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Urban forests sustain diverse carrion beetle assemblages in the New York City metropolitan area

Nicole A. Fusco[1], Anthony Zhao[2] and Jason Munshi-South[1,*]

[1]Louis Calder Center – Biological Field Station, Fordham University, 31 Whippoorwill Road, Armonk, NY 10504, USA.
[2]Department of Entomology, University of Maryland, College Park, MD 20742, USA.

*Corresponding author:
Jason Munshi-South
Louis Calder Center, Fordham University, 31 Whippoorwill Road, Armonk, NY 10504 USA
jmunshisouth@fordham.edu
Phone: (914) 273-3078 x20

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Abstract

Urbanization is an increasingly pervasive form of land transformation that reduces biodiversity of many taxonomic groups. Beetles (Order: Coleoptera) exhibit a broad range of responses to urbanization, likely due to the high functional diversity in this order. Carrion beetles (Family: Silphidae) provide an important ecosystem service by promoting decomposition of small-bodied carcasses, and have previously been found to decline due to forest fragmentation caused by urbanization. However, New York City (NYC) and many other cities have fairly large continuous forest patches that support dense populations of small mammals, and thus may harbor relatively robust carrion beetle communities in city parks. In this study, we investigate carrion beetle community composition, abundance and diversity in forest patches along an urban-to-rural gradient spanning the urban core (Central Park, NYC) to outlying rural areas. Additionally, we conducted a more in-depth study of the carrion beetle community at a single suburban site in Westchester County, NY that was intensively surveyed in the early 1970’s. We collected a total of 2,170 carrion beetles from eight species at 13 sites along this gradient. We report little to no effect of urbanization on carrion beetle diversity, although two species were not detected in any urban parks. *Nicrophorus tomentosus* was the most abundant species at all sites and seemed to dominate the urban communities, potentially due to its generalist habits and shallower burying depth. Variation between species in body size, habitat specialization, and area of largest continuous forest tract also did not influence carrion beetle communities. Lastly, we found few significant differences between 10 carrion beetle relative abundance between the early 1970’s and 2015 at a single site in Westchester County, NY, although two of the rare species in the early 1970’s were not detected in 2015. These results indicate that NYC’s forested parks have the potential to sustain carrion beetle communities and the ecosystem services they provide.

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Introduction

The ecological influence of urbanization is increasingly pervasive around the world. In 2014, 54% of the world's human population resided in urban areas (United Nations 2014) and urban populations increased by 12% between 2000 and 2010 in the United States (U.S. Census Bureau 2010). Urban landscapes are highly modified for human use, with natural habitats typically occurring only in small, fragmented patches (Saunders, et al. 1991). Fragmentation in cities often decreases species richness, changes community composition, and alters ecosystem processes (Didham 2010). Many species are impacted negatively by urbanization (*carnivores*- Ordeñana, et al. 2010; *arthropods*- Sattler, et al. 2010; *amphibians*- Hamer and Parris 2011; *birds & plants*- Aronson, et al. 2013), but effects vary based on the taxonomic group in question (McKinney 2008). For example, studies of arthropod diversity along urban-to-rural gradients have documented a wide variety of responses to urbanization (Hornung, et al. 2007; Niemelä and Kotze 2009; Varet, et al. 2011; Magura, et al. 2013; Savage, et al. 2015; Diamond, et al., 2015). Given the extreme variety of life history traits and habitat use among arthropods, responses to urbanization may be difficult to predict.

Carrion beetles use small mammal carcasses as food sources for their young (Scott 1998). These beetles bury carcasses to avoid competition with other scavengers, thus facilitating decomposition and providing considerable ecosystem services. Availability of carrion likely influences the abundance and diversity of carrion beetles. Carrion beetle species compete with each other as well as with other scavenging vertebrates (Scott 1998; Trumbo and Bloch 2002;

DeVault, et al. 2010), and invertebrates for this resource (Ratcliffe 1996; Gibbs and Stanton 2001). Urbanization alters natural habitats in myriad ways (Grimm, et al. 2008) that may cause local extirpations or reduced abundance of small mammals (e.g. likely carrion) and carrion beetles in cities.

Gibbs and Stanton (2001) previously reported that forest fragmentation reduced carrion beetle species richness and abundance in Syracuse, New York. Beetles that persisted in these fragments were primarily small-bodied habitat generalists, and other carrion beetles may have declined in abundance due to lower carcass availability, increased prevalence of other scavengers, or reduced soil and litter quality. Wolf and Gibbs (2004) also found that forest fragmentation decreased carrion beetle diversity and abundance in Baltimore, Maryland. They argued that forest contiguity was an important factor affecting richness, abundance, and diversity of carrion beetles in this city. However, these studies did not directly address whether large parks within core urban areas harbor a substantial diversity of carrion beetles.

In this study we investigated species richness, diversity, relative abundance and community similarity of carrion beetles (Family: Silphidae) across an urban-to-rural gradient in the New York City (NYC) metropolitan area. NYC is the most densely populated area in North America, but 20% of the city's land area is comprised of vegetated natural areas, particularly within several large urban parks. These parks are characterized by substantial forest cover and high densities of small mammals (Munshi-South and Kharchenko 2010), and thus may provide high-quality habitat for a diverse assemblage of carrion beetles. Alternatively, NYC's urban forests may harbor less carrion beetle diversity relative to suburban and rural areas outside of NYC as was found in Baltimore and Syracuse (Gibbs and Stanton 2001; Wolf & Gibbs 2004). We also compared historical records from a single site (Pirone 1974), the Louis Calder Center in

Armonk, New York, with our 2015 estimates of carrion beetle diversity and abundance to examine changes over the last four decades. The forest area at the Louis Calder Center has not changed in that time, but urbanization of the surrounding area and a rapid increase in deer herbivory may have resulted in altered diversity of community composition of carrion beetles.

Urban forests have the potential to harbor substantial biodiversity in cities worldwide (Faeth, et al. 2011; Elmqvist, et al. 2013; La Sorte, et al. 2014; Aronson, et al. 2014). Diamond, et al. (2015) argued that increases in biodiversity may be due to introduction of non-native species as well as increased habitat heterogeneity in densely populated areas, but many native species still persist in these urban remnants. Urban carrion beetle diversity that rivals surrounding rural areas would indicate that urban forests in NYC are currently undervalued as reservoirs of arthropod biodiversity.

Materials & Methods

Study site and sampling techniques

This study was conducted across an urban-to-rural gradient spanning 120 km from the urban core of NYC (Central Park, Manhattan) to southern New York State and western Connecticut. Carrion beetles were collected from five urban sites in New York City, five suburban sites and three rural sites (Table 1, Figure 1). Urban, suburban and rural site classifications followed Munshi-South et al. (2016) and were based on percent impervious surface cover. Many of our sampling sites were previously used by Munshi-South et al. (2016) to examine population genomics of white-footed mice (*Peromyscus leucopus*) and thus classifications were already available. For sites unique to this study, we used the same methods to quantify urbanization (Table 1, Figure 1). In brief, we created 2 km boundary buffers around our study sites in ArcGIS 10.3 (ESRI, 2014) and then used zonal statistics to calculate mean percent impervious surface from the Percent Developed Imperviousness data layer imported from the National Land Cover Database 2011 (Xian, et al. 2011).

For comparison with previous carrion beetle surveys in other cities, we followed the sampling methods employed in Gibbs and Stanton (2001) and Wolf and Gibbs (2004). We constructed traps from open-topped cylinders by cutting the top off 1 L plastic bottles, adding a loop of string to hang the trap, and attaching a rain cover (cardboard covered in plastic cling wrap) by threading it through the string. Most traps contained 200 mL of a 1:1 mixture of ethylene glycol and water, although soapy water was substituted at the Manhattan sites due to public safety regulations. A small glass jar containing bait (~6.5 cm^2 of rotting chicken thigh) was topped with a punctured lid to prevent insects from destroying the bait but permitting odors to attract carrion beetles. This jar was placed inside each plastic trap that was then filled with the ethylene glycol mixture. We set three traps at each site, close to forest edges and at least 100 m apart. Traps were hung from small tree branches approximately 1-1.5 m from the ground to prevent other wildlife from disturbing the traps. Traps were set out for seven consecutive days at each site, where beetles were collected upon the last day. We conducted all trapping from 22 June to 05 August 2015. At each study location, we separated beetles from other insects, and stored beetles in 80% ethanol before bringing all specimens to the laboratory for identification. We identified all carrion beetles species following Hanley and Cuthrell (2008). After collection, all beetles were stored in ethanol at -20 °C. Permission to collect carrion beetles was granted by the New York City Department of Parks and Recreation, the Rockefeller State Park Preserve, and the Connecticut Department of Energy and Environmental Protection.

