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Fusco NA, Zhao A, Munshi-South J. 2017. Urban forests sustain diverse carrion beetle assemblages in the New York City metropolitan area. PeerJ 5:e3088 <https://doi.org/10.7717/peerj.3088>

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

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## 1 Abstract

2 Urbanization is an increasingly pervasive form of land transformation that reduces biodiversity  
3 of many taxonomic groups. Beetles exhibit a broad range of responses to urbanization, likely due  
4 to the high functional diversity in this order. Carrion beetles (Order: Coleoptera, Family:  
5 Silphidae) provide an important ecosystem service by promoting decomposition of small-bodied  
6 carcasses, and have previously been found to decline due to forest fragmentation caused by  
7 urbanization. However, New York City (NYC) and many other cities have fairly large  
8 continuous forest patches that support dense populations of small mammals, and thus may harbor  
9 relatively robust carrion beetle communities in city parks. In this study, we investigated carrion  
10 beetle community composition, abundance and diversity in forest patches along an urban-to-rural  
11 gradient spanning the urban core (Central Park, NYC) to outlying rural areas. We conducted an  
12 additional study focusing on comparing the current carrion beetle community at a single  
13 suburban site in Westchester County, NY that was intensively surveyed in the early 1970's. We  
14 collected a total of 2,170 carrion beetles from eight species at 13 sites along this gradient. We  
15 report little to no effect of urbanization on carrion beetle diversity, although two species were not  
16 detected in any urban parks. *Nicrophorus tomentosus* was the most abundant species at all sites  
17 and seemed to dominate the urban communities, potentially due to its generalist habits and  
18 shallower burying depth compared to the other beetles surveyed. Variation between species in  
19 body size, habitat specialization, and % forest area also did not influence carrion beetle  
20 communities. Lastly, we found few significant differences in relative abundance of 10 different  
21 carrion beetle species between 1974 and 2015 at a single site in Westchester County, NY,  
22 although two of the rare species in the early 1970's were not detected in 2015. These results

23 indicate that NYC's forested parks have the potential to sustain carrion beetle communities and  
24 the ecosystem services they provide.

25

## 26 **Introduction**

27       The ecological influence of urbanization is increasingly pervasive around the world. In  
28 2014, 54% of the world's human population resided in urban areas (United Nations 2014) and  
29 urban populations increased by 12% between 2000 and 2010 in the United States (U.S. Census  
30 Bureau 2010). Urban landscapes are highly modified for human use, with natural habitats  
31 typically occurring only in small, fragmented patches (Saunders, et al. 1991). Fragmentation in  
32 cities often decreases species richness, changes community composition, and alters ecosystem  
33 processes (Didham 2010). Many species are impacted negatively by urbanization (*carnivores-*  
34 *Ordeñana, et al. 2010; arthropods-* Sattler, et al. 2010; *amphibians-* Hamer and Parris 2011;  
35 *birds & plants-* Aronson, et al. 2013), but effects vary based on the taxonomic group in question  
36 (McKinney 2008). For example, studies of arthropod diversity along urban-to-rural gradients  
37 have documented a wide variety of responses to urbanization (Hornung, et al. 2007; Niemelä and  
38 Kotze 2009; Varet, et al. 2011; Magura, et al. 2013; Savage, et al. 2015; Diamond, et al., 2015).  
39 Given the extreme variety of life history traits and habitat use among arthropods, responses to  
40 urbanization may be difficult to predict.

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

46 DeVault, et al. 2010), and invertebrates for this resource (Ratcliffe 1996; Gibbs and Stanton  
47 2001). Urbanization alters natural habitats in myriad ways (Grimm, et al. 2008) that may cause  
48 local extirpations or reduced abundance of native small mammals (e.g. likely carrion) and  
49 carrion beetles in cities.

