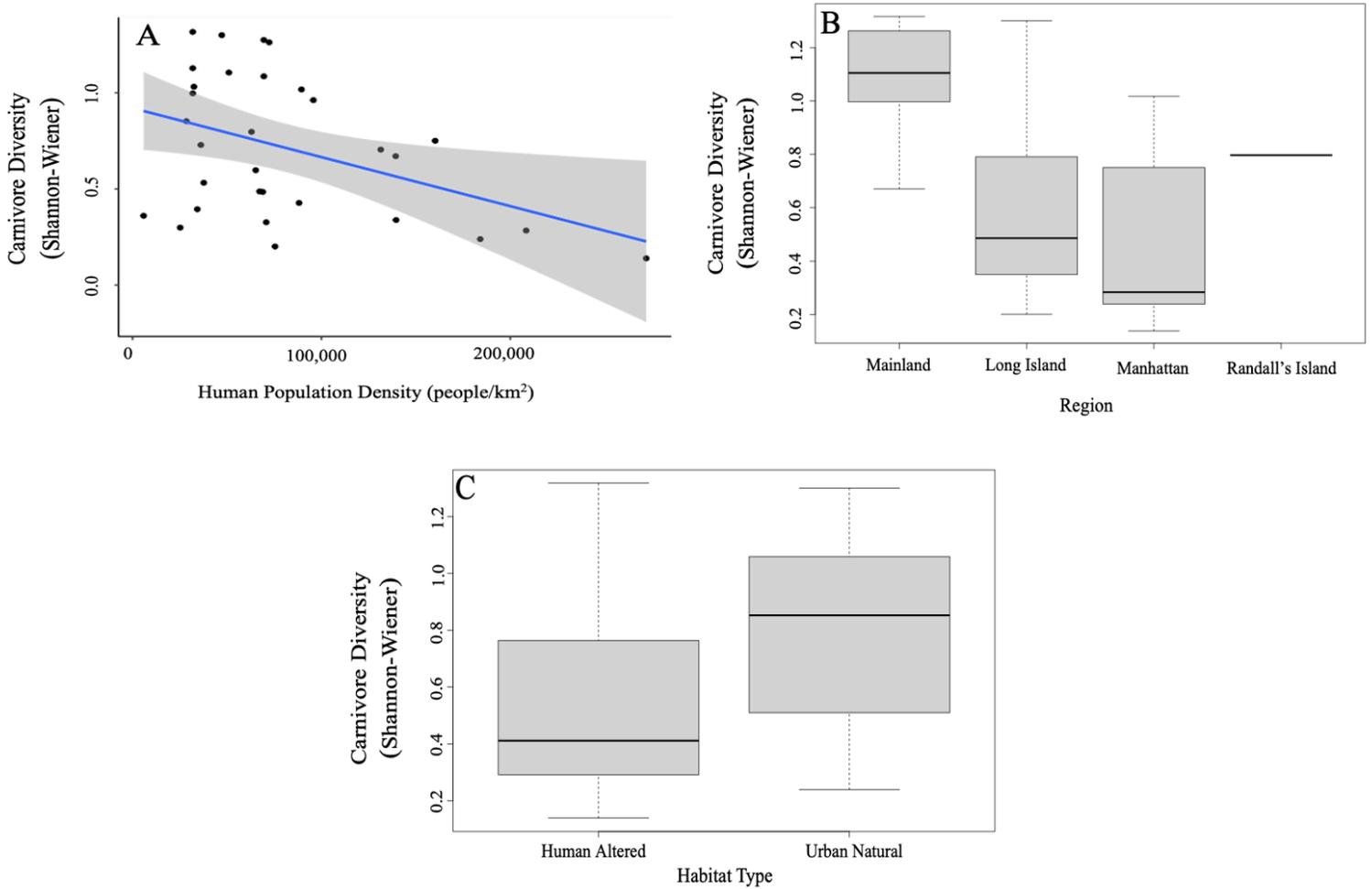


Figure 1.8. Patterns among Carnivore taxa diversity (Shannon-Wiener index) and (a) human population density; (b) region; and (c) habitat type across the 31 study sites. Points and whiskers on the plot represent the mean and standard error.

Table 1.9. Best supported model for Carnivore Shannon-Wiener diversity (500 m scale) based on averaging of parameter estimates. Model-average coefficients (conditional average), standard error, *t*-value, and *P* value of the averaged models are shown.

Predictor Variable	Fixed Effects	Estimate	Std. Error	<i>t</i> value	<i>P</i> value
Carnivore Shannon-Wiener diversity (500 m scale)	Human population density	0.00001	0.000003	2.942	0.007**
	Region – Long Island	0.777	0.223	3.484	0.002**
	Region – Manhattan	0.157	0.474	0.331	0.743
	Region – Randall’s Island	-0.124	0.591	-0.210	0.836
	Habitat type (natural)	-0.528	0.256	-2.065	0.049*

* denotes significance of <.05

** denotes significance of <.01

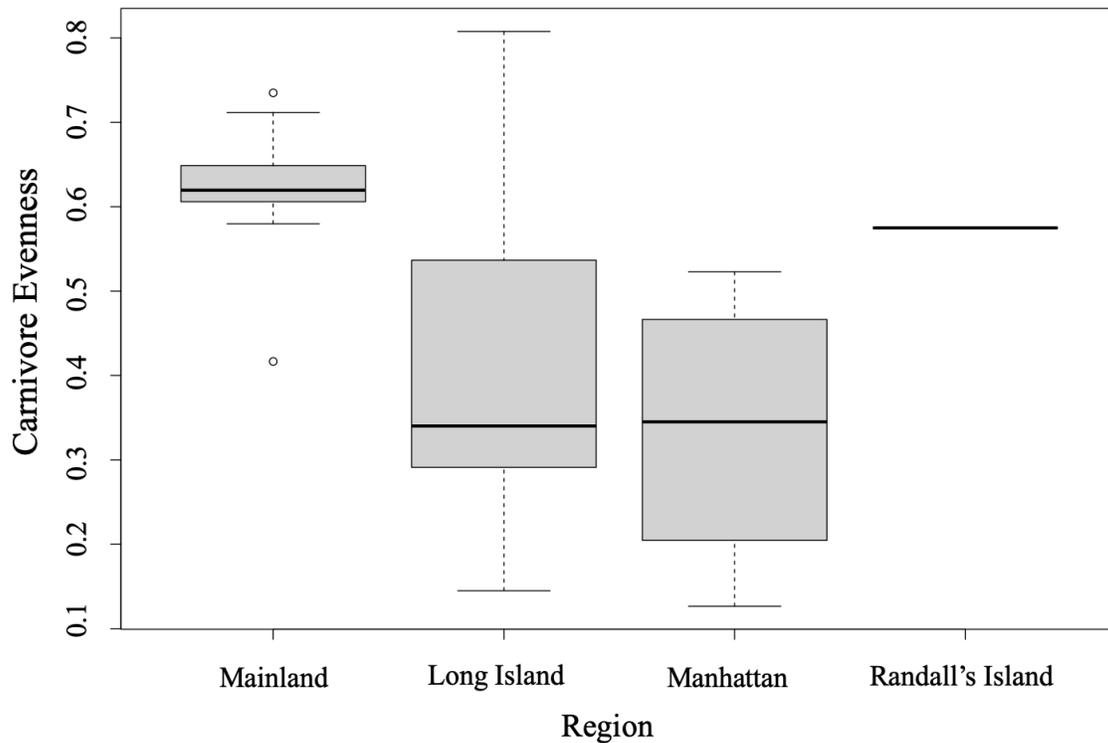


Figure 1.9. Patterns among Carnivore evenness and region across the 31 study sites. Points and whiskers on the plot represent the mean and standard error.

Table 1.10. Best supported model for Carnivore evenness (500 m scale). Standard error, adjusted SE, z-value, and *P* value of the best model is shown.

Predictor Variable	Fixed Effects	Estimate	Std. Error	Adjusted SE	z value	<i>P</i> value
Carnivore evenness (500 m scale)	Patch size	-0.040	0.024	0.026	1.581	0.114
	Percent developed	0.001	0.001	0.001	1.193	0.233
	Human population density	-0.000001	0.000001	0.000001	1.813	0.070 ·
	Region – Long Island	-0.203	0.067	0.070	2.895	0.004**
	Region – Manhattan	-0.177	0.132	0.136	1.300	0.194
	Region – Randall’s Island	0.003	0.172	0.180	0.016	0.988
	Habitat type (natural)	0.122	0.060	0.063	1.956	0.050 ·

· denotes $P < 0.1$

** denotes significance of <0.01

Discussion

In this investigation of predictors of mammalian diversity in the New York metropolitan area, I found ample support for the hypothesis that mammalian diversity is associated with anthropogenic factors and geographical barriers. Consistent with my predictions, I found that mammal taxa richness was higher in greenspaces with larger patch sizes and less developed land cover suggesting that species richness is a function of habitat area (Arrhenius, 1921). Moreover, mammal taxa richness and Shannon-Wiener diversity were greater on the continent (Bronx/Westchester) than Long Island suggesting that there are barriers to dispersal that limit the movement of species between regions (Weckel et al., 2015). Further, both Shannon-Wiener diversity and evenness were higher in urban natural habitats than human-altered habitats. Measures of carnivore diversity were also associated with anthropogenic factors and geographical barriers. Among carnivores, Shannon-Wiener diversity was significantly lower in greenspaces with higher human population densities and in human-altered habitats. Further, both Shannon-Wiener diversity and evenness were significantly higher among carnivores on the mainland (Bronx/Westchester) than in Long Island. Collectively, these results provide insights into the drivers of mammalian community composition and are helpful for drawing inferences on what factors contribute to mammalian diversity in urban environments.

Throughout the greenspaces of the New York metropolitan area, some mammalian taxa were more common than others. Three species were identified in all 31 study sites: free-ranging cats, gray squirrels, and raccoons. In addition to these three species, the greenspaces that exhibited low taxa diversity also tended to harbor rodents (Family Muridae) and opossums. The five taxa found at these low diversity sites— free-ranging cats, gray squirrels, raccoons, small rodents (Family Muridae), and opossums—are known as urban adapters (McKinney, 2002;

Adams and Lindsey, 2010; Gehrt et al., 2013; Lombardi et al., 2017). This is largely because these mammals have the capacity to exploit both urban greenspaces while also supplementing their diets with anthropogenic food sources (Cove et al., 2017; Guiry and Buckley, 2018; Nicholson and Cove, 2022). One of these urban adapters, free-ranging cats, are associated with several negative impacts, including the local extinction of native wildlife and the spread of certain pathogens (Gehrt et al., 2013).

In contrast to these animals, three mammalian species were rare among the greenspace of the New York metropolitan area: minks, groundhogs, and white-tailed deer. Minks were identified in only one of the 31 greenspaces. This is probably because minks require wetland habitats and tend to reside in freshwater streams and rivers (Allen, 1984). Most of my study sites were not situated in wetland habitats, which might explain why the only mink identified was located in a greenspace adjacent to the Hudson River. Previous studies indicate that minks are typically found in sparsely populated rural areas and only occasionally in urban settings (Silva-Rodríguez et al., 2020). White-tailed deer were identified in six of the 31 greenspaces surveyed in this study. Five of these greenspaces were located on the mainland; one was located on Long Island. These findings suggest that the roads and waterways that separate the mainland from the islands make it particularly challenging for large-bodied mammals such as deer to disperse to highly urbanized islands with high human population densities (Michael, 1965; Long et al., 2010). Although there are white-tailed deer found on Long Island, they are typically further east, suggesting that since Brooklyn and Queens are more urbanized, they may serve as an urban matrix and as barriers for repopulation. Like deer, groundhogs were also identified in six of the 31 greenspaces surveyed in this study. Surveys indicate that both white-tailed deer and groundhogs are more likely to reside in rural and suburban habitats; however, both of these

species have increasingly become more abundant in urban greenspaces in recent years (Gaughan and Destefano, 2005; Lehrer and Schooley, 2010). These findings suggest that minks, groundhogs, and white-tailed deer are urban avoiders (McKinney 2002), but still have the capacity to exploit some urban habitats. My findings suggest that urban greenspaces can be refuges for many mammalian taxa, especially urban adapters; however, in some cases, even urban avoiders can make use of certain urban greenspaces.