Relative abundance at urban, suburban and rural sites

To explore the overall association of site classification (urban, suburban, rural) and species identity (beetle species names; Table 2) with total relative abundance we performed two separate one-way ANOVA analyses and calculated post hoc comparisons using Tukey's HSD (Sokal and Rohlf 2011). To summarize this variation we calculated the relative proportion of each species sampled for the entire study across the three habitat classes: urban, suburban, and rural.

To examine changes over the summer season in carrion beetle diversity and abundance at the Louis Calder Center (a suburban site), we conducted three separate trapping surveys, from 22-29 June, 14-21 July, and 22-29 July 2015. Only data collected from the third survey were used in the main urban-to-rural analysis. We calculated the relative proportion of each species for each of the three surveys at the Louis Calder Center to examine changes throughout the study period.

Historical comparison of carrion beetle presence and abundance

Data from all three surveys at the Louis Calder Center site were used to compare the current carrion beetle species (2015) with historical data collected in the 1970's (Pirone 1974). A student's t-test was conducted to compare total relative abundance in 1970 to 2015 (Sokal and Rohlf 2011).

Species diversity and species richness along an urban-to-rural gradient

For the analysis along the urban-to-rural gradient we used two different measures; species richness and species diversity. To compare species diversity across sites, we calculated the

Simpson's reciprocal index (1/D; Simpson 1949) of diversity. We then calculated community similarity using the Jaccard Index of community similarity (Jaccard, 1901):

$$CC_J = S_J = a / (a + b + c),$$

where S_J is the Jaccard similarity coefficient, a is the number of species shared by all sites, b is the number of species unique to the first site, and c is the number of species unique to the second site. Then we calculated the Jaccard coefficient of community similarity for all the data pooled across sites classes (urban, suburban and rural) to analyze overall carrion beetle community assemblages.

To examine the influence of urbanization on species richness and diversity, we calculated general linear regressions of mean percent impervious cover versus species richness and species diversity at each site using R v.3.2.3 (R Core Team 2015). Additionally, we performed a gradient analysis by creating a Non-metric Multidimensional Scaling (NMDS) plot using the Vegan package (Oksanen, et al. 2016) in R to investigate population dissimilarity based on site class (urban, suburban, and rural). NMDS compares species changes from one community to the next by using rank order comparison and calculates the pairwise dissimilarity of points in low-dimensional space (Buttigieg and Ramette 2014). Thus, NMDS allows us rto obustly estimate dissimilarity between site locations based on the type of site and the species located in each site.

Species-specific differences compared across urban, suburban, and rural sites.

Many studies on beetles have focused on specific characteristics that may underlie differences in species richness and diversity within sites and across studies (Davies, et al. 2000). We conducted a factorial ANOVA to examine the interaction effect of species body size (small < 5 mm, medium = 5-6.5 mm, large > 6.5 mm; estimations based on data from Gibbs and Stanton

2001) and site classification (urban suburban, rural) based on mean relative abundance. We also used a student's t-test to examine mean relative abundance when species are classified as habitat generalists versus habitat specialists (Gibbs and Stanton 2001). Lastly, we performed a general linear regression to explore if a relationship exists between species richness or species diversity and the area of the largest continuous forest tracts (km^2) existing at each site (Sokal and Rohlf 2011). At each site the largest continuous forest area encompassing at least one trap was measured using ArcGIS 10.3 (ESRI 2014)..

Results

Relative abundance at urban, suburban and rural sites

We collected a total of 2,170 carrion beetles comprising eight Silphid species, (Table 2) across all sites (Table 1, Figure 1). There was no significant difference in the mean relative abundance of all species across urban, suburban and rural site classes, ($F_{2,96}$=0.23, p=0.80; Figure S1). There was a significant difference in relative abundance between different species across all sites, ($F_{7,16}$=19.92, p<0.0001), where the mean relative abundance of *Nicrophorus tomentosus* was significantly greater than all other species (p<0.0001; Figure S2) across all sites, accounting for 56.8% of all beetles captured (Figure 2A). Other species also varied in presence or abundance between urban, suburban and rural forests (Figure 2A); specifically, *Oiceoptoma noveboracense* was captured more often in urban and suburban areas (21.9% and 23.5% of the total samples, respectively) than at rural sites (1.6%), whereas *Nicrophorus defodiens* was captured predominantly in rural areas (7.1% versus 0.3% in urban areas and 0.2% in suburban areas). Similarly, *Necrophila americana* was recorded in suburban and rural areas (8.4% and 4.3% of the total sample, respectively) but was not found in any urban sites. *Nicrophorus sayi*

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was only recorded at one rural park, accounting for 1.4% of the total number of beetles captured at rural sites (Table, 1, 2, and Figure 2A).

We captured 358 individuals (including all species) across the three surveys at the Louis Calder Center in Summer 2015. *Ni. tomentosus* became more prevalent (34.4%, 54.5%, 74.0% of the total sample from the three surveys) throughout the Summer and *O. noveboracense* decreased in relative abundance. We did not capture *Ne. americana* or *Nicrophorus pustulatus* during the first survey (Figure 2B).

Historical comparison of carrion beetle presence and abundance

Compared to data collected at the Louis Calder Center in 1974 (Pirone 1974), 2015 data show an increase (5.8% to 54.3% in 1974 vs 2015) in the relative abundance of *Ni. tomentosus*, and a decrease in relative abundance of *Ne. americana* (41.8% to 6.7%) and *O. noveboracense* (38% to 21.9%) since 1974. *Ni. defodiens* and *Ni. sayi* were absent from both studies at this site. Two species were not captured in 2015 that were already low in relative abundance in 1974, *Necrodes surinamensis* (0.2%) and *Necrophilus pettiti* (0.3%; Figure 2C).

Species diversity and species richness along an urban-to-rural gradient

Across the urban-to-rural gradient there was no significant relationship between mean percent impervious surface of a site and carrion beetle species richness ($R^2 = 0.028$, $p > 0.05$; Figure 3A) or species diversity ($R^2 = 0.0213$, $p > 0.05$; Figure 3B). However, NMDS ordination plots exhibit dissimilarity in carrion beetle assemblages in rural and urban sites. NMDS also showed that beetle assemblages in suburban sites were more similar to those in the urban sites.

Based on the size of the convex hulls, heterogeneity of carrion beetle species composition was the greatest for suburban sites and least for urban sites (Figure 4).

We observed relatively high community similarity indices across most pairwise comparisons (CC*j* = 0.333-1.000; Table 3). Several pairs of nearby sites had very high community similarity, such as two urban sites: Inwood Hill Park and New York Botanical Garden (CC*j*= 1.000); and two suburban sites: Convent of the Sacred Heart School and Louis Calder Center (CC*j* = 1.000). The most distant pairs of sites were less similar, most notably between highly urbanized Central Park and rural Clarence Fahnestock State Park (CCj = 0.333). The pooled urban carrion beetle community was found to be more similar to the pooled suburban community (CC*j* = 0.857) than to the pooled rural community (CC*j* = 0.750), as also demonstrated in the NMDS ordination (Figure 4). The pooled rural community was equally similar to both the pooled urban and suburban communities (CC*j* = 0.750; Table 4).

Species-specific differences compared across urban, suburban, and rural sites.

We found no significant effect between beetle body size and site class (urban, suburban, rural) for relative abundance of carrion beetle species in this study (Table S1). Additionally, when focusing on habitat specialization, we also found no significant difference in habitat specialization between urban, suburban, and rural sites (Table S2). Lastly, we found no trend in species richness (Figure S3) or species diversity (Figure S4) across increasing continuous forest areas throughout sampled sites.

Discussion

Contrary to our predictions, we observed few differences in beetle diversity or richness along an urban-to-rural gradient in the NYC metropolitan area. Along this gradient, urban and suburban sites were nearly equally diverse and species-rich as rural sites. We also detected little to no influence of urbanization (measured by mean percent impervious surface) on relative species abundance, species diversity or species richness of carrion beetles throughout these sites (Figure 3A, 3B). Additionally, we observed relatively high carrion beetle community similarity values between most pairs of sites in this study regardless of their urbanization status (Jaccard Index= 0.333-1.000; Table 3). Overall, this study demonstrates that a diverse community of carrion beetles are able to thrive in rural, suburban and urban forests in and around New York City. Gibbs and Stanton (2001) and Wolf and Gibbs (2004) reported that carrion beetle diversity is significantly reduced around Syracuse, NY and Baltimore, MD due to forest fragmentation associated with urbanization, but our results indicate that forested city parks in the most urbanized areas of North America (i.e. Manhattan and the Bronx, NYC) do harbor substantial carrion beetle diversity. We did not directly examine variation in fragment size within urban, suburban, and rural areas, but the discrepancy between these earlier results and ours may be due to the fact that urban forests in NYC parks are relatively large compared to other cities.