I found support for the idea that mammalian diversity is characterized by species-area effects. In support of this idea, patch size was positively correlated with species richness. This result is consistent with other studies that have also reported higher mammal taxa richness in greenspaces with relatively larger patch sizes (Yates et al., 1997; Hodgkinson et al., 2007; Nielsen et al., 2014). These results also lend support to the species-area hypothesis, the idea that species richness is a function of the amount of available habitat (Arrhenius, 1921; Turner et al., 2005). In the case of the current study, I find evidence of the species-area effect in an urban context.

Habitat type was a significant predictor of two measures of biodiversity: Shannon-Wiener diversity and evenness. First, I found that Shannon-Wiener diversity was higher in study sites where the dominant habitat was an urban natural habitat rather than a human-altered habitat. Although some mammals may thrive in human-altered habitats, like golf courses and cemeteries (Gallo et al., 2017; Wurth et al., 2020), most mammals tend to have higher persistence in urban natural areas, or habitats that consist of large patches of secondary growth forest and shrubs (Atwood et al., 2004; Baker and Harris, 2007). It has also been found that manicured lawns and artificial nocturnal illumination, as seen in parks, golf courses, and cemeteries, may limit dispersal (Mahan and O'Connell, 2005; Fitzgibbon et al., 2007). Second, I also found a positive correlation between habitat type and evenness. Specifically, I found that evenness was higher in

study sites where more than fifty percent of the patch area was an urban natural habitat. These findings are consistent with previous research that suggest that diversity in urban natural habitats is higher than in human-altered habitats (Parsons et al., 2018). Taken together, these two findings—higher Shannon-Wiener diversity and higher taxa evenness among mammals in urban natural habitats—suggest that it is important for park managers to maintain at least 50% natural area within urban parks to support mammalian diversity.

Consistent with my predictions, I found that greenspaces surrounded by more developed land cover exhibited lower mammal taxa richness than greenspaces surrounded by less developed land cover. This result was only significant at a scale of 1000 meters, but at this scale, it masked the effects of any of the other predictor variables. This finding appears to contradict the urban refugia hypothesis (Haffer, 1969), which suggests that urban greenspaces in highly developed areas are oases for biodiversity. More specifically, my results differ from the findings of a recent study in the New York metropolitan Area that found support for the urban refugia hypothesis: Stark et al. (2020) found that the relative abundance of mammalian carnivores was higher in greenspaces with higher surrounding human development. In my analysis of mammalian carnivores, I found no significant relationship between human development and carnivore species richness. However, the Stark et al. (2020) study was conducted in nature preserves outside of New York City and in less populous areas than the current study. Specifically, the mean (\pm SD) human population density for the Stark et al. (2020) study was 7,305 (\pm 11,222) humans per square kilometer while the mean human population density in the current study was 81,451 (\pm 60,515) humans per square kilometer. Perhaps in highly urbanized, densely populated areas, a minimum amount of greenspace is required for urban greenspaces to function as refugia for mammals especially carnivores. Another factor that might explain my

result is that in highly developed areas, buildings, roads, and other anthropogenic structures reduce connectivity between habitats (LaPoint et al., 2015; Beninde et al., 2016). Obstruction in connectivity can also lead to resource depletion, habitat disturbance, and ultimately reduced species richness (Blair and Launer, 1997; Fidino et al., 2020). Additionally, my result might also be attributed to higher mortality rates caused by humans, including vehicle collisions (Trombulak and Frissell, 2000; Seiler, 2001; Collins and Kays, 2011) and poisoning (Brooks et al., 2020). Overall, my results suggest that highly developed areas pose a particularly daunting challenge for maintaining high levels of mammalian diversity.

Urban greenspaces located on the mainland (Bronx and Westchester) harbored greater mammal taxa richness and Shannon-Wiener diversity than urban greenspaces located on urban islands (Long Island, Manhattan, Randall's Island). These findings suggest that geographical barriers to dispersal might impact patterns of mammalian diversity. In support of this idea, previous studies have documented multiple barriers to dispersal between the mainland (Bronx and Westchester) and the other three regions (Long Island, Manhattan, and Randall's Island) (Weckel et al., 2015; Nagy et al., 2016). Additionally, roads and waterways, as well as other barriers, play a large role in limiting dispersal (Oxley et al., 1974; Merriam et al., 1989; Baker and Harris, 2007). For example, coyotes have not established strong breeding populations yet in Long Island mainly because of bridges and rivers that separate the island from the Bronx and Westchester (Nagy et al., 2017). My results lend support to the hypothesis that islands, even those in close proximity to the continent, can serve as barriers to dispersal.

The New York metropolitan area harbors several carnivore species that vary in their abundance and distribution. I found that the greenspaces surveyed in this study supported one or more of the following carnivores: coyotes (*C. latrans*), free-ranging cats (*F. catus*), domestic

dogs (*Canis familiaris*), minks (*M. vison*), opossums (*D. virginiana*), raccoons (*P. lotor*), red foxes (*V. vulpes*), and striped skunks (*Mephitis mephitis*). Because of their low densities, need for large habitat area, and conflict with humans, many large carnivores once native to this region, including black bears (*Ursus americanus*), bobcats (*Lynx rufus*), fishers (*Pekania pennanti*), and long-tailed weasels (*Neogale franata*), were not observed in any of the greenspaces surveyed in this study, although these mammals persist in nature preserves outside of New York City (Spinola et al., 2008; Stark et al., 2020; Nagy, unpublished data). In the present study, I found that Shannon-Wiener diversity among carnivores was higher in urban natural habitats and in greenspaces with lower human population densities. In support of these findings, previous studies have found that many carnivores tend to avoid human interaction, preferring less developed urban habitats with lower human population densities (Grinder and Krausman, 2001; George and Crooks, 2006; Gehrt et al., 2009). I also found that carnivore evenness was significantly higher in the mainland than in sites located in Long Island and Manhattan. This finding suggests that there might be differences in the habitat characteristics between the mainland sites (Bronx and Westchester) and the island sites (Manhattan and Long Island) including differences in floral diversity (Ekernas and Mertes 2006), resource availability (Matthies et al., 2017), the historical range of various species (e.g., Rooney, 2001; Hody and Kays, 2018), and management strategies (McPhearson et al., 2016). Furthermore, the asymmetric distribution of carnivore communities on the islands might also be explained by barriers to dispersal between the mainland and island sites. Although large mammals, like carnivores, are more adept at crossing bridges and waterways than smaller mammals, these barriers still hinder and reduce the likelihood of movement between regions (Weckel et al., 2015; Henger et al.,

2020). Collectively, these findings suggest that carnivores are particularly sensitive to urbanization and barriers to dispersal such as bridges and large bodies of water.

Limitations

Because I did not trap or tag species and relied solely on camera data, one limitation of this study was that I was unable to identify individuals. Therefore, the abundance indices that I calculated are rough estimates and may not be representative of actual mammal abundances. In future studies, the use of mark-recapture or identification techniques to assess individual sightings would ensure a more accurate representation of abundance (Ekernas and Mertes, 2006; Lewis et al., 2015; Lombardi et al., 2017). The current study surveyed sixteen sites on Long Island, thirteen of which were located in Queens, two in Brooklyn, and one in Nassau County. Since the majority of the Long Island study sites were located in Queens, the results may not be representative of mammal diversity for all of the island. For future studies, it would be beneficial to have a more even distribution of study sites across the island to allow for more accurate comparison of regions.

Conclusions and Future Directions

My findings that anthropogenic variables, such as percent developed land cover, patch size, and habitat type, influence patterns of mammalian diversity suggest that it is crucial to understand and study the consequences of increasing urbanization on mammalian communities. There were some mammals in the current study that appeared to flourish across all urban greenspaces (i.e., urban exploiters) and were less sensitive to urbanization, apparently because they can take better advantage of anthropogenic food resources. On a more nuanced level, my

findings suggest that there are some habitat features that are more suitable for mammals that are sensitive to urbanization (i.e., urban avoiders), including large patch sizes and high proportions of secondary growth forest. Hence, while urbanization is generally detrimental to biodiversity, I found that there were greenspaces in the New York metropolitan area where mammalian diversity was high. This suggests that there is a potential to make cities more suitable habitats for many mammalian species and that a barren ecology is not inevitable. The current study provides correlative evidence that some features of urbanization are associated with patterns of mammalian biodiversity. My findings might be helpful in terms of management and conservation efforts within similarly large urban centers. Based on my results, I recommend that planners and managers of cities focus their efforts on maintaining large, connected, natural greenspaces, especially when surrounded by highly developed areas with high human population densities. Urban ecological research would benefit from longitudinal studies conducted across multiple large cities that can document changes in diversity, abundance, and evenness of mammals.

Footnotes

1. <https://www.nycgovparks.org/parks/Q001/>
2. <https://www.nycgovparks.org/parks/bronx-park/highlights/11414>
3. <https://www.centralparknyc.org/about>
4. <https://www.nycgovparks.org/parks/clearview-park-golf-course/history>
5. <https://www.nycgovparks.org/parks/cunningham-park/history>
6. <https://www.nycgovparks.org/parks/ferry-point-park/history>
7. <https://www.nycgovparks.org/parks/Q015/>
8. <https://www.nycgovparks.org/parks/fort-washington-park/history>
9. <https://www.nycgovparks.org/parks/francis-lewis-park>
10. <https://www.nycgovparks.org/parks/highbridge-park>
11. <https://www.nycgovparks.org/greening/nature-preserves/site?FWID=32>
12. <https://www.nycgovparks.org/parks/inwood-hill-park>
13. <https://www.gnparks.org/499/Major-Parks>
14. <http://www.maplegrove.biz/about/rich-history/>
15. http://pelhambaypark.org/?page_id=71
16. <https://www.dec.ny.gov/outdoor/57289.html>
17. <https://www.prospectpark.org/learn-more/archives/park-tree-history/>
18. <https://www.nycgovparks.org/parks/B073/>
19. <https://www.nycgovparks.org/parks/pugsley-creek-park/highlights/11647>
20. <https://www.nycgovparks.org/parks/railroad-park-q412>
21. <https://www.inaturalist.org/guides/1430>
22. <https://randallsisland.org/visit/waterfront-natural-areas/>
23. <https://queensmuseum.org/2020/02/ridgewood-reservoir-for-the-21st-century>
24. <https://www.nycgovparks.org/parks/riverdale-park>
25. <https://riversideparknyc.org/overview/>
26. <https://www.idealists.org/en/nonprofit/0e0735788f8e45a68144cf7449493f91-smiling-hogshead-ranch-queens>
27. <https://www.nycgovparks.org/parks/soundview-park>
28. <https://www.seagrant.sunysb.edu/hriver/pdfs/coastalchange/SoundviewPark/ProjectSummary-Narrative.pdf>
29. <https://www.nycgovparks.org/parks/starlight-park>
30. <https://www.nycgovparks.org/parks/flushing-meadows-corona-park/highlights/12907>
31. <https://www.unitedstateszipcodes.org/>
32. <https://www.google.com/maps>
33. <https://www.mrlc.gov/data/legends/national-land-cover-database-2019-nlcd2019-legend>
34. <https://www.R-project.org/>
35. <http://vegan.r-forge.r-project.org/>
36. <https://r-forge.r-project.org/projects/mumin/>

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**PREDICTORS OF COYOTE AND FREE-RANGING CAT OCCUPANCY
AND DETECTION PROBABILITY IN THE NEW YORK
METROPOLITAN AREA**

by

Angelinna Bradfield

Abstract

Although urbanization can have a variety of detrimental effects on mammalian carnivore communities, some carnivore species have the capacity to exploit and even thrive in urban habitats. Coyotes and free-ranging cats are two examples of mammalian carnivores that make use of greenspaces in urban areas. Their distribution is thought to be influenced by several factors including human population density, patch area, habitat type, habitat heterogeneity, developed land cover, biogeographical barriers, and competitive interactions. The goal of this study was to investigate the influence of anthropogenic, biogeographical, and ecological variables on the distribution of coyotes and free-ranging cats in urban greenspaces, and to assess whether free-ranging cats avoid habitats occupied by coyotes. I deployed 138 motion-activated camera traps across 31 urban greenspaces in the most densely populated region of the United States: the New York metropolitan area. I used occupancy models to investigate which factors best explain coyote and free-ranging cat occupancy and detection probability. I found that several variables influence the distribution of coyotes and free-ranging cats in the New York metropolitan area. Specifically, coyotes were more likely to be detected in urban natural habitats and in sites with relatively low human population densities; however, despite this finding, coyotes were still found more often in human-altered habitats. These results suggest that some anthropogenic factors, including fragmentation and development, influence coyote detection probability, while other anthropogenic factors, such as access to human-derived food resources, influence coyote occupancy. Moreover, coyote occupancy was greater on the continent (Bronx and Westchester) than nearby islands (Long Island, Manhattan, and Randall's Island). Measures of free-ranging cat distribution were driven by several anthropogenic factors, including patch area, percent developed land cover, and habitat type, as well as the presence or absence of

coyotes. Notably, I found that free-ranging cat detection probability was lower in habitats where coyotes were present than in habitats where coyotes were absent. Collectively, these results reveal the complexities of a highly urbanized city in terms of harboring mesocarnivores such as coyotes and free-ranging cats, and the dynamic interplay between anthropogenic, biogeographical, and ecological variables.

Introduction

While most large carnivores in North America, such as wolves (*Canis lupus*) (Thurber and Peterson, 1991; Berger and Gese, 2007; Levi and Wilmers, 2012; Benson et al., 2017), cougars (*Puma concolor*) (Ripple and Beschta, 2006; Lindzey and Boyce, 2010; Crawford et al., 2022), and bears (*Ursus* spp.) (Berger et al., 2001; Beschta and Ripple, 2009; Shivik, 2014), have been decimated by anthropogenic change, one species has thrived: the coyote (*Canis latrans*) (Gese and Bekoff, 2004; Ripple et al., 2013; Schuttler et al., 2016; Hody and Kays, 2018). Remarkably, coyotes have expanded from their ancestral range in the western United States, taking the place of extirpated apex predators, and now have populations across all 48 contiguous states (Hody and Kays, 2018). In recent decades, coyotes have colonized densely populated cities including Chicago (Morey et al., 2007; Gehrt et al., 2009, 2011, 2013; Gese et al., 2012; Hennessy et al., 2012), Los Angeles (Shargo, 1988; Tigas et al., 2002; Riley et al., 2003), Toronto (Adkins and Stott, 1998), and most recently, the New York metropolitan area (Weckel et al., 2015; Nagy et al., 2016; Lombardi et al., 2017; Stark et al., 2020). The emergence of coyotes in the New York metropolitan area can have important ecological implications, which raises questions about how coyotes will adapt to a novel, highly urbanized landscape, and their potential impact on other mesocarnivores, including free-ranging cats.

The expansion of coyotes into the New York metropolitan area is of particular interest because this region is comprised of over 23 million humans (*Homo sapiens*) and a plethora of complex landscape gradients (Weckel et al., 2015; Nagy et al., 2016; Stark et al., 2020; United States Census Bureau, 2021). Strikingly, New York City, the most populous city in the United States, has a population density of over 43,000 humans per square kilometer (New York City Department of City Planning, 2022). In addition to being highly urbanized, New York City presents an additional challenge to coyote expansion because other than the Bronx, which is located on the continent, all other boroughs are located on islands. Coyotes have become well-established in the larger tri-state area (New York, New Jersey, and Connecticut) around New York City, and despite the geographic challenges, a number of individuals have crossed from mainland New York and established territories in Manhattan and Long Island (Nagy et al. 2017; Henger et al., 2020). Coyotes are predicted to continue their range expansion further into Long Island, one of the few remaining large land masses in the United States in which there are apparently no viable breeding populations (Fener et al., 2005; Weckel et al., 2015; Nagy et al., 2016; but see Nagy et al., 2017).

One species predicted to be impacted by the expansion of coyotes is the free-ranging cat (*Felis catus*), which includes those that are owned by humans and have access to the outdoors, those that are not owned and live independently of humans, and those that live primarily outdoors but receive human provisions in the form of food and shelter (Elizondo and Loss, 2016). These predictions are derived from the mesopredator release hypothesis (Soulé et al., 1988), which posits that the removal or release of apex predators, such as wolves and bears, results in a dramatic increase in mesopredators (Estes, 1996; Crooks and Soulé, 1999; Gehrt and McGraw, 2007). Among mesopredators, coyotes have relatively larger body sizes and broad

dietary niches; therefore, if coyotes occupy the ecological niche formerly occupied by apex predators, the expansion of coyotes into urban environments might have trophic impacts on smaller mesocarnivores, including free-ranging cats (Johnson et al., 1996; Crooks and Soulé 1999; Faeth et al., 2005; Weckel et al., 2015). In support of this idea, several studies have documented coyote predation on cats (Quinn, 1997; Crooks and Soulé, 1999; Grubbs and Krausman, 2009; Brashares et al., 2010; Gehrt et al., 2013). Moreover, some studies suggest that cats avoid coyote-dominated habitats to escape predation (Crooks and Soulé, 1999; Gehrt et al., 2013; Kays et al., 2015), while other studies suggest that coyotes steer clear of cat-dominated habitats to avoid close proximity to humans (Krauze-Gryz et al., 2012). Whether these patterns are evident in a large metropolitan area like New York remains largely unknown.

In addition to competitive interactions, several anthropogenic and ecological factors are thought to be drivers of coyote and free-ranging cat distribution (occupancy and detection probability) in urban greenspaces. These include (1) human population density; (2) habitat type; (3) patch area; (4) percent developed land cover; and (5) fine-scale habitat heterogeneity. The direction and intensity of these anthropogenic and ecological drivers on coyotes and free-ranging cats might be species-specific (e.g., Laliberte and Ripple, 2004; Newsome et al., 2015; Brain and Anderson, 2020), or alternatively, driven by processes that impact these species similarly (Ekernas and Mertes, 2006; Gallo et al., 2017; Fidino et al., 2020; Moll et al., 2020). Additionally, because coyotes have distinct pup-rearing and non-pup-rearing seasons, the direction and intensity of these anthropogenic and ecological drivers on coyote occupancy and detection probability may differ between these two periods (Nagy et al., 2016).

Coyote distribution (occupancy and detection probability) has been found to be positively correlated with urban natural areas (Gibeau, 1998; Way et al., 2004; Weckel et al. 2015), patch

area (Gittleman et al., 2001; Dobson et al., 2006; Ordeñana et al., 2010; Ripple et al., 2014; Šálek et al., 2014), and fine-scale habitat heterogeneity (Beckoff, 1977; Hodgkinson et al., 2007; Cove et al., 2017). Although several studies have found that coyotes prefer natural areas as their primary habitat, they tend to use urban areas with anthropogenic cover as secondary habitats where they can search for prey and other resources (Gibeau, 1998, Way et al., 2004; Weckel et al., 2015). Indeed, urban coyotes tend to shift their activities so that they are more active at night, most likely to avoid human interaction (Grinder and Krausman, 2001; Morey et al., 2007; Gese et al., 2012). Because coyotes require large home ranges and maintain low densities, this makes them particularly sensitive to habitat fragmentation (Gittleman et al., 2001; Dobson et al., 2006; Ordeñana et al., 2010; Ripple et al., 2014; Šálek et al., 2014). Therefore, coyote abundance is typically a function of habitat patch area (Crooks and Soulè, 1999; Crooks, 2002; Gese et al., 2012; Cherry et al., 2016). Accordingly, Crooks, (2002) found that coyotes have low abundance and occupancy in small, isolated habitats due to their sensitivity to fragmentation. Within suitable patches, coyotes are thought to prefer heterogenous habitats rather than more homogenous habitats (Ekernas and Mertes, 2006; Fuhlendorf et al., 2010). MacArthur and MacArthur (1961) proposed the habitat heterogeneity hypothesis, in which they posit that biodiversity is positively correlated with the number of habitats in that area. Considering coyotes are opportunistic and situationally exploit different habitats (Beckoff, 1977; Cove et al., 2017), patches with multiple habitats are thought to be highly beneficial to them (Hodgkinson et al., 2007).

The relationship between coyote distribution with two measures of urbanization—human population density and percent developed land cover—is quite complex. In some studies, human population density has been found to be negatively correlated with coyote distribution (e.g.,

Gehrt et al., 2011; Larson et al., 2020; Sugden et al., 2021) while in other studies, human population density has been found to be positively correlated with coyote distribution (e.g., Dodge and Kashian, 2013; Poessel et al., 2016; Parsons et al., 2018; Brooks et al., 2020). Likewise, some studies have reported a negative correlation between coyote distribution and developed land cover (e.g., Atwood et al., 2004, Gese et al., 2012; Dodge and Kashian, 2013), while other studies have reported a positive correlation between coyote distribution and developed land cover (e.g., Tigas et al., 2002; Ordeñana et al., 2010; Stark et al., 2020). Since coyotes are generalists, they have a broad diet consisting of insects, fruits, small mammals, and anthropogenic food sources (Andelt et al., 1987; Mastro et al., 2012; Weckel et al., 2015); this generalist lifestyle might explain their successful expansion into city centers with high human population densities. Morey et al., (2007), for example, found that up to 25% of coyotes' diets in Chicago were comprised of food sources found in human garbage.

Similar to coyotes, free-ranging cat distribution (occupancy and detection probability) is also impacted by anthropogenic and ecological variables, although not always in the same direction as coyotes. The distribution of free-ranging cats in urban areas has been found to be positively associated with human population density (Cove et al., 2017; Morin et al., 2018; Vanek et al., 2020), human-altered habitats (Tennent and Downs, 2008; Gehrt et al., 2013; Kays et al., 2015) and developed land cover (Sims et al., 2007; Krauze-Gryz et al., 2012; Flockhart et al., 2016; Vanek et al., 2020), but negatively associated with patch area (Crooks, 2002; Kays and DeWan, 2004; Schwenk, 2014). The association between free-ranging cat distribution and fine-scale habitat heterogeneity remains inconclusive. Because of their reliance on anthropogenic food sources, cats tend to thrive in urban centers and have been found to substantially surpass their carrying capacities in areas with high human population densities (Sims et al., 2007; Cove

et al., 2017; Morin et al., 2018). For example, Vanek et al., (2020), found that cat occupancy was more than triple in areas with high human population densities than areas that were less populated. However, in contrast to coyotes, free-ranging cats have been found to favor human-altered habitats over natural habitats (Kays and DeWan, 2004; Gehrt et al., 2013; Kays et al., 2015). While cats are generalist predators and like coyotes, can hunt in both natural and human-altered habitats (Turner and Bateson, 2000; Kays and DeWan, 2004; Tennent and Downs, 2008), unlike coyotes, cats tend to spend little time in forested areas instead selecting for forest edges and urbanized areas (Ray, 2000; Crooks, 2002; Elizondo and Loss, 2016; Vanek et al., 2020; Gehrt et al., 2013). Moreover, studies have found higher cat densities in areas surrounded by more developed land cover, which is thought to be attributed to limited habitat space and less competition with other mesocarnivore taxa (Riley et al., 2006; Crooks et al. 2010; Lewis et al. 2017). The “home range pile-up” hypothesis (Riley et al., 2006), for instance, posits that anthropogenic constructions, like roads and buildings, can increase free-ranging cat densities and lead to higher detection probability. In support of this hypothesis, cat population distribution in urban areas has been found to increase with increasing human population and housing density (Sims et al., 2007, Fischer et al., 2012; Thomas et al., 2012; Flockhart et al., 2016). Considering larger carnivores, like coyotes, are sensitive to habitat fragmentation (Gittleman et al., 2001; Dobson et al., 2006; Ordeñana et al., 2010; Šálek et al., 2014), small habitat fragments that can only support relatively smaller mesocarnivores are available for use by species like cats (Ordeñana et al., 2010; LeFlore et al., 2019). Accordingly, unlike coyotes, studies have found that free-ranging cats tend to select for smaller patch areas (Crooks, 2002; Kays and DeWan, 2004; Schwenk, 2014). Because research suggests that free-ranging cats select for smaller patch areas, this suggests that cats might prefer more homogenous landscapes than coyotes and thus

limit the overlap among the two species; however, the relationship between free-ranging cat distribution and habitat heterogeneity remains largely unknown.