Arthropods have exhibited highly variable, even dichotomous, responses to urbanization around the world (Lessard and Buddle 2005; Sattler, et al., 2010). Other studies show that the influence of urbanization varies based on taxonomic group, geographic location, climate and spatial scale (McKinney 2008; Kotze, et al. 2011, Martinson and Raupp 2013). Carabid beetles are the most well-studied arthropod group: carabid species richness has been found to decrease (Gaublomme, et al. 2008) or not change (Dieschel 2006) in urban areas. In a meta-analysis of carabids and urbanization, Magura, et al. (2010) argued that this variation was due to site-specific effects operating in each study. Urbanization did not homogenize carabid assemblages in cites in England, Denmark, and Helsinki, Finland, but urbanization did affect species assemblages in other Finnish cities, Hungary, Japan and Bulgaria (Kotze, et al. 2011). Other than location, discrepancies across studies may be related to the choice of variables for analysis. Differing climates, different measures of urbanization (e.g. human population density, economics, housing density, or impervious surface), different times of the year studies were conducted, and spatial scale (Faeth, et al. 2011) all could affect species presence, richness, and diversity results in urban areas. These factors may also explain some of the differences between the NYC results presented here, and those of Gibbs and Stanton (2001) and Wolf and Gibbs (2004) for Syracuse, NY and Baltimore, MD.

When quantifying and classifying urbanization, many studies use measures based on forest fragmentation, extent of forest cover, isolation caused by human-induced disturbance, impervious surface, or human population density (Macdonnell and Hahs 2008). The use of a common index to represent urbanization is necessary to compare results across studies, but there are no common indices currently in wide use. Macdonnell and Hahs (2008) and Kotze, et al. (2011) stress the need for such common measures to examine the generality the influence of urbanization on biodiversity patterns. Comparing our study to other carrion beetle studies, we used mean percent impervious surface to quantify urbanization, whereas Gibbs and Stanton (2001), Wolf and Gibbs (2004) and Klein (1989) utilized continuous forest cover and fragmentation to classify the level of urbanization at each site. Our study specifically quantified urbanization with mean percent impervious surface using 2 km buffers as was previously reported by Munshi-South, et al. (2016) for many of the same study sites. Although many metrics can be employed to measure urbanization, we believe that impervious surface cover is particularly useful for urban-to-rural gradient studies because it is measurable for nearly any terrestrial area and directly related to urban landscape modification.

We also examined species abundance changes over three sampling periods at a suburban site: the Louis Calder Center in Westchester County, NY. Despite no significant change in total abundance across samples throughout the summer season, we did see slight changes in species abundance over different collection periods (Figure 2B). In comparison to Wolf and Gibbs (2004) our study showed opposite trends in species presence across the collection period. This difference could be due to difference in climate and temperature across June, July, and August in NYC versus the more southern Baltimore, MD. In Armonk, NY, *Ni. tomentosus*, *O. noveboracense,* and *Oiceoptoma inaequale* were more abundant later in the summer, and *Ni. orbicollis* was more abundant earlier in the summer. Scott (1998) describes *Ni. tomentosus* as a late summer / early fall breeder, which was corroborated by our observation that *Ni. tomentosus* was most abundant in the latest summer survey. *Ni. orbicollis* begins breeding in late spring (Ratcliffe 1996), and was the most abundant in our first sample session at this site. *Ni. sayi* is most active in very early spring, which may explain the absence of this species at this site during the Summer. Lastly, the absence of *Ni. pustulatus* may be due to their habitat preference for = wetlands (Gibbs and Stanton 2001), which were not very extensive close to our trap sites in this study.

Species richness of carrion beetles generally did not differ between 1970 and 2015 at the Louis Calder Center site. However, we did record pronounced species-specific differences in abundance between the past study (Pirone 1974) and this current study in 2015 (Figure 2C). Species differences over time could be due to anthropogenic modification of the landscape in and around the Louis Calder Center site since the early 1970s. There was an increase in human population density in the town of North Castle, NY in Westchester County from 9,591 (1970) to 11,841 (2010) according to the Decennial Census 1950-2010 (U.S Census Bureau, 2010). An increase in population density often results in construction of more housing and roads and subsequent fragmentation of forests, which could alter current species assemblages. We identified the most drastic change in relative abundance over time for 3 species; *Ni. tomentosus*, *O. noveboracense* and *Ne. americana* (Figure 2C). In contrast, relative abundance of *Ni. tomentosus* increased, which could be due to the fact that this species is an ecological generalist that becomes more common after habitat degradation. There was a substantial decrease in *O. noveboracense* since 1974, perhaps due to its univoltine nature and inability to effectively compete with multivoltine species (Kotze, et al. 2011), as well as its limited dispersal ability in warmer temperatures (Ratcliffe 1996). Lastly, the most drastic decline was in *Ne. americana*, which is perhaps due to its large body size (smaller bodied generalists can survive in more disturbed habitat; Gibbs and Stanton 2001) and its preference for field habitat (Ratcliffe 1996), which may be more limited in the area in 2015 due to fragmentation and the reduction in agriculture. Two previously-observed species, *Necrodes surinamensis* and *Necrophilus pettiti,* were completely absent in our contemporary sample. *Ne. surinamensis* is nocturnal and highly attracted to artificial lights, causing Ratcliffe (1998) to state concern for this species in cities where increased nocturnal lighting is common. This may be the reason for the decrease or even the extirpation of this species at this site. As for *Ne. pettiti*, it is a flightless carrion beetle species (Peck 1991), possibly limiting its dispersal and survivability in increasingly urbanized areas.

In their study, Gibbs and Stanton (2001) discuss several ecological factors that may influence the presence and relative abundance of carrion beetles in urban areas. The first limiting factor is the availability of carcasses. However, urbanization can lead to an increase in abundance of some birds and small mammals (Faeth, et al. 2011; Pickett, et al. 2011). Forests in New York City typically contain large rodent populations (particularly white-footed mice and chipmunks), as well as abundant songbird populations (Ekernas and Mertes 2006; Seewagen and Slayton 2008). Availability of bird and small mammal carcasses in urban parks may be higher than previously appreciated, and may explain the abundance of some generalist species (*Ni. tomentosus*) in NYC.

Competition with scavengers may also limit carrion beetle abundance and diversity. Competitors for carrion include other invertebrates (*flies and mites*- Gibbs and Stanton 2001) and many vertebrate mesopredators that are abundant in cities (*raccoons, opossums, coyotes, skunks*- DeVault, et al. 2011). However, Suguira, et al. (2013) recently reported that resource competition between invertebrates and vertebrates for carrion was less prevalent than previously thought. Vertebrate competitors are likely present at all of our study sites but may not substantially influence carrion beetle abundance, particularly if they are utilizing food resources provided by humans in cities. As for intraspecific competition with other carrion beetle species, Scott (1998) found there to be competition between *Ni. orbicollis* and *Ni. defodiens* based on temperature. Trumbo & Bloch (2002) found that *Ni. defodiens* can locate carcasses sooner than other species, but *Ni. orbicollis* uses cues from *Ni. defodiens* to locate and subsequently dominate carrion. We identified a higher abundance of *Ni. orbicollis* than *Ni. defodiens*, especially in urban and suburban sites (Figure 2A). Greater abundance of *Ni. orbicollis* in our sites could be due to these competitive abilities that aid *Ni. orbicollis* in locating and dominating prey more effectively. Lastly, intraspecific invertebrate competitors such as flies are often very prevalent in human altered landscapes (Kavazos and Wallman 2012). Flies are known to quickly locate carcasses and may outcompete beetles on carrion (Scott 1998; Gibbs and Stanton 2001). If there is fly abundance in NYC parks, our study indicates that this intraspecific competition is not restricting beetle abundance in urban forests compared to suburban and rural forests. Some carrion beetles have also evolved adaptations to thwart fly competition. For example, *Ni. tomentosus* was the most abundant carrion beetle in urban forests in this study, and may be thriving partially due to its cooperative burying behavior rapidly conceals carcasses from flies during times of day when flies are most active (Scott, et al. 1987).

Gibbs and Stanton (2001) also identify soil compaction as a negative influence on carrion beetles in urban areas. Soil compaction is characteristic of urban forests due to trampling by humans and other factors, and may impede the ability of beetles to dig and bury carcasses in urban soils (Gibbs and Stanton 2001; Pouyat et al. 1994). The relatively shallow burying of *Ni. tomentosus* may be another factor promoting the success of this species in NYC (Figure 2A). In the study by Wolf and Gibbs (2004) they found soil compaction to not be correlated with urbanized land, but was partially correlated with forest extent. Additionally, larger forest area has been shown to support greater diversity of burying beetles (Gibbs and Stanton 2001). NYC's urban parks seem to contain sufficiently extensive tracts of forest for carrion beetles to persist despite possible soil compaction.