In addition to anthropogenic and ecological factors, biogeographical variables, such as the type of landmass, can also impact coyote and free-ranging cat distribution. Several hypotheses have been proposed related to variation in landmass variables including: (1) the “fence effect” (Krebs et al., 1969) and the (2) the “island syndrome” (Adler and Levins 1994). These hypotheses propose that bounded populations, like islands, have high densities due to reduced opportunities for dispersal. These hypotheses are especially important when examining coyote and free-ranging cat distribution in a region like the New York metropolitan area because of its many geographical barriers separating the continent and islands. Because free-ranging cats are an invasive species that have been introduced to islands by humans (Fischer et al., 2012; Loss et al., 2013; Nogales et al., 2013), they might be more prevalent on islands than on the continent. Coyotes are more prevalent on the continent because islands are barriers to dispersal because they are bounded by water on all sides (Weckel et al., 2015). It is not surprising that New York Harbor serves as a barrier to dispersal because coyotes must either swim across the Long Island Sound or venture across heavily trafficked bridges in order to disperse to Long Island (Harrison, 1992; Mitchell et al., 2015; Weckel et al., 2015; Nagy et al., 2016).

The aim of the current study was to determine what factors best explain coyote and free-ranging cat occupancy and detection probability in various greenspaces of the New York metropolitan area and to assess whether free-ranging cats avoid habitats occupied by coyotes. The study addresses three major research questions: (1) What factors contribute to coyote occupancy and detection probability in the New York metropolitan area? (2) What factors contribute to free-ranging cat occupancy and detection probability in the New York metropolitan

area? (3) Do free-ranging cats avoid habitats occupied by coyotes? To address these questions, I set up motion-activated camera traps across 31 study sites (Table 2.1). I hypothesized that coyote and cat occupancy and detection probability are influenced by multiple factors including human population density, habitat type, patch area, percent developed land cover, fine-scale habitat heterogeneity, and biogeographical variables. Specifically, I predicted that coyote occupancy and detection probability would be higher in sites where there were lower human population densities, urban natural habitats, larger patch areas, more surrounding developed land cover, and more habitat heterogeneity. I also predicted that during the pup-rearing season, coyote detection probability would be higher in study sites with lower human population densities. Additionally, I predicted that cat occupancy and detection probability would be higher in sites where there were higher human population densities, smaller patch areas, human-altered habitats, more surrounding developed land cover, and less habitat heterogeneity. Considering the geographical barriers between the continent and islands, I predicted that coyote occupancy would be higher on the continent (Bronx/Westchester) than on the islands (Long Island, Manhattan, and Randall's Island), while I expected free-ranging cat occupancy and detection probability to exhibit the opposite pattern.

With the continuing expansion of coyotes, it is necessary to explore relationships between their changing distribution with potentially meaningful geographic and anthropogenic factors. As the largest carnivore in the region, coyotes have the potential to impact the ecology of particular species or even the ecology of the overall wildlife community, not to mention potential interactions with humans and pets. Furthermore, cats are currently a major threat to biodiversity (Elizondo and Loss, 2016; Krauze-Gryz et al., 2012, 2017), so exploring the potential of top-down effects of coyotes on free-ranging cats may inform the conservation of a variety of taxa.

Methods

Field Sites

This research is the third in a series of analyses focused on examining the distribution, occupancy, and detection probability of coyotes in the New York metropolitan area (Fig. 2.1). The first analysis was based on data collected between 2011-2014; for each of these four years, coyotes were studied in anywhere from 10 to 13 sites in the New York boroughs of the Bronx, Queens, Manhattan, and Brooklyn (Nagy et al., 2016). The second analysis, based on data collected from 2016 to 2019, extended the total number of study sites to 45 sites across the Bronx, Manhattan, and Queens (Nagy et al., 2017). In the present study, I focused on 31 sites from the 2016-2019 dataset for sampling and comparison (Table 2.1). In addition to coyote occupancy and detection probability, the present study also investigated free-ranging cat occupancy and detection probability across the 31 study sites and their spatial interactions with coyotes.

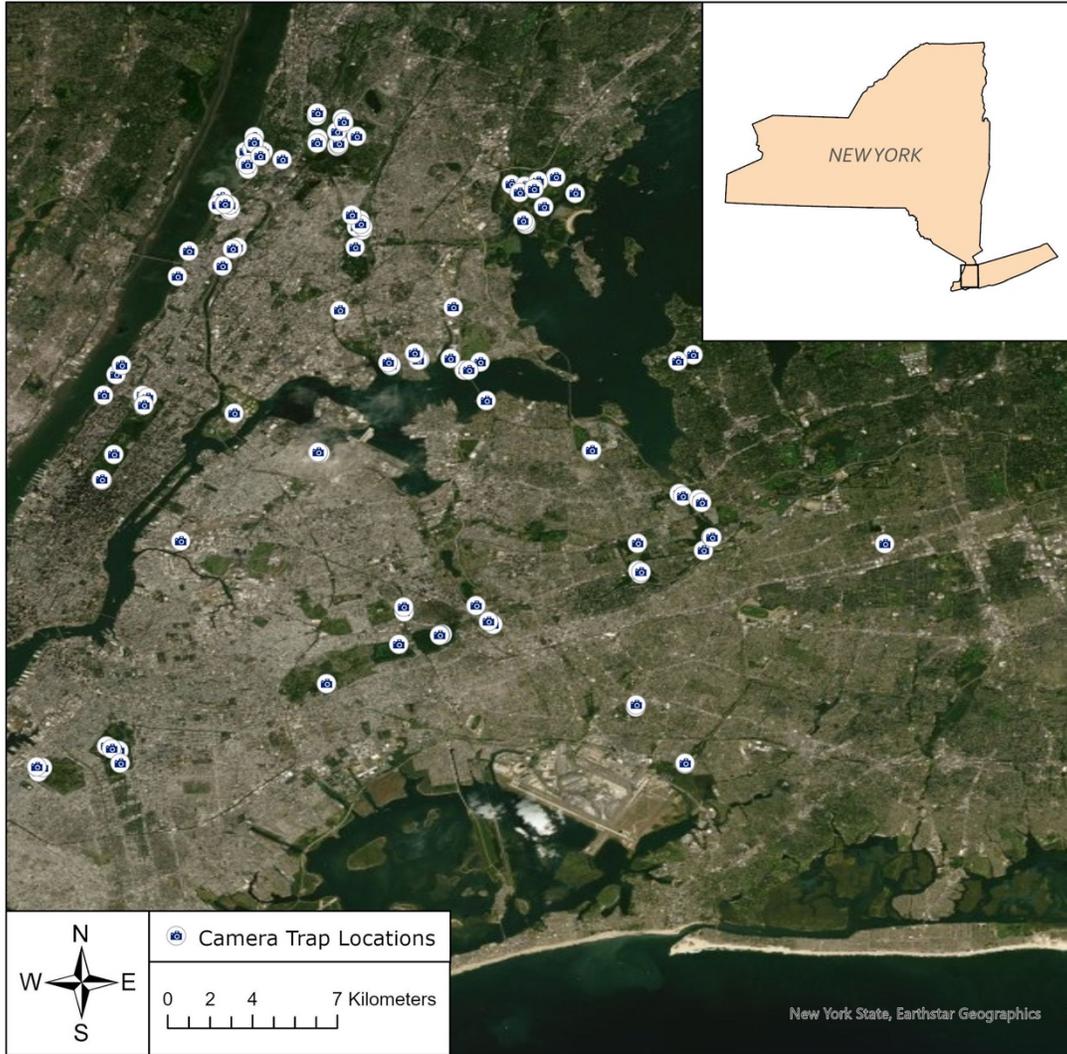


Figure 2.1. Map of camera trap sites across 31 greenspaces where coyote and free-ranging cat distributions were examined in the New York metropolitan area, 2015-2019.

Table 2.1. Dates, coordinates, and characteristics of the 31 greenspaces surveyed between 2015-2019

Study Site	Survey Dates	Latitude, Longitude ^A	Human Population Density (people/km ²) ^B	Patch Area (km ²)	Habitat Type	Percent Developed Land cover (1000 m)	Habitat Heterogeneity (100 m)	Landmass Type	Number of Cameras/km ²	Number of Cameras Deployed
Alley Pond	2/1/16 – 5/7/19	40.75742, -73.74266	28,552.03	2.82	Urban Natural Habitat	82.86	4	Island	2.48	7
Bronx Park	1/30/16 – 6/13/19	40.86273, -73.87398	139,345.89	2.95	Urban Natural Habitat	85.71	5	Continent	3.39	10
Central Park	2/17/16 – 7/24/17	40.76635, -73.97463	271,920.26	3.43	Human-Altered Habitat	30.56	3	Island	2.62	9
Clearview Golf Course	2/1/16 – 3/29/19	40.77767, -73.78519	34,319.93	0.48	Human-Altered Habitat	0	1	Island	6.25	3
Cunningham	2/3/16 – 5/7/19	40.74176, -73.76742	37,726.40	2.25	Urban Natural Habitat	33.33	4	Island	2.67	6
Elmjack Ingrams Field	5/27/16 – 5/10/19	40.77693, -73.89096	65,241.80	0.058	Human-Altered Habitat	51.43	5	Island	51.72	3
Ferry Point	2/1/16 – 5/16/19	40.81174, -73.82832	31,890.52	1.32	Human-Altered Habitat	50	3	Continent	3.03	4
Forest Park	6/13/16 – 5/10/19	40.70644, -73.84295	68,951.44	1.30	Urban Natural Habitat	0	1	Island	3.08	4
Fort Washington	2/18/16 – 9/1/16	40.84486, -73.94538	160,249.04	0.51	Urban Natural Habitat	28.13	4	Island	5.88	3
Francis Lewis	2/3/16 – 2/8/19	40.79685, -73.82587	36,189.90	0.039	Human-Altered Habitat	43.75	5	Island	25.64	1
Green-wood Cemetery	1/26/17 – 5/13/19	40.65319, -73.99909	75,492.97	1.90	Human-Altered Habitat	54.29	2	Island	1.58	3
Highbridge Park	7/9/17 – 7/28/17	40.84889, -73.92803	184,104.12	0.262	Urban Natural Habitat	19.44	4	Island	7.63	2
Hutchinson	3/7/16 – 5/8/19	40.833, -73.83879	31,890.52	0.031	Urban Natural Habitat	83.33	4	Continent	32.26	1
Idlewild Park	2/10/16 – 3/23/19	40.6564, -73.74908	32,512.12	1.65	Urban Natural Habitat	0	3	Island	1.21	2
Inwood Hill Park	12/26/15 – 5/10/19	40.87247, -73.92971	89,468.55	0.789	Urban Natural Habitat	0	1	Island	10.14	8
Kings Point Park	6/29/16 – 9/1/16	40.81459, -73.74606	5,881.86	0.70	Urban Natural Habitat	0	1	Island	2.86	2
Maple Grove Cemetery	3/7/16 – 5/10/19	40.71028, -73.82334	88,168.38	0.272	Human-Altered Habitat	80	3	Island	7.35	2
Pelham Bay Park	2/2/16 – 5/11/19	40.86636, -73.81177	31,890.52	2.23	Human-Altered Habitat	2.86	2	Continent	6.73	15
Prospect Park	7/7/17 – 5/13/19	40.65661, -73.96745	139,567.73	2.46	Urban Natural Habitat	5.41	6	Island	1.63	4
Pugsley Creek	2/18/16 – 5/7/19	40.81244, -73.85221	69,530.82	2.40	Urban Natural Habitat	20	5	Continent	1.67	4
Queensline	2/10/16 – 5/10/19	40.71709, -73.85794	95,769.99	0.198	Urban Natural Habitat	89.19	4	Island	15.15	3
Railroad	2/10/16 – 5/10/19	40.67924, -73.76794	47,282.82	0.152	Urban Natural Habitat	16.67	3	Island	13.16	2
Randall's Island	2/3/16 – 5/4/19	40.79188, -73.9234	63,011.82	.092	Human-Altered Habitat	87.88	4	Island	21.74	2
Ridgewood Highland	1/26/18 – 5/16/18	40.68739, -73.8877	70,792.15	1.71	Human-Altered Habitat	8.33	3	Island	0.58	1
Riverdale	1/31/16 – 5/12/19	40.89881, -73.91566	72,364.27	0.51	Urban Natural Habitat	8.82	8	Continent	21.57	11
Riverside Park	2/17/16 – 4/16/19	40.81059, -73.96693	208,386.12	0.35	Human-Altered Habitat	22.86	8	Island	11.43	4
Smiling Hogshead Ranch	1/27/17 – 4/29/18	40.74252, -73.94411	25,236.84	0.008	Human-Altered Habitat	100	2	Island	125	1
Soundview	7/3/16 – 5/7/19	40.81164, -73.86387	69,530.82	0.719	Urban Natural Habitat	0	3	Continent	4.17	3
Starlight Park	2/18/16 – 5/12/16	40.83183, -73.88263	131,408.23	0.011	Urban Natural Habitat	75.76	4	Continent	90.91	1
Van Cortlandt	1/27/16 – 5/16/19	40.90697, -73.89154	51,011.11	4.65	Urban Natural Habitat	0	3	Continent	3.44	16
Willow Lake	2/10/16 – 1/9/17	40.71763, -73.82987	67,286.60	0.665	Urban Natural Habitat	0	2	Island	1.5	1