We found no trend in body size (as classified via Scott 1998 and Gibbs and Stanton 2001), across habitat specialization (from Gibbs and Stanton, 2001), or with continuous forest habitat area compared to abundance of species found in urban, suburban and rural sites (Supplementary Fig. 3,4,5). Our results of body size and habitat specialization were again contradictory to past burying beetle literature where Ulrich, et al. (2007) found a negative association between body size of necrophagous beetles and distance from the city center in northern Poland. Gibbs and Stanton (2001) also reported that carrion beetles thriving in urban

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areas were often small-bodied and habitat generalists. In a broader analysis of 69 beetle species, body size was not correlated with fragmentation. The relationship between extinction risk and body size may be very complex and influenced by other factors like spatial scale, population fluctuation, and longevity (Davies, et al. 2000). This complex relationship could be why we do not see a trend in body size or habitat specialization of carrion beetles in and around NYC. In general, our study shows that within NYC, urban parks are able to house nearly the same community as continuous forest tracts in the rural surrounding areas despite local impervious surface and ecological / life history variability across species. These results highlight the importance of maintaining and conserving large areas of forest throughout NYC within city parks commonly used for human recreation.

Conclusions:

Urban parks have the potential to house diverse habitats rich in biodiversity (Kotze, et al. 2011) of both plants and animals (Angold, et al. 2006). Even highly modified landscapes containing small reserves comprising ample green space have the potential to house large beetle diversity (Watts and Lariviere 2004) and high abundance of other arthropod species (Bolger, 2008; Faeth, et al. 2011). The maintenance of arthropod biodiversity in urban parks may ultimately be mediated by human influence on plant communities (Faeth, et al. 2011). Alternatively, arthropod species thriving in urban habitats may be preadapted for tolerance to fragmentation and high colonization potential (Sattler, et. al 2010). A current review on biodiversity in cities suggests that patch area and corridors have the strongest positive effect on biodiversity and that we need to maintain sites with larger than 50 hectares to prevent rapid loss of sensitive species (Beninde, et al. 2015). Maintenance of carrion beetle diversity in NYC will

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stabilize the interconnectedness of urban food webs, aid in nutrient cycling, and promote natural decomposition of carcasses (Beasley, et al. 2015) in our urban parks. Sustaining the ecosystem services provided by carrion beeltes will require conservation of large, continuous forest tracts in urban parks. Greater connectivity between small green areas, and connectivity between the urban core and surrounding forested areas will promote the biodiversity potential of small patches (Doo and Joo, 2011). A "land sparing city" approach is one way to maintain essential ecosystem services (Stott, et al. 2015) provided by carrion beetles in the New York City area.

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Tables & Figures

Table 1. Characteristics, classification and quantification of urbanization at each sample sites, along with species richness, and species diversity measures at each site (urban=orange, suburban=teal, rural=purple).

Site Code	Site Name	Site Classification	Mean % Impervious Surface	Species Richness (species number)	Species Diversity (Simpson's 1/D)
NYBG	New York Botanical Garden	Urban	60.88%	2	1.61
HBP	High Bridge Park	Urban	60.54%	6	1.84
CP	Central Park	Urban	60.24%	6	2.66
IHP	Inwood Hill Park	Urban	29.97%	6	2.94
VCP	Van Cortlandt Park	Urban	27.97%	5	2.34
SWP	Saxon Woods Park	Suburban	17.63%	5	2.37
LCC	Louis Calder Center	Suburban	10.57%	-	-
-LCC1	Louis Calder Center Sample 1	-	-	3	3.20
-LCC2	Louis Calder Center Sample 2	-	-	4	2.59
-LCC3	Louis Calder Center Sample 3	-	-	5	2.87
CSH	Convent of Sacred Heart	Suburban	11.14%	4	2.31
RSP	Rockefeller State Park	Suburban	4.74%	5	1.75
MRG	Mianus River Gorge Preserve	Suburban	0.64%	6	2.59
CT	Western Connecticut	Rural	0.89%	3	2.38
CAT	Catskills	Rural	0.46%	5	1.68
CFP	Clarence Fahnestock State Park	Rural	0.20%	4	1.77

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Table 2. Presence data for eight carrion beetle (Family: Silphidae) species ("X" indicates species is present at that site) at all site locations (site abbreviations and classification found in Table 1).

Species	***Nicrophorus orbicollis***	***Nicrophorus tomentosus***	***Nicrophorus defodiens***	***Nicrophorus pustulatus***	***Nicrophorus sayi***	***Oiceoptoma inaequale***	***Oiceoptoma noveboracense***	***Necrodes americana***
								
NYBG	X	X	X	X		X	X	
HBP	X	X				X	X	
CP		X					X	
IHP	X	X	X	X		X	X	
VCP	X	X		X		X	X	
SWP	X	X		X		X	X	
LCC	X	X					X	X
-LCC1	X	X					X	
-LCC2	X	X					X	X
-LCC3	X	X					X	X
CSH	X	X		X		X	X	
RSP	X	X	X				X	
MRG	X	X					X	X
CT	X	X					X	X
CAT	X	X					X	X
CFP	X	X		X	X		X	X

Table 3. Pairwise Jaccard community similarity index values calculated between all sample sites (site abbreviations and classification located in Table 1).

	NYBG	HBP	CP	IHP	VCP	SWP	LCC	CSH	RSP	MRG	CT	CAT	CFP
NYBG	-	0.667	0.333	1.000	0.833	0.833	0.571	0.571	0.571	0.500	0.571	0.625	0.500
HBP		-	0.500	0.667	0.800	0.800	0.500	0.500	0.500	0.750	0.500	0.750	0.429
CP			-	0.333	0.400	0.400	0.400	0.400	0.400	0.667	0.400	0.500	0.333
IHP				-	0.833	0.833	0.571	0.571	0.571	0.500	0.571	0.750	0.500
VCP					-	1.000	0.667	0.667	0.429	0.600	0.429	0.875	0.571
SWP						-	0.667	0.667	0.429	0.600	0.429	0.875	0.571
LCC							-	1.000	0.667	0.600	0.667	0.875	0.833
CSH								-	0.667	0.600	0.667	0.571	0.833
RSP									-	0.600	1.000	0.625	0.833
MRG										-	0.600	0.875	0.500
CT											-	0.875	0.600
CAT												-	0.875
CFP													-

Table 4. Pairwise Jaccard community similarity values calculated for pooled sample sites classified as urban (orange), suburban (teal) and rural (purple).

	Urban	**Suburban**	**Rural**
Urban	-	0.857	0.750
Suburban		-	0.750
Rural			-

Figure 1. Geographic location of study sites surrounded by 2 km buffer circles. Urban (orange), suburban (teal), and rural (purple) sites were classified according to impervious surface in these buffers as described in the text. Green areas represent no impervious surface, whereas areas of increasing pink coloration denote increasing percent impervious surface as reported in the 2011 National Landcover Database (Xian, et al. 2011). Site abbreviations follow Table 1.