^A For sites containing multiple camera sites, the latitude and longitude was recorded based on the location at which there were the most photo captures.

^B The human population density was calculated by averaging the population density of all of the zip codes surrounding each site.

Camera Surveys

Following Nagy et al., (2016), 138 camera traps were deployed across 31 different study sites throughout five regions in the New York metropolitan area. There were three varieties of Reconyx cameras deployed across the five years of the study (December 2015 to June 2019): heat and motion activated HC500, RC55, and PC800 cameras (Reconyx, Inc., Holmen, WI). Two different models of the RC55 were used: (1) an older model, mainly used for nighttime photos (5.0 x 7.6 cm red/infrared flash); (2) a newer model with only one LED bulb (“semi-convert” infrared flash). All three camera varieties had similar infrared flash ranges (PC800: 21m, HC500 and RC55: 15m), the same trigger speeds (0.2s), and the same resolutions (1080p). Locations for camera deployment were randomly selected for each greenspace using ArcGIS 9 and ArcGIS10 (ESRI, Redlands, California), and were at least 500m apart. Each camera within a study site was deployed in an adequate forest patch or undeveloped area. Due to a limited number of camera traps, in some cases, they were shifted to different locations within a greenspace in order to increase sampling coverage. Some cameras were relocated within ~50 m of the original location due to legal complications, vandalism, theft, or for a more suitable placement. Across the span of the study, the same general camera placements were used each year barring areas found to be susceptible to theft or natural disasters. Each greenspace contained a different number of cameras with most study sites having at least one camera per 0.5km².

Predictors of coyote and free-ranging cat occupancy and detection probability

To test what factors best explain coyote and free-ranging cat occupancy and detection probability in various greenspaces of the New York metropolitan area, I modeled six predictor variables: (1) human population density; (2) habitat type; (3) patch area; (4) percent developed land cover; (5)

fine-scale habitat heterogeneity; and (6) type of landmass. For analyses of detection probability, I included cameras per km² in my models to control for variation in camera deployment (Table 2.1).

- (1) **Human population density.** I measured human population density by accessing the number of people per square mile based on the zip code location of each study site¹. I converted these measurements to number of humans per square kilometer. In cases in which there were more than one zip code situated in a study site, I measured the human population density of each study site by calculating the average human population density among these zip codes.
- (2) **Habitat type.** I categorized each study site into one of two habitat types: *urban natural*, defined as an urban greenspace comprised of greater than 50 percent secondary growth forest and *human-altered*, defined as an urban greenspace comprised of greater than 50 percent manicured lawns, athletic fields, golf courses, or playgrounds (Gallo et al., 2017). In cases in which study sites were comprised of both habitat types, I categorized the habitat based on which of the two habitats was dominant.
- (3) **Patch area.** I calculated patch area of each greenspace using the “measure distance” tool on Google Maps². To do so, I traced the perimeter of the greenspace in which each study site was situated, and then converted the output to km².
- (4) **Percent developed land cover.** I calculated percent developed land cover within a 1 km buffer surrounding each study site using ArcGIS Pro 2.6 (ESRI, Redlands, CA) and the National Land Cover Database (NLCD, 2019). I used a 1000 m buffer to analyze whether the amount of developed land cover surrounding a habitat influenced coyote and cat distribution (e.g., Gomes et al., 2011). I combined percent land cover from three different NLCD classes (“developed, low intensity”; “developed, medium intensity”; and

“developed, high intensity”) into one broad category: developed land cover (Callaghan et al., 2019; Stark et al., 2020; Goldstein et al., 2022) (Fig. 2.2). Developed land cover consists of at least 20 percent impervious surface cover and a mixture of constructed materials and vegetation (NLCD 2019)³.

- (5) **Fine-scale habitat heterogeneity.** I calculated fine-scale habitat heterogeneity by counting the number of different habitat categories as defined by the National Land Cover Database within a 100 m buffer of the study site (Fig 2.2; Table 2.2).
- (6) **Landmass type.** I classified each study site into one of two categories based on landmass: *island*, designated for study sites located in Long Island, Manhattan, or Randall’s Island; and *continent*, designated for study sites located in Bronx and Westchester.

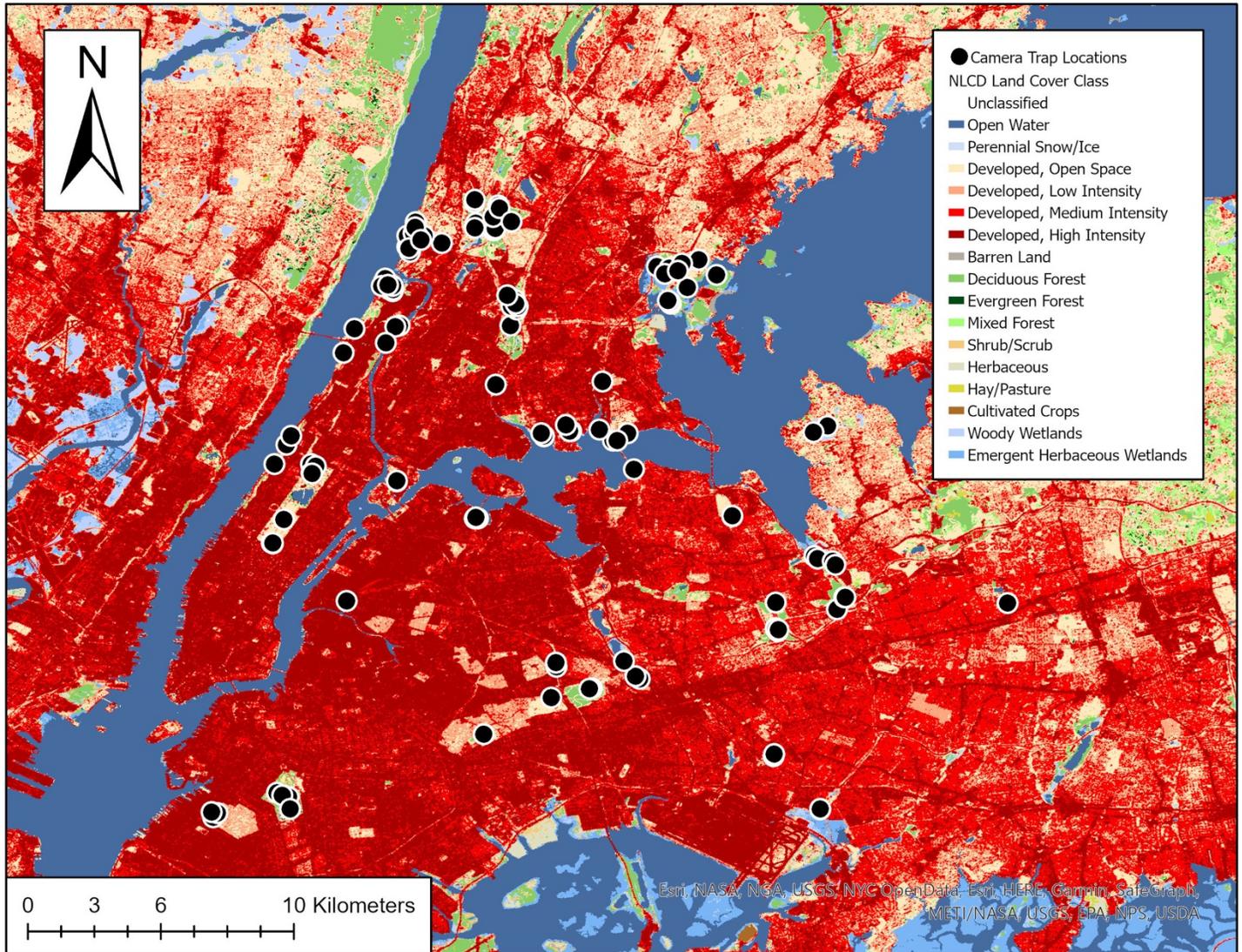


Figure 2.2. Map displaying land cover classes and camera trap locations to analyze coyote and free-ranging cat distributions in the New York metropolitan area.

Table 2.2. Classification of spaces based on the National Land Cover Database (2019)

Class	Classification Description
Open water	spaces composed of bodies of open water with no more than 25% soil or vegetation
Developed: Open space	spaces containing a mixture of manicured grasses and manmade materials with less than 20% impervious surfaces (i.e., trimmed lawns, urban parks golf courses, housing structures)
Developed: Low intensity	spaces composed of a mixture of natural vegetation and manmade material with impervious surfaces accounting for 20-49% of the land cover composition
Developed: Medium intensity	spaces consisting of a combination of natural vegetation and manmade materials with 50-79% impervious land cover
Developed: High intensity	spaces where 80-100% of the land cover is an impervious surface resulting from high development due to commercial and industrial activities
Barren land	spaces composed mainly of native earthen materials with vegetation accounting for less than 15% of the land
Deciduous forest	spaces that have greater than 20% vegetation cover that consists mainly of trees that are taller than five meters and trees that shed leaves seasonally (75%)
Evergreen forest	spaces with more than 20% of total land cover being encompassed by vegetation and trees that do not change color or shed leaves every season
Mixed forest	spaces s with more than 20% of their land cover consisting of vegetation with neither deciduous nor evergreens comprising more than 75% of the tree cover
Shrub/scrub	spaces composed of shrubs that are less than five meters in height, and account for more than 20% of their land cover
Grassland/herbaceous	spaces consisting of grassy vegetation that composes 80% or more of their total land cover
Pasture/hay	spaces composed of at least 21% of their land cover existing as legumes or grasses for either hay or animal grazing
Crops	spaces that are constantly cultivated for the production of annual crops such that this vegetation accounts for over 20% of the total land cover
Woody/wetlands	spaces consisting of more than 20% shrubland or forests where the soil is sporadically drenched with water
Emergent herbaceous wetlands	spaces where perennial herbaceous vegetation comprises more than 80% of the land cover and there is intermittent soaking of the soil with water

Spatial overlap between free-ranging cats and coyotes

To test whether free-ranging cats avoid habitats occupied by coyotes, I modeled one additional predictor variable: **presence or absence of coyotes**. I coded a camera trap location as 0 if there were no coyotes identified and a camera trap location as 1 if one or more coyotes were present.