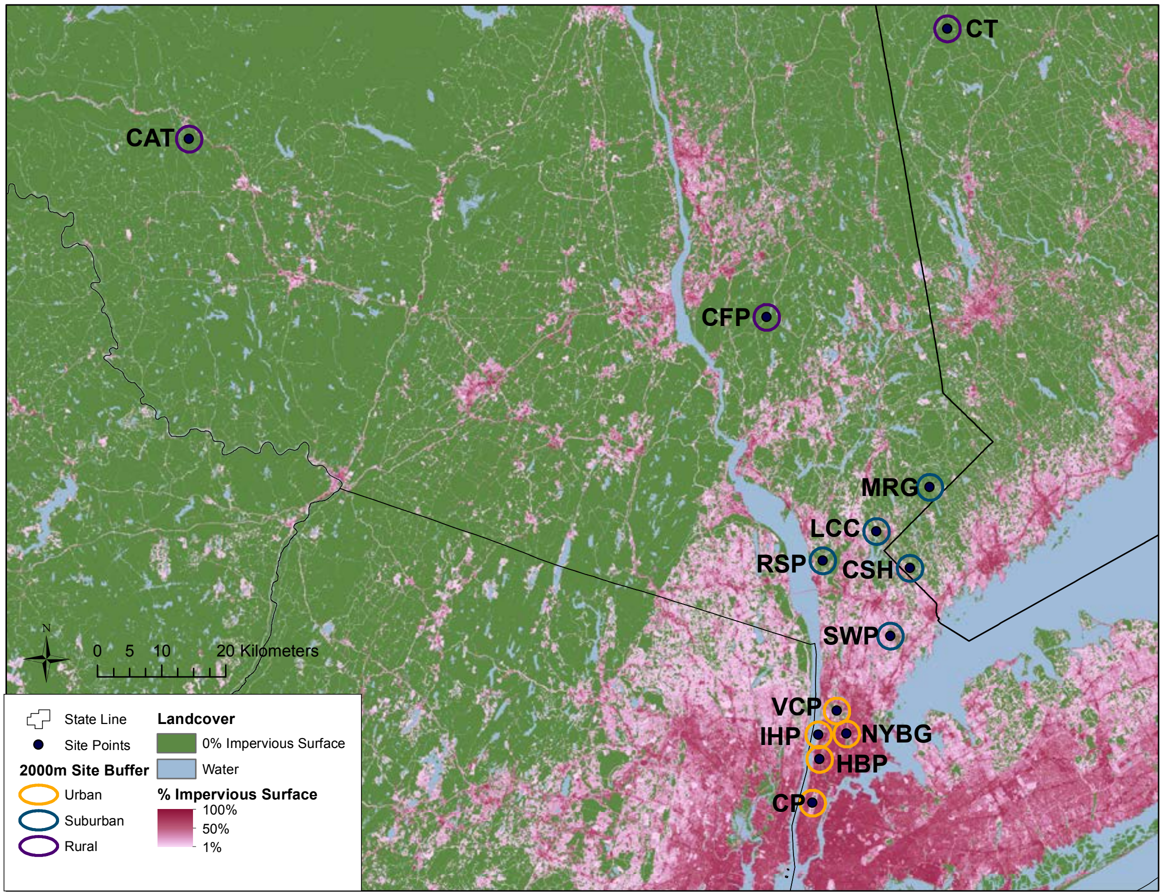

Figure 2A. Relative abundance of species across site classes urban (orange), suburban (teal), rural (purple) sites.

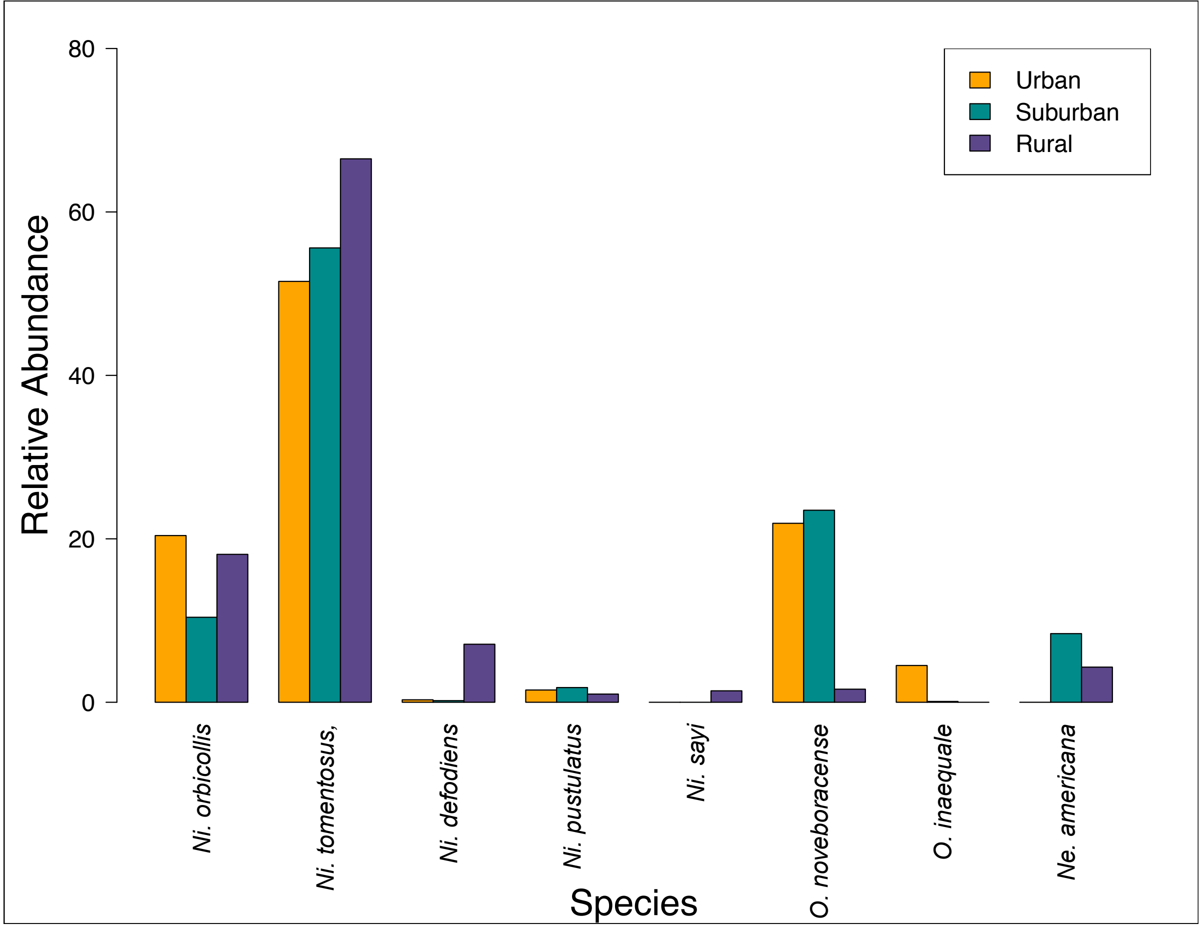

Figure 2B. Relative abundance of species across three sampling surveys at the Louis Calder Center site (sample 1=light teal, sample 2= medium teal, sample 3=dark teal).

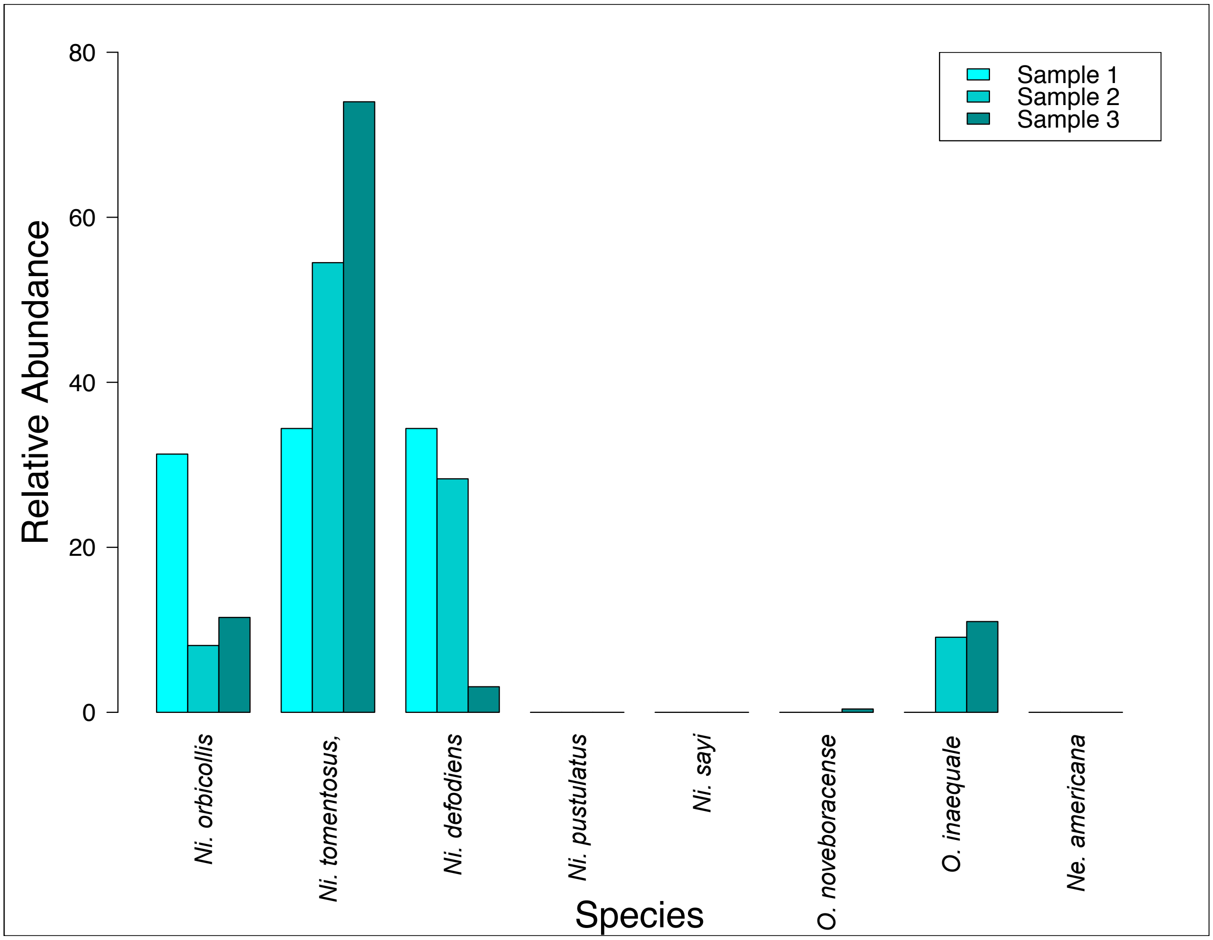

Figure 2C. Relative abundance of species at the Louis Calder Center site in 1970 (light purple; Pirone, 1974) and in 2015 (dark purple).

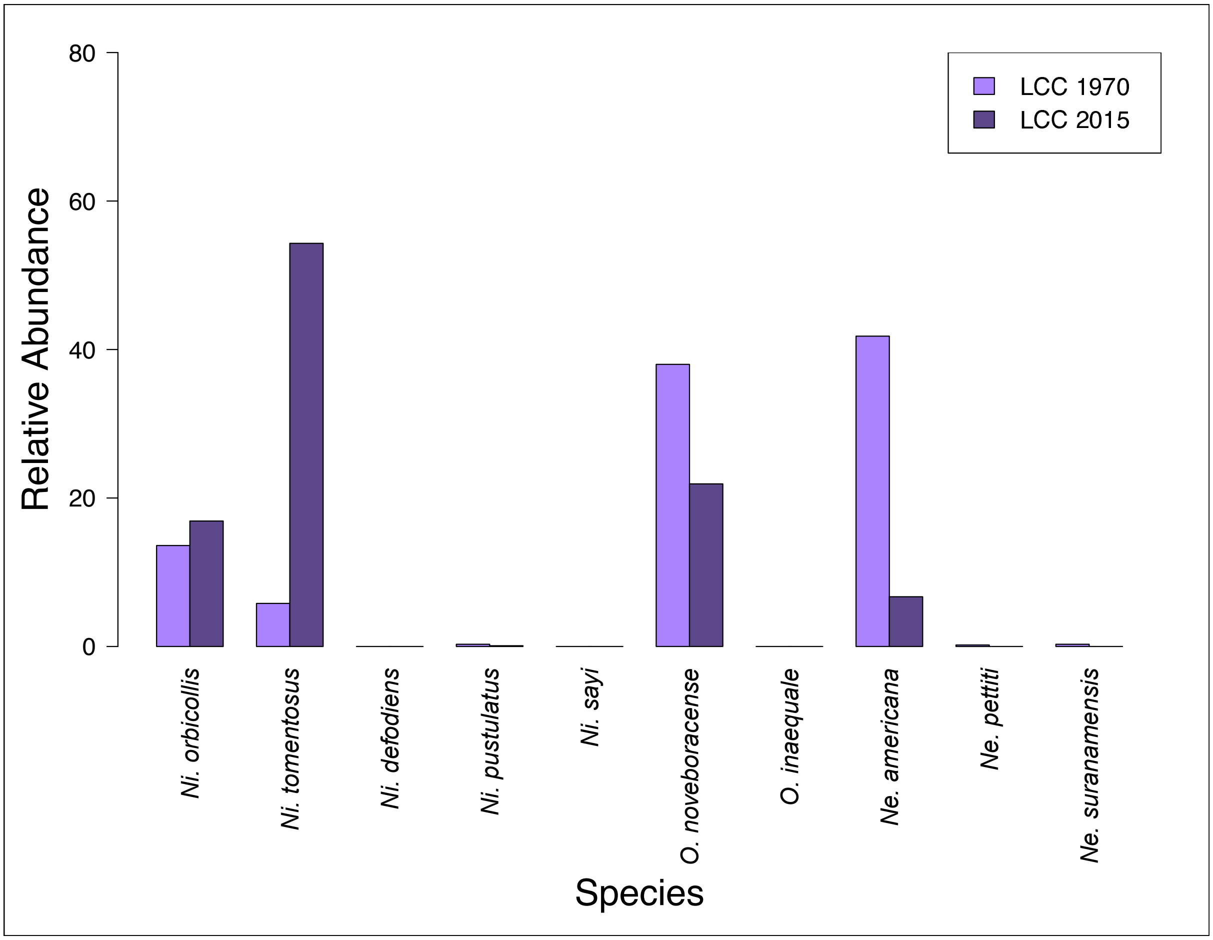

Figure 3A. Relationship between carrion beetle species richness and mean percent impervious surface at all sampled sites (site abbreviations and classification found in Table 1, Figure 1).

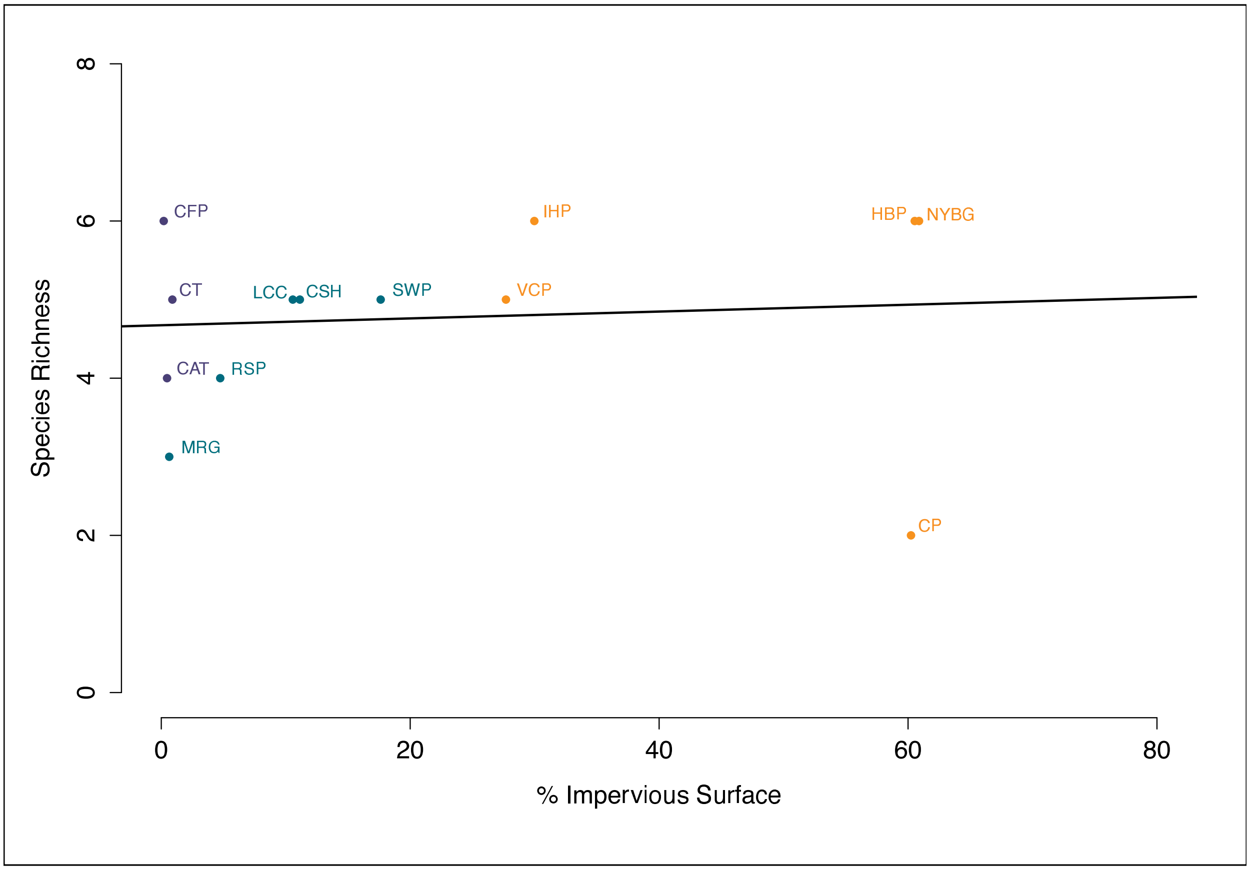

Figure 3B. Relationship of carrion beetle species diversity (Simpson's reciprocal index= 1/D) and mean percent impervious surface at all sampled sites (site abbreviations and classification found in Table 1, Figure 1).