Statistical analyses

All statistical analyses were conducted using the R Project for Statistical Computing⁴. I used occupancy models to investigate factors that best explain coyote and free-ranging cat occupancy and detection probability in the New York metropolitan area. To perform occupancy and detection probability analyses, I used the *unmarked* package (Fiske and Chandler, 2011).

Occupancy was defined as the probability that an individual camera trap survey site is occupied by a given species (Parsons et al., 2018), while detection probability was defined as the probability of detecting a specific species at a camera trap survey site (Parsons et al., 2018).

Independent photographs of coyotes or cats were calculated by counting the maximum number of individuals in the same photograph during 24-hour intervals (Cove et al., 2012; Lombardi et al., 2017; Egan et al., 2020).

To account for seasonal fluctuations in coyote activity during the breeding and non-breeding season, the data were divided into pup-rearing seasons and non-pup-rearing seasons for each study site. Pup-rearing seasons took place from April 1st - September 30th of each year, while non-pup-rearing seasons occurred from October 1st - March 31st of each year (Harrison and Gilbert, 1985; Way et al., 2001; Gehrt et al., 2009; Nagy et al., 2016). Occupancy models of pup-rearing seasons included four seasons of data (2015-2016; 2016-2017; 2017-2018; 2018-2019); occupancy models of non-pup-rearing seasons also included four seasons of data (2016 through 2019). Occupancy and detection probability models of free-ranging cats were not sub-divided because these animals breed year-round (Cove et al., 2012).

I modeled six response variables: (1) coyote occupancy (pup-rearing season); (2) coyote detection probability (pup-rearing season); (3) coyote occupancy (non-pup-rearing season); (4) coyote detection probability (non-pup-rearing season); (5) free-ranging cat occupancy, and (6)

free-ranging cat detection probability. A complete list of the predictor and response variables included in each model is summarized in Table 2.3.

Table 2.3. Response and predictor variables for coyote and free-ranging cat occupancy and detection probability models

Response Variables	
Occupancy	the probability that an individual camera trap survey site is occupied by a given species
Detection probability	the probability of detecting a specific species at a camera trap survey site
Predictor Variables	
Population density	the average population density per km ² in the zip code where the study area and surrounding zip codes were located in
Habitat type	the kind of landscape that comprises greater than 50% of the patch area of the study location (coded as either <i>urban natural habitat</i> or <i>human-altered landscape</i>)
Patch area	area of each of the study sites (km ²)
Percent developed land cover	the percent of different land cover types within a 1km buffer that surrounds a study area.
Fine-scale habitat heterogeneity	the number of different habitat types that comprised each study area based on classifications set by the National Land Cover Database (2019) (Fig. 2.2; Table 2.2)
Landmass type	the type of landmass that the study site is found on (coded as either <i>island</i> (Long Island, Manhattan, or Randall’s Island sites), or <i>continent</i> (Bronx and Westchester sites).
Cameras per km ²	for detection probability models only, the number of camera traps per km ² in each study area was modeled to control for camera density
Presence/Absence of coyotes	the presence or absence of coyotes within a study area, used for free-ranging cat analyses only

Results

Distribution of coyotes and free-ranging cats in the New York metropolitan area

Throughout the 31 study locations, coyotes were found at eleven of these sites; of these eleven locations, coyote pups were detected at four of these sites (Fig. 2.3; Table 2.4). Coyote occupancy was 14.1% higher during the non-pup-rearing (NPR) than the pup-rearing seasons (PR) (NPR: 0.456; PR: 0.396) and coyote detection probability was 27.8% higher during the non-pup-rearing than pup-rearing seasons (NPR: 0.085; PR: 0.069). Free-ranging cats were found at all 31 study locations. Across the duration of the study, cat occupancy was 0.653, while cat detection probability was 0.103. Overall, cat occupancy and detection probability were greater than that of coyotes.

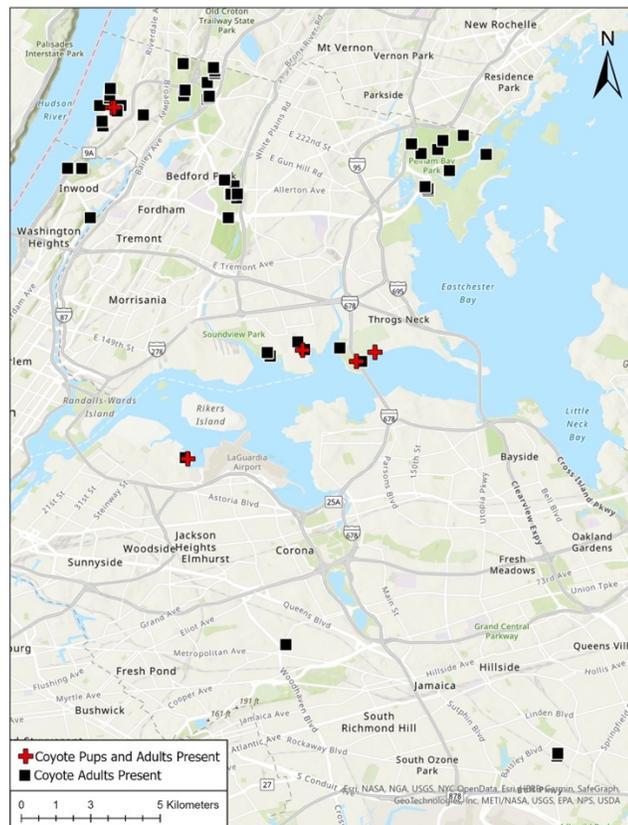


Figure 2.3. Camera trap locations where adult coyotes and coyote pups were detected between 2015-2019. Black squares indicate locations in which adult coyotes were present. Red plus marks indicate locations in which both adult coyotes and pups were present.

Table 2.4. Detections of adult coyotes or adult coyotes and coyote pups at each of the 31 greenspaces during pup-rearing and non-pup-rearing seasons from 2015-2019

Study Site	2015-2016		2016-2017		2017-2018		2018-2019	
	NPR	PR (2016)	NPR	PR (2017)	NPR	PR (2018)	NPR	PR (2019)
Alley Pond Park	0	0	0	0	0	0	0	0
Bronx Park	1	1	1	1	1	1	1	1
Central Park	0	0	0	0	X	X	X	X
Clearview Golf Course	0	0	0	0	0	0	0	0
Cunningham Park	0	0	0	0	0	0	0	0
Elmjack Ingrams Field	X	2	1	1	0	0	1	1
Ferry Point Park	1	1	1	2	0	1	1	1
Forest Park	X	0	0	0	0	0	0	0
Fort Washington Park	0	0	X	X	X	X	X	X
Francis Lewis Park	0	0	0	0	0	0	0	X
Green-wood Cemetery	0	0	0	0	0	0	0	0
Highbridge Park	X	X	X	0	X	X	X	X
Hutchinson	0	0	0	0	0	0	0	0
Idlewild Park	0	0	0	0	0	0	0	X
Inwood Hill Park	0	0	0	1	0	0	1	0
Kings Point Park	X	0	X	X	X	X	X	X
Maple Grove Cemetery	0	0	0	0	0	0	0	0
Pelham Bay Park	1	1	1	1	1	1	1	1
Prospect Park	X	X	X	0	0	0	0	0
Pugsley Creek Park	1	2	1	0	1	0	0	0
Queensline	1	0	0	0	0	0	0	0
Railroad Park	1	1	1	0	0	0	1	1
Randall's Island	0	0	0	0	0	0	0	0
Ridgewood Highland	0	0	0	0	0	0	X	X
Riverdale Park	1	2	1	1	1	1	1	1
Riverside Park	0	0	0	0	0	0	0	0
Smiling Hogshead Ranch	X	X	0	0	0	0	X	X
Soundview Park	X	1	0	0	1	1	0	0
Starlight Park	0	0	X	X	X	X	X	X
Van Cortlandt Park	1	1	1	1	1	1	1	1
Willow Lake	0	0	0	X	X	X	X	X

NPR = non-pup-rearing season; PR = pup-rearing season

0 = no detections; 1 = adult coyote detections; 2 = adult coyote and pup detections

“X” = site was not surveyed that season

Predictors of coyote occupancy

Based on model averaging, I found that there were two variables that significantly predicted coyote occupancy during both the non-pup-rearing (NPR) and pup-rearing (PR)

seasons (Table 2.5): habitat type and type of landmass. Specifically, coyote occupancy was higher in human-altered habitats than urban natural habitats (NPR: estimate = -1.422, Table 2.5; $p = 0.026$; PR: estimate = -3.936; $p = 0.003$, Table 2.5). Coyote occupancy was also higher on the continent (Bronx and Westchester) than on the islands (Manhattan, Long Island, Randall's Island) (NPR: estimate = -3.728, Table 2.5; $p = <0.001$; PR: estimate = -4.449; $p = <0.001$, Table 2.5).

I found one variable that was a significant predictor of coyote occupancy during the non-pup-rearing seasons, but not during the pup-rearing seasons: percent developed land cover. Specifically, during the non-pup-rearing seasons, coyote occupancy was significantly higher in greenspaces surrounded by more developed than less developed land cover (NPR: estimate = 2.550; $p = 0.019$; Table 2.5).

I also found two variables that were significant predictors of coyote occupancy during the pup-rearing seasons, but not during the non-pup-rearing seasons: habitat heterogeneity and human population density. Specifically, during the pup-rearing seasons, coyote occupancy was higher in more heterogeneous than less heterogenous habitats (PR: estimate = 0.429; $p = 0.039$; Table 2.5). Further, during the pup-rearing seasons, coyote occupancy was higher in greenspaces with higher human population densities than greenspaces with lower human population densities (PR: estimate = 7.548; $p = 0.004$; Table 2.5).

Predictors of coyote detection probability

Based on model averaging, I found that there were two variables that significantly predicted coyote detection probability during both the non-pup-rearing and pup-rearing seasons in which the response was in the same direction: human population density and habitat type

(Table 2.5). Specifically, coyote detection probability was higher in greenspaces with lower human population densities than higher human population densities (NPR: estimate = -1.890; $p = <0.001$, Table 2.5; PR: estimate = -3.676; $p = 0.002$, Table 2.5). Coyote detection probability was also higher in urban natural habitats than in human-altered habitats (NPR: estimate = 0.657; $p = <0.001$, Table 2.5; PR: estimate = 0.956; $p = 0.034$, Table 2.5).

I found that there were two variables that significantly predicted coyote detection probability during both the non-pup-rearing and pup-rearing seasons in which the response was not in the same direction: habitat heterogeneity and patch area. Coyote detection probability was higher in more heterogenous habitats during the non-pup-rearing seasons (NPR: estimate = 0.133; $p = 0.040$; Table 2.5) and in less heterogenous habitats during the pup-rearing seasons (PR: estimate = -0.342; $p = <0.001$; Table 2.5). Moreover, coyote detection probability was higher in greenspaces with smaller patch areas during the non-pup-rearing seasons (NPR: estimate = -0.684; $p = <0.001$, Table 2.5) and larger patch areas during the pup-rearing seasons (estimate = 0.352; $p = 0.036$; Table 2.5).

Predictors of free-ranging cat occupancy

Based on my best supported model, I found that there were three variables that significantly predicted free-ranging cat occupancy: habitat type, patch area, and percent developed land cover. Specifically, free-ranging cat occupancy was higher in human-altered habitats than urban natural habitats (estimate = -0.182; $p = 0.027$; Table 2.5). Free-ranging cat occupancy was also higher in greenspaces with smaller patch areas than larger patch areas (estimate = -0.363; $p = 0.002$; Table 2.5). Finally, greenspaces surrounded by less developed

land cover exhibited higher free-ranging cat occupancy than greenspaces surrounded by more developed land cover (estimate = -1.479; $p = 0.019$; Table 2.5).