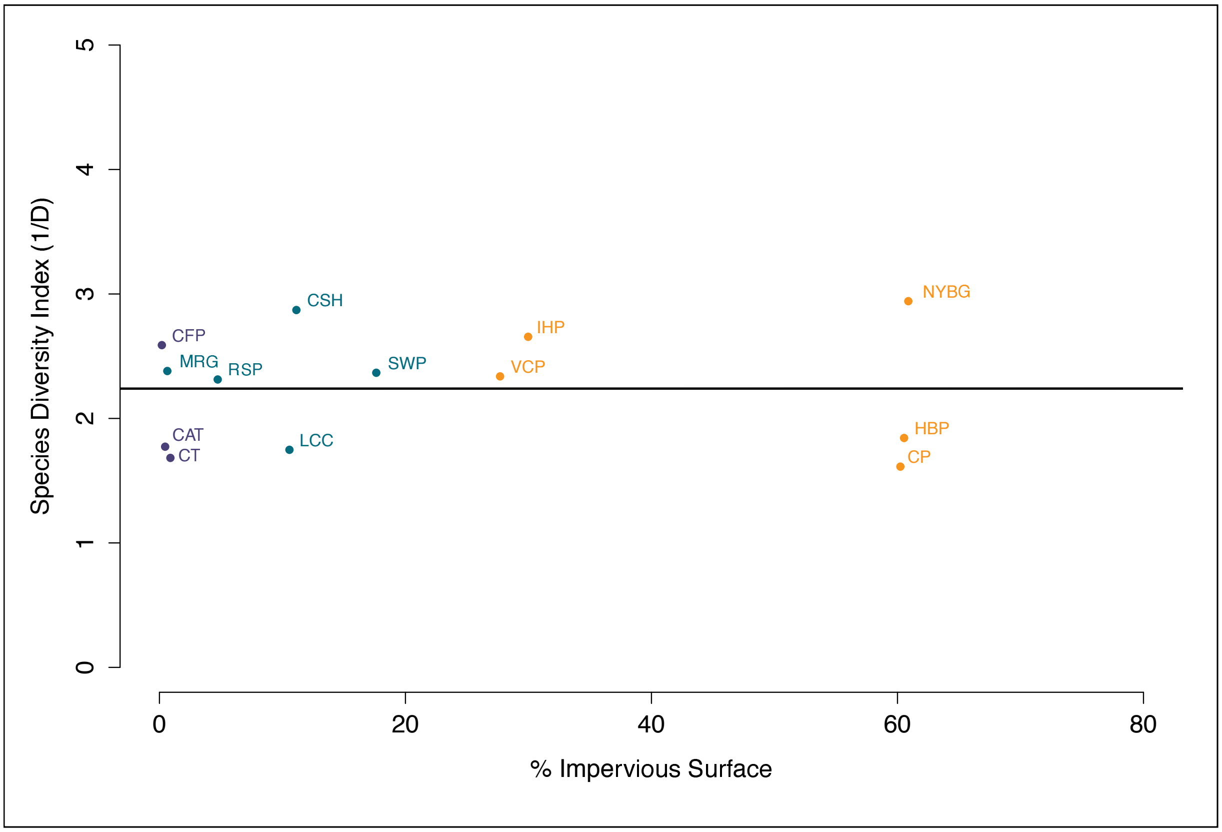

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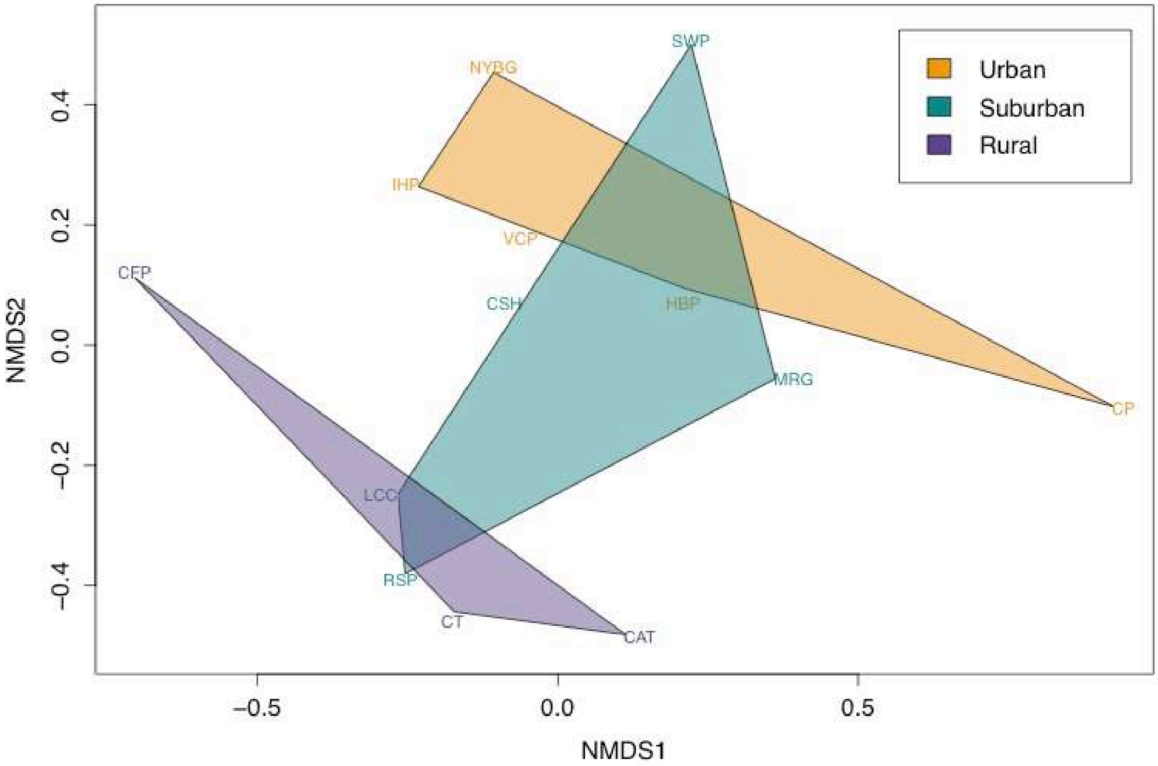
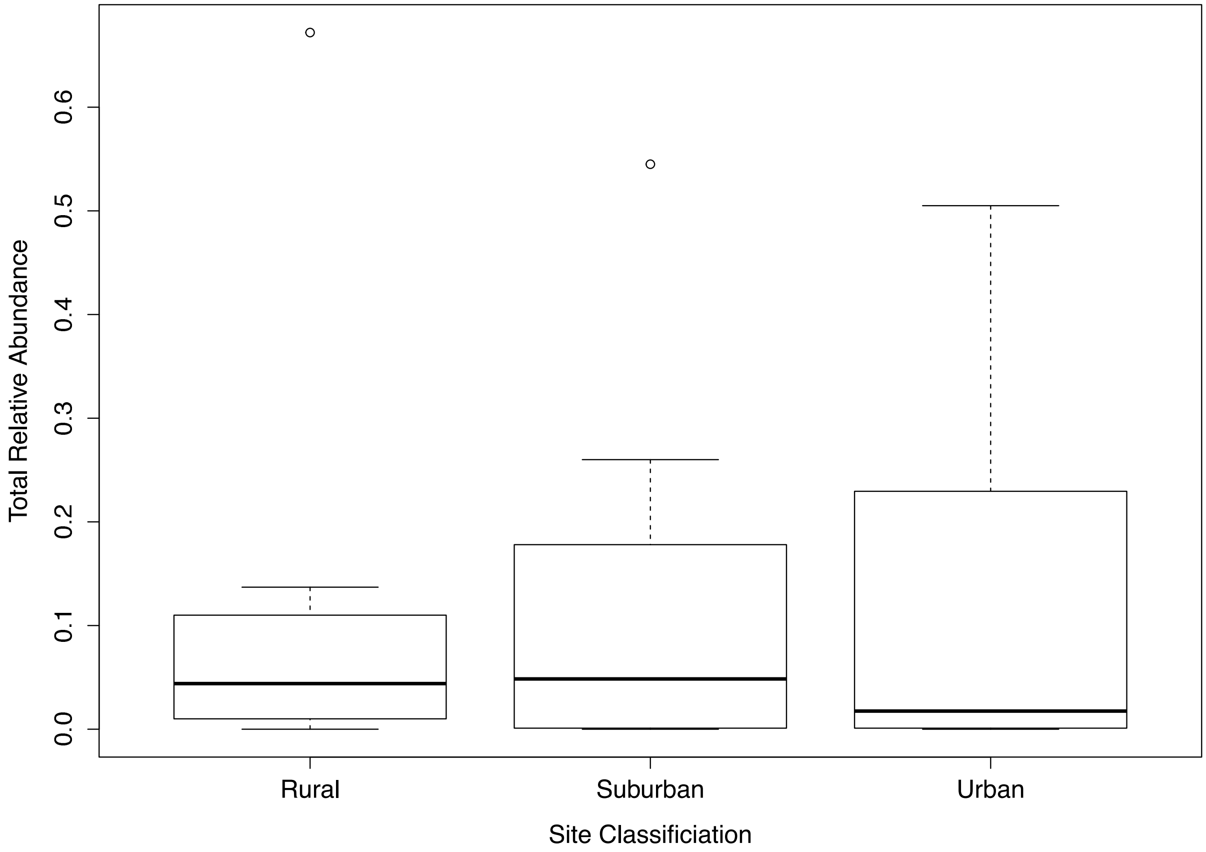
Figure 4. Non-metric multidimensional scaling (NMDS) of abundance of carrion beetle species at each site grouped by site class as a convex hull (urban=orange, suburban=teal, rural=purple).

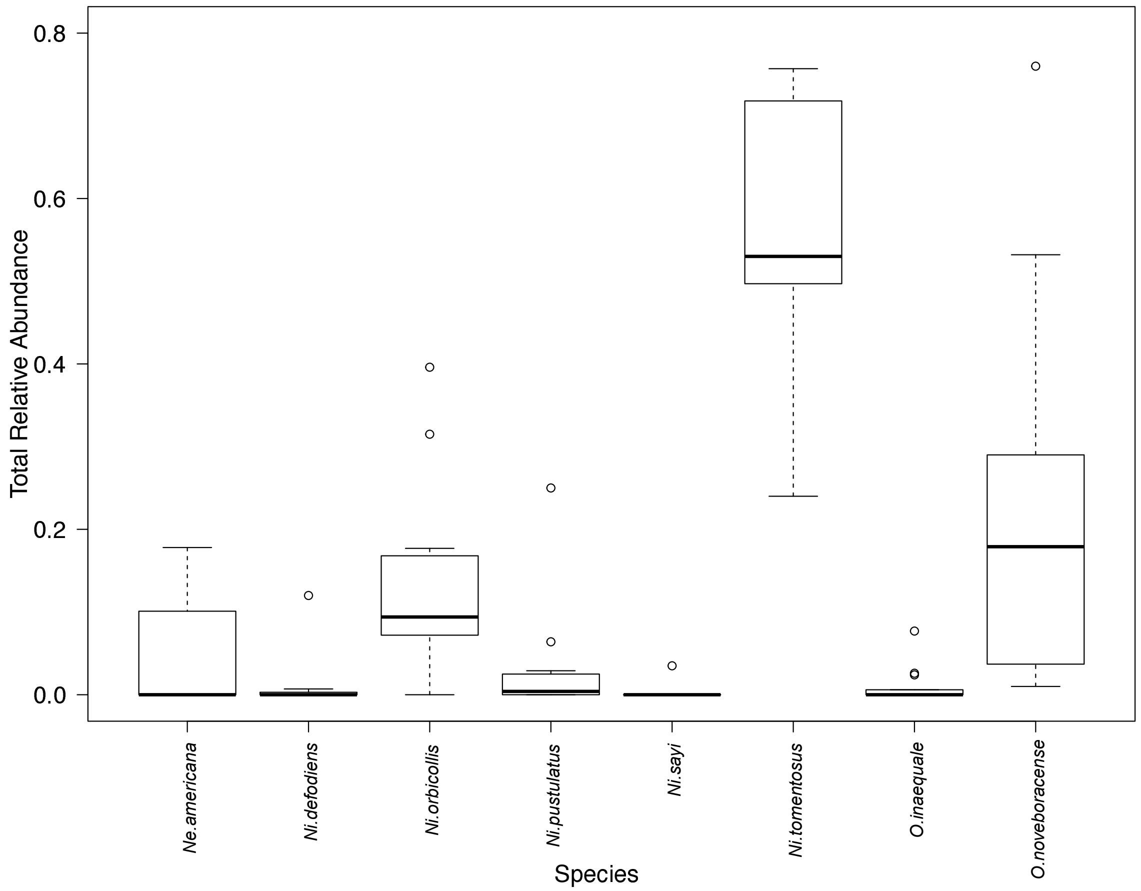


Supplementary Figures

Supplemental Figure S1. Box plot of mean relative abundance of all carrion beetle species across site classification.



Supplemental Figure S2. Box plot of mean relative abundance of all sites across species.



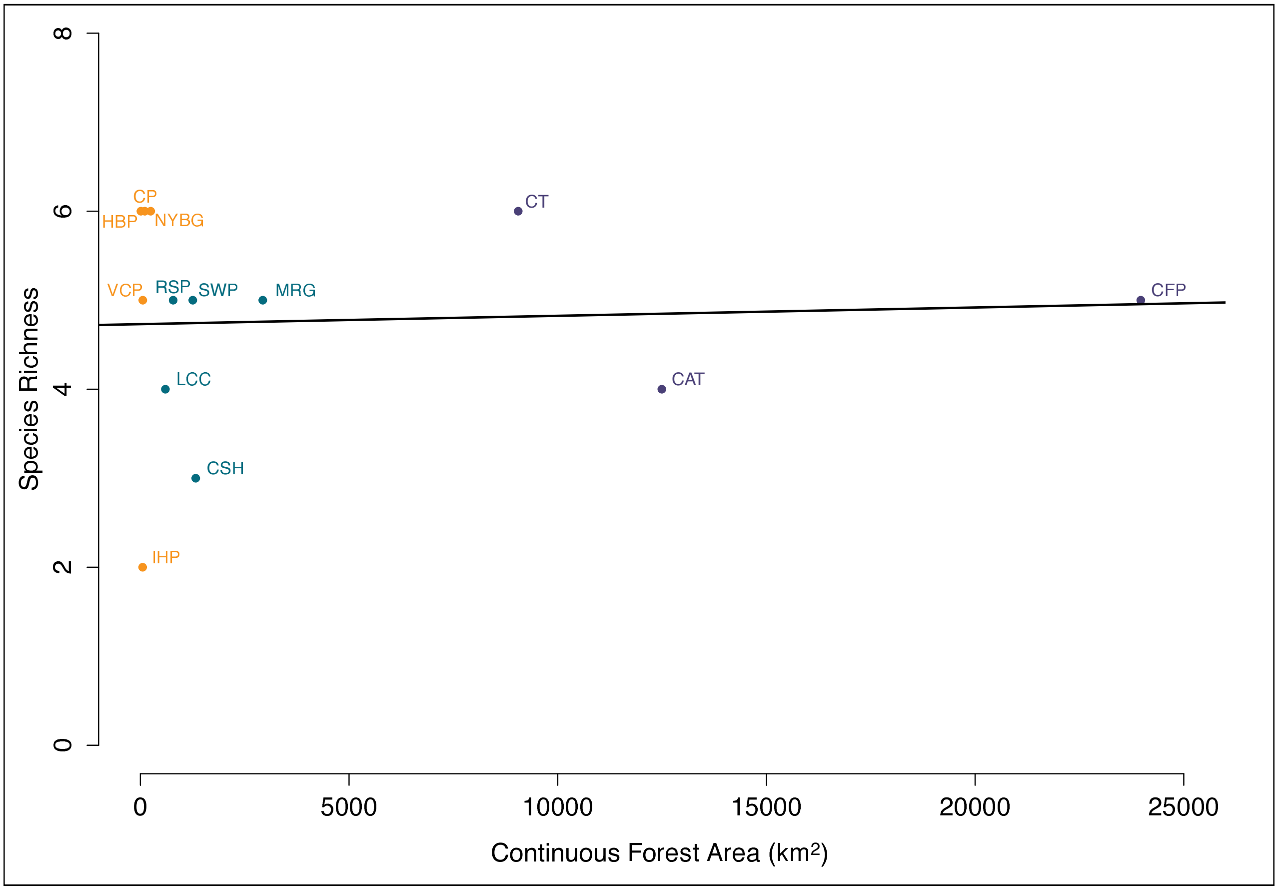
Supplemental Table S1. Mean relative abundance across different site classification (urban, suburban, rural) comparing beetle size classes (small, medium, large; Gibbs and Stanton 2001).

	Mean Relative Abundance			ANOVA	
Beetle Size	***Urban***	***Suburban***	***Rural***	***F***	***p***
Small *(<5mm)*	0.253	0.273	0.356	0.216	0.807
Medium *(6-6.5mm)*	0.121	0.089	0.049	2.948	0.057
Large *(>6.5mm)*	0.253	0.273	0.356	2.502	0.104

Supplemental Table S2. Mean relative abundance across different site classification (urban, suburban, rural) comparing habitat specialization (generalist versus specialist; Gibbs and Stanton 2001).

	Mean Relative Abundance			ANOVA	
Specialization	***Urban***	***Suburban***	***Rural***	***F***	***p***
Generalist	0.256	0.282	0.340	0.138	0.872
Specialist	0.081	0.073	0.053	0.244	0.784

Supplemental Figure S3. Relationship between carrion beetle species richness and continuous forest area at all sampled sites (site abbreviations found in Table 1, Figure 1).



Supplemental Figure S4. Relationship between carrion beetle species diversity and continuous forest area at all sampled sites (site abbreviations found in Table 1, Figure 1).