Predictors of free-ranging cat detection probability

Based on my best supported model, I found that there were five variables that significantly predicted free-ranging cat detection probability: presence of coyotes, habitat type, human population density, patch area, and percent developed land cover. First, free-ranging cat detection probability was lower in habitats where coyotes were present than in habitats where coyotes were absent (estimate = -0.432; $p = <0.001$; Table 2.5). Second, free-ranging cat detection probability was higher in urban natural habitats than human-altered habitats (estimate = 0.218; $p = 0.003$; Table 2.5). Third, free-ranging cat detection probability was higher in greenspaces with lower human population densities than higher human population densities (estimate = -0.717; $p = <0.001$; Table 2.5). Fourth, free-ranging cat detection probability was higher in greenspaces with smaller patch areas than greenspaces with larger patch areas (estimate = -0.327; $p = <0.001$; Table 2.5). Fifth, free-ranging cat detection probability was significantly higher in greenspaces surrounded by less developed land cover than more developed land cover (estimate = -1.132; $p = <0.001$; Table 2.5).

Table 2.5. Best supported models for each response variable for coyote and free-ranging cat occupancy and detection probability

Response Variables	Fixed Effects	Estimate	Std. Error	z value	P value
Coyote occupancy (non-pup-rearing season)	Habitat type	-1.422	0.638	2.229	0.026*
	Landmass type	-3.728	0.596	6.258	<0.001***
	Percent developed land cover	2.450	1.046	2.343	0.019*
Coyote occupancy (pup-rearing season)	Habitat type	-3.936	1.316	2.991	0.003**
	Fine-scale habitat heterogeneity	0.429	0.208	2.061	0.039*
	Landmass type	-4.449	0.863	5.158	<0.001***
	Human population density	7.548	2.643	2.856	0.004**
Coyote detection probability (non-pup-rearing season)	Habitat type	0.657	0.191	3.441	<0.001***
	Fine-scale habitat heterogeneity	0.133	0.065	2.056	0.040*
	Human population density	-1.890	0.529	3.574	<0.001***
	Patch area	-0.684	0.113	6.033	<0.001***
	Cameras per squared kilometer	-1.350	0.356	3.797	<0.001***
Coyote detection probability (pup-rearing season)	Habitat type	0.956	0.450	2.125	0.034*
	Fine-scale habitat heterogeneity	-0.342	0.094	3.648	<0.001***
	Human population density	-3.676	1.173	3.133	0.002**
	Patch area	0.352	0.168	2.092	0.036*
	Percent developed land cover	-1.559	0.841	1.853	0.064
	Cameras per squared kilometer	1.923	0.428	4.488	<0.001***
Free-ranging cat occupancy	Habitat type	-0.182	0.082	-2.210	0.027*
	Patch area	-0.363	0.115	-3.160	0.002**
	Percent developed land cover	-1.479	0.632	-2.340	0.019*
Free-ranging cat detection probability	Coyote presence/absence	-0.432	0.069	-6.240	<0.001***
	Habitat type	0.218	0.073	2.990	0.003**
	Human population density	-0.717	0.135	-5.320	<0.001***
	Patch area	-0.327	0.041	-8.000	<0.001***
	Percent developed land cover	-1.132	0.135	-8.400	<0.001***
	Cameras per squared kilometer	-0.475	0.090	-5.260	<0.001***

· denotes P < 0.1
* denotes significance of <0.05
** denotes significance of <0.01
*** denotes significance of < 0.001

Discussion

My analysis of predictors of coyote and free-ranging cat occupancy and detection probability in the New York metropolitan area suggests that anthropogenic variables play key roles in determining the distribution of both cats and coyotes, that biogeographical variables heavily shape coyote distribution, and that the presence of coyotes influences the detection probability of free-ranging cats. In support of my predictions, I found that coyote detection probability was higher in urban natural habitats and in sites with relatively low human population densities. However, contrary to my predictions, coyote occupancy was higher in human-altered habitats rather than urban natural habitats. Hence, while coyotes were more likely to be detected in natural habitats and in sites with relatively low human population densities, despite this finding, coyotes were still found more often in human-altered habitats. These results suggest that some anthropogenic factors, including fragmentation and development, influence coyote detection probability (Cove et al., 2012; Parsons et al., 2018; Stark et al., 2020), while other anthropogenic factors, such as access to human-derived food resources, influence coyote occupancy (Riley et al., 2003; Morey et al., 2007; Gehrt et al., 2009; Dodge and Kashian, 2013). I also found that several anthropogenic factors influenced coyote distribution differently depending on whether it was the pup-rearing season versus the non-pup-rearing season, which suggests that coyotes shift their behavior during reproductive months (Grinder and Krausman, 2001; McClennen et al., 2001; Kenaga et al., 2013). Finally, I found that biogeographical barriers contributed to coyote distribution. Specifically, coyote occupancy was greater on the continent (Bronx and Westchester) than on the nearby islands (Long Island, Manhattan, and Randall's Island).

Measures of free-ranging cat distribution were driven by several anthropogenic factors as well as the presence or absence of coyotes. Consistent with my predictions, I found that both

occupancy and detection probability were higher in greenspaces with smaller patch areas, and that free-ranging cat occupancy was higher in human-altered habitats than urban natural habitats. These findings support my hypothesis that free-ranging cats are attracted to human habitats (Thomas et al., 2012; Flockhart et al., 2016; Casteñada et al., 2018). However, contrary to my predictions, free-ranging cat occupancy and detection probability were higher in greenspaces with less surrounding developed land cover, and detection probability was higher in habitats that were comprised mainly of urban natural habitats that consisted of low human population densities. Lastly, in support of my prediction, I found that free-ranging cat detection probability was lower in habitats where coyotes were present than in habitats where coyotes were absent. Collectively, these results reveal the complexities of a highly urbanized city in terms of harboring mesocarnivores such as coyotes and free-ranging cats, and the dynamic interplay between anthropogenic, biogeographical, and ecological variables. I elaborate on my findings in the sections below.

Coyotes are expanding their range in the New York metropolitan area

I found that coyotes are expanding their range into additional greenspaces in the New York metropolitan area. In a previous camera trap study conducted in the New York metropolitan area from 2011-2016, coyotes were identified in six greenspaces on the continent (Bronx/Westchester) and in two greenspaces on nearby islands (one greenspace in Long Island and one greenspace in Manhattan) (Nagy et al., 2016). In the current study, coyotes were identified in all six continental sites where they were detected previously as well as in one additional greenspace (Soundview Park; Table 3). Moreover, in the previous study (Nagy et al., 2016), coyotes were identified in one greenspace on Long Island, whereas in the current study,

coyotes were found in two additional greenspaces for a total of three greenspaces on Long Island. However, coyotes were only detected in one greenspace in Manhattan (Inwood Hill Park), both in the current and historical study. I also sampled an additional nearby island (Randall's Island), but no coyotes were detected at this study site. These findings suggest that while coyotes in the New York metropolitan area are expanding their range, they have yet to establish appreciable populations in Long Island and Randall's Island, which might be attributed to both anthropogenic influences and barriers to dispersal (Fener et al., 2005; Curtis et al., 2007; Toomey et al., 2012; Weckel et al., 2015).

Coyote occupancy and detection probability are influenced by anthropogenic factors

Consistent with my hypothesis that coyotes take advantage of urban habitats, but largely avoid highly urbanized areas, I found that coyote detection probability was higher in urban natural habitats and in sites with relatively low human population densities. Coyotes might select urban natural habitats because they provide natural food sources and forest cover (Person and Hirth, 1991; Quinn, 1997; Morey et al., 2007; Gese et al., 2012; Dodge and Kashian, 2013). Moreover, while coyotes are attracted to urban habitats, they tend to avoid areas with high human presence (Grinder and Krausman, 2001; Way et al., 2004; Gehrt et al., 2009; Gallo et al., 2017; Parsons et al., 2018). This probably explains why detection probability was also lower in greenspaces with high human population densities.

Although coyote detection probability was higher in urban natural habitats compared to human-altered habitats, contrary to my predictions, I found the opposite pattern when assessing coyote occupancy. Specifically, coyote occupancy was higher in human-altered rather than urban natural habitats. While coyotes are known to avoid humans, they also tend to maximize their

resources, which might be more plentiful in some human-altered greenspaces (i.e., manicured grasses that harbor an abundance of rabbits, mice, deer, etc.) (Atwood et al., 2004; Way et al., 2004; Gese et al., 2012). Since coyotes have a wide-ranging diet, when prey is limited, they tend to supplement their diets with human food scraps as well as garbage (Gosselink et al., 2003; Contesse et al., 2004; Stark et al., 2020). Therefore, while coyotes are more likely to be detected in urban natural habitats, these findings suggest that they are also exploiting the resources of human-altered habitats. “Occupied” status is also assigned to a site by a single observation within a season, which could be observations of a single individual that did not stay in the area for long (i.e., a lone individual traveling through or looking for suitable habitat). Thus, while short-term occupancy status is a snapshot of distribution, only long-term persistence and reproduction should be used as an index of habitat quality, especially for a highly mobile generalist like the coyote.

Anthropogenic factors impact coyote distribution differently in pup-rearing versus non-pup-rearing seasons

There were several cases in which anthropogenic factors influenced coyote distribution differently when comparing non-pup-rearing to pup-rearing seasons. First, percent developed land cover was a significant predictor of coyote occupancy during the non-pup-rearing seasons, but not during the pup-rearing seasons. Specifically, during the non-pup-rearing seasons, coyote occupancy was higher in greenspaces surrounded by more developed than less developed land cover. During the non-pup-rearing season, coyotes tend to utilize developed areas to search for anthropogenic food resources, but during the pup-rearing season, coyotes tend to be less mobile and select greenspaces with higher forest cover (Riley et al., 2003; Gese et al., 2012). Contrary to

my findings, Gese et al., (2012) found that developed land cover consisting of impervious surfaces, like roads, buildings, and parking lots, correlated with decreased coyote occupancy largely due to habitat fragmentation. However, considering the extent of urbanization in “super-urban” centers like the New York metropolitan area (DeCandia et al., 2019), some carnivores, have adapted to high levels of habitat fragmentation by using developed areas as corridors for movement (Tigas et al., 2002; Atwood et al., 2004; Way et al., 2004; Stark et al., 2020). Moreover, my findings lend support to the urban refugia hypothesis, which suggests that urban greenspaces surrounded by highly developed areas serve as shelter for animals, and lead to higher occupancies (Haffer, 1969; Stark et al., 2020).

Second, habitat heterogeneity was a significant predictor of coyote occupancy during the pup-rearing seasons, but not during the non-pup-rearing seasons. During the pup-rearing seasons, coyote occupancy was higher in more heterogeneous habitats than less heterogeneous habitats. This result suggests that heterogeneous habitats are more suitable locations for coyote dens, and that heterogeneous habitats provide better shelter and more cover for coyote pups (Grinder and Krausman, 2001; Atwood, 2006; Dodge and Kashian, 2013). Additionally, coyotes have been found to exploit heterogeneous habitats to improve their foraging efforts (Gese et al., 2012), especially during pup-rearing seasons where coyotes acquire food and resources needed for their pups (Way et al., 2004; Lombardi et al., 2017; Poessel et al., 2014, 2017).

Third, during the pup-rearing seasons, coyote occupancy was higher in greenspaces with higher human population densities, but not during the non-pup-rearing seasons. This result is somewhat counterintuitive; however, I also found that coyote detection probability was higher in habitats with relatively low human population densities. Therefore, while coyotes are more likely to be detected in habitats with low human population densities, they are still more likely to be

found in habitats with high human population densities, specifically during the pup-rearing seasons. This suggests that coyotes make use of habitats surrounded by low human population densities more often, but still regularly utilize more densely populated areas, possibly for anthropogenic food resources (Gehrt et al., 2009). Indeed, coyotes have been found to take advantage of human resources when needed, especially if there is enough surrounding forest cover for shelter and protection (Atwood et al., 2004; Gehrt et al., 2009). Coyotes also exploit habitats that have high surrounding human population densities, but not necessarily high human activity (Boone et al., 2008; Gallo et al., 2017). Many of my study sites were situated in golf courses, cemeteries, and parks that have limited-use-hours. Previous studies have found that coyotes tend to occupy golf courses and cemeteries due to their semi-natural landscape and decreased human activity at night (Boone et al., 2008; Dodge and Kashian, 2013; Gallo et al., 2017).

Fourth, habitat heterogeneity was a significant predictor of coyote detection probability, but the response was opposite when comparing non-pup-rearing and pup-rearing seasons. Specifically, coyote detection probability was higher in less heterogeneous habitats during the pup-rearing seasons and in more heterogeneous habitats during the non-pup-rearing seasons. This finding contradicts previous research that found that during the pup-rearing season, coyotes tend to select for more heterogeneous habitats because they provide more forest cover for protection and an abundance of resources (Gehrt et al., 2009; Poessel et al., 2014). However, coyotes in the current study were more likely to occupy heterogeneous habitats during the pup-rearing seasons. Moreover, coyotes are known to move less during the pup-rearing season as they spend considerable time guarding their dens (Harrison and Gilbert, 1985; Mastro et al., 2012). This might explain why they were more likely to be found in a heterogeneous habitat, but less likely to

be detected by my cameras. Additionally, it is important to note that between one-third and one-half of urban coyotes are typically solitary animals, and that these individuals tend to travel over large ranges and exploit a variety of habitat types (Grinder and Krausman, 2001; Way et al., 2002; Gehrt and McGraw, 2007).

Finally, coyote detection probability was higher in greenspaces with smaller patch areas during the non-pup-rearing seasons and in greenspaces with larger patch areas during the pup-rearing seasons. Because smaller mammals tend to occupy small patch areas (Crooks and Soulé, 1999; Vanek et al., 2020), the availability of prey might explain why coyotes venture into greenspaces with smaller patch areas during the non-pup-rearing seasons. However, my finding that coyotes were detected more often in greenspaces with larger patch areas during the pup-rearing seasons, suggests that these habitats provide more cover and protection than more patchy greenspaces (Atwood, 2006; Kenaga et al., 2013; Cherry et al., 2016). My results are also consistent with previous literature that have noted higher detection probability in larger patch areas than smaller patch areas (Crooks and Soulé, 1999; Lombardi et al., 2017). Overall, these findings suggest that during the non-pup-rearing season, coyotes exploit habitats based on food availability, but during the pup rearing season, coyotes must balance between foraging and the protection of their pups.

Coyote occupancy is influenced by biogeographical barriers

One of the strongest predictors of coyote occupancy was biogeographical barriers to dispersal. Specifically, coyote occupancy was significantly higher on the continent (Bronx/Westchester) than on the islands, including Long Island. This finding suggests that biogeographical barriers, such as the Long Island Sound and heavily trafficked bridges, continue

to hinder the expansion of coyotes (Weckel et al., 2015; Nagy et al., 2016; Ali and Vences, 2019). However, in the present study, coyotes were found in three of 16 Long Island sites, suggesting that at least some coyotes are either swimming across waterways or crossing major bridges, making the difficult journey to new habitats (Nagy et al., 2016; Henger et al., 2019). During the present study, there were no pups identified in any of the greenspaces in Long Island, aside from the ones located at the Elmjack Ingrams site that were culled in 2017 (Nagy et al., 2017). These findings suggest that solitary coyotes, most likely males, are making the long trek to Long Island. However, it is probably only a matter of time before Long Island harbors significant breeding populations (Weckel et al., 2015; Nagy et al., 2017).

Free-ranging cat occupancy and detection probability are influenced by anthropogenic factors

Consistent with my hypothesis that free-ranging cats are attracted to urbanized habitats, I found that both occupancy and detection probability were higher in greenspaces with smaller patch areas, and that free-ranging cat occupancy was higher in human-altered habitats. My first finding, higher cat distribution in smaller patch areas, is supported by previous studies that have shown that cats tend to select smaller habitat patches, probably because these greenspaces are less likely to support larger carnivores (Crooks, 2002; Schwenk, 2014; LeFlore et al., 2019). Hence, considering that large carnivores are less likely to occupy these smaller patches, cats may roam freely without the threat of being preyed upon (Crooks and Soulé, 1999; Vanek et al., 2020).

My second finding, higher cat occupancy in human-altered habitats, is also consistent with the literature (e.g., Baker et al., 2005; Sims et al. 2007; Thomas et al., 2012; Vanek et al., 2020). Free-ranging cats have a long-standing relationship with humans (Kays and DeWan,

2004; Thomas et al., 2012; Cove et al., 2017; Casteñada et al., 2018), and as generalists, cats take advantage of readily available and abundant food resources found in human-altered environments (e.g., mice, birds, human garbage) (Contesse et al., 2004; Tennent and Downs, 2008; Flockhart et al., 2016). In support of my findings, previous studies have found that free-ranging cat populations tend to be considerably larger in more urbanized areas (Turner and Bateson, 2000; Tennent and Downs, 2008). Therefore, my results lend support to the hypothesis that free-ranging cats depend on human-altered habitats for food resources and protection from predation (Horn et al., 2011; Flockhart et al., 2016; Cove et al., 2017)

However, contrary to my hypothesis that free-ranging cats are most attracted to urbanized habitats, I found that free-ranging cat occupancy and detection probability were higher in greenspaces with less surrounding developed land cover, and that detection probability was higher in areas with lower human population densities. Moreover, while free-ranging cats in the current study were more likely to occupy human-altered habitats, they were also more likely to be detected in urban natural habitats, which suggests that urban natural habitats in the New York metropolitan area might resemble human-altered habitats of less densely populated cities (DeCandia et al., 2019). Collectively, these findings contradict previous studies that have found higher cat occupancy and detection probability in greenspaces with more surrounding development (Ogan and Jurek, 1997; Tennent and Downs, 2008; Casteñada et al., 2018) and in areas with more human population and housing density (Baker et al., 2005; Sims et al. 2007; Thomas et al., 2012; Vanek et al., 2020). Overall, these inconsistencies might be attributed to the uniqueness of the New York metropolitan area, the most densely populated city in the United States (DeCandia et al., 2019; Henger et al., 2019; United States Census Bureau, 2021; New York City Department of City Planning, 2022). While there have been several studies

documenting the impact of urbanization on free-ranging cat distribution (Shargo, 1988; Adkins and Stott, 1998; Tigas et al., 2002; Riley et al., 2003; Morey et al., 2007; Gehrt et al., 2009, 2011, 2012, 2013; Gese et al., 2012; Hennessy et al., 2012), none of these “urban” areas exhibit the scale of human population and housing density of the New York metropolitan area. Hence, in a “super-urban” center like the New York metropolitan area (Ellis and Weiss, 2018; DeCandia et al., 2019), there might be an urbanization threshold in which extreme development and human population density are no longer suitable habitat for free-ranging cats.

Free-ranging cat detection probability is influenced by the presence or absence of coyotes

In support of the mesopredator release hypothesis (Soulé et al., 1988), free-ranging cat detection probability was lower in habitats where coyotes were present than in habitats where coyotes were absent. This result suggests that the expansion of coyotes into the New York metropolitan area in recent decades is having an impact on free-ranging cat behavior, and that coyotes might be occupying an ecological niche historically occupied by apex predators (Estes, 1996; Crooks and Soulé, 1999; Gehrt and McGraw, 2007). While this is the first documentation of coyotes influencing the activity and behavior of free-ranging cats in the New York metropolitan area, research in other urban centers have found that coyotes limit the distribution of free-ranging cats either spatially, temporally, or both (Crooks, 2002; Kays and DeWan, 2004; Gehrt et al., 2009, 2011, 2013; Kays et al., 2015; Vanek et al., 2020). As coyotes continue their expansion into Long Island, their presence might have yet-to-be-determined trophic impacts. Notably, if the expansion of coyotes limits free-ranging cat distribution, this might result in indirect ecological effects, potentially impacting avian and small mammal populations (Crooks and Soulé, 1999; Sims et al., 2007; Gehrt et al., 2013; Weckel et al., 2015; Cove et al., 2017).

Limitations

While my research has provided insights regarding how anthropogenic, biogeographical, and ecological variables influence coyote and free-ranging cat occupancy and detection probability, I recognize that there are some limitations to this study. First, considering that coyotes and cats were not trapped or tagged, and that I relied only on camera evidence, I was unable to distinguish individual animals. Therefore, it is hard to distinguish between many photographs of the same individual coyote or cat at a site versus multiple individuals. Second, relationships between occupancy and covariates can be interpreted as habitat selection or habitat suitability, but there is no difference in these model predictions from a park that had a single coyote versus a site that supports a pack since both are modeled as “occupied”, even though the latter likely has better habitat overall. Similarly, patterns regarding detection rates associated with covariates are difficult to interpret. For example, I observed lower detection of cats at camera sites that also photographed coyotes. This was interpreted as a change in cat activity around the cameras due to the presence of coyotes, but I cannot say specifically that this was due to fewer cats in the area or that cats used the area differently, or both. Third, I was unable to estimate the ranging behavior of individual coyotes and free-ranging cats, which would have been useful for comparing differences in spatial distribution. Future research using mark-recapture techniques (Ekernas and Mertes, 2006; Lewis et al., 2015; Lombardi et al., 2017) and radio-tracking collars (Gibeau, 1998; Tigas et al., 2002; Riley et al., 2003; Gehrt et al., 2009; Mastro et al., 2012; Sugden et al., 2021) to identify and track individuals can discern more detailed interactions, where the density of these species can be compared across space and time rather than merely using a binary (occupied versus not occupied states). Finally, in terms of the camera traps, some sites did not allow for deployment across all five years of the study and

cameras were not always deployed evenly throughout the parks due to theft, vandalism, legal ramifications, and logistical reasons. While I included cameras per km² in my models to control for variation in camera deployment, the study would have benefitted if cameras had been deployed more proportionally across all greenspaces.

Conclusions and Future Directions

I found that coyotes and free-ranging cats make use of many of the greenspaces in the most heavily urbanized region of the United States: the New York metropolitan area. My findings indicate that both coyote and free-ranging cat distribution are influenced by several anthropogenic variables, including human population density, patch area, habitat type, fine-scale habitat heterogeneity, and percent developed land cover, but not always in the direction predicted by urban ecologists. For example, contrary to my predictions, coyotes exhibited higher occupancy in greenspaces surrounded by more developed land cover whereas free-ranging cats exhibited higher occupancy in greenspaces surrounded by less developed land cover, which suggests that “super-urban” centers like the New York metropolitan have a complex influence on mesocarnivore distribution that is probably mediated by impervious surface cover and human population density as well as spatiotemporal patterns of human activity (Greenspan et al., 2018). For example, in the current study, both coyotes and free-ranging cats were more likely to be detected in greenspaces surrounded by low human population densities. Furthermore, coyotes and free-ranging cats were more likely to occupy, but less likely to be detected, in human-altered habitats than urban natural habitats. These findings suggest that in urban habitats, anthropogenic food sources are an important driver of mesocarnivore distribution (Bateman and Fleming, 2012; Parsons et al., 2018; Brooks et al., 2020). While coyotes and free-ranging cats were influenced

by some of the same anthropogenic variables and occupied some of the same habitats, I also found that free-ranging cats largely avoid coyotes. In support of the mesopredator release hypothesis (Soulé et al., 1988), free-ranging cat detection probability was significantly lower in habitats where coyotes were present than in habitats where coyotes were absent. Finally, biogeographical variables, including major bodies of water and heavily trafficked bridges, continue to limit coyote dispersal into islands, but had no significant impact on free-ranging cat distribution, likely because their distribution is governed by where people have brought and released them. As coyotes continue to expand their range, the collection of baseline data in habitats unoccupied by coyotes, including the documentation of avian and mammalian community composition, will allow for a natural experiment in which we can compare communities before and after the expansion of coyotes into new habitats (Weckel et al., 2015). With that in mind, I suggest that urban ecologists establish ecological studies further onto Long Island, especially Nassau and Suffolk counties, to allow for baseline data of animal communities before the apparent inevitable establishment of coyotes.

Footnotes

1. <https://www.unitedstateszipcodes.org/>
2. <https://www.google.com/maps>
3. <https://www.mrlc.gov/data/legends/national-land-cover-database-2019-nlcd2019-legend>
4. <https://www.R-project.org/>.

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