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

59         In this study we investigated species richness, diversity, relative abundance and  
60 community similarity of carrion beetles (Family: Silphidae) across an urban-to-rural gradient in  
61 the New York City (NYC) metropolitan area. NYC is the most densely populated area in North  
62 America, but 20% of the city's land area is comprised of vegetated natural areas, particularly  
63 within several large urban parks. These parks are characterized by substantial forest cover and  
64 high densities of small mammals (Munshi-South and Kharchenko 2010), and thus may provide  
65 high-quality habitat for a diverse assemblage of carrion beetles. Alternatively, NYC's urban  
66 forests may harbor less carrion beetle diversity relative to suburban and rural areas outside of  
67 NYC as was found in Baltimore and Syracuse (Gibbs and Stanton 2001; Wolf & Gibbs 2004).  
68 We also compared historical records from a single site (Pirone and Sullivan, 1980), the Louis

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

74 Urban forests have the potential to harbor substantial biodiversity in cities worldwide  
75 (Faeth, et al. 2011; Elmqvist, et al. 2013; La Sorte, et al. 2014; Aronson, et al. 2014). Diamond,  
76 et al. (2015) argued that increases in biodiversity may be due to introduction of non-native  
77 species as well as increased habitat heterogeneity in densely populated areas, but many native  
78 species still persist in these urban remnants. Urban carrion beetle diversity that rivals  
79 surrounding rural areas would indicate that urban forests in NYC currently provide ample habitat  
80 and resources to sustain these native beetle communities.

81

## 82 **Materials & Methods**

### 83 *Study site and sampling techniques*

84 This study was conducted across an urban-to-rural gradient spanning 120 km from the  
85 urban core of NYC (Central Park, Manhattan) to southern New York State and western  
86 Connecticut. Carrion beetles were collected from five urban sites in New York City, five  
87 suburban sites and three rural sites (Table 1, Figure 1). Urban, suburban and rural site  
88 classifications followed Munshi-South et al. (2016) and were based on percent impervious  
89 surface cover. Many of our sampling sites were previously used by Munshi-South et al. (2016) to  
90 examine population genomics of white-footed mice (*Peromyscus leucopus*) and thus  
91 classifications were already available. For sites unique to this study, we used the same methods

92 to quantify urbanization (Table 1, Figure 1). In brief, we created 2 km boundary buffers around  
93 our study sites in ArcGIS 10.3 (ESRI, 2014) and then used zonal statistics to calculate mean  
94 percent impervious surface from the Percent Developed Imperviousness data layer imported  
95 from the National Land Cover Database 2011 (Xian, et al. 2011).

96 For comparison with previous carrion beetle surveys in other cities, we followed the  
97 sampling methods and trap design employed by Gibbs and Stanton (2001) and Wolf and Gibbs  
98 (2004). We constructed traps from open-topped cylinders by cutting the top off 1 L plastic  
99 bottles, adding a loop of string to hang the trap, and attaching a rain cover (cardboard covered in  
100 plastic cling wrap) by threading it through the string. Most traps contained 200 mL of a 1:1  
101 mixture of ethylene glycol and water, although soapy water was substituted at the Manhattan  
102 sites due to public safety regulations. A small glass jar containing bait (~6.5 cm<sup>2</sup> of rotting  
103 chicken thigh) was topped with a punctured lid to prevent insects from destroying the bait but  
104 permitting odors to attract carrion beetles. This jar was placed inside each plastic trap that was  
105 then filled with the ethylene glycol mixture. We set three traps at each site, close to forest edges  
106 and at least 100 m apart. Traps were hung from small tree branches approximately 1-1.5 m from  
107 the ground to prevent other wildlife from disturbing the traps. Traps were set out for seven  
108 consecutive days at each site, where beetles were collected upon the last day. We conducted all  
109 trapping from 22 June to 05 August 2015. At each study location, we separated beetles from  
110 other insects, and stored beetles in 80% ethanol before bringing all specimens to the laboratory  
111 for identification. We identified all carrion beetle species following Hanley and Cuthrell (2008).  
112 After collection, all beetles were stored in ethanol at -20 °C. Permission to collect carrion beetles  
113 was granted by the New York City Department of Parks and Recreation, the Rockefeller State  
114 Park Preserve, and the Connecticut Department of Energy and Environmental Protection.

115 *Relative abundance at urban, suburban and rural sites*

116 To describe variation among sites and site classes we calculated relative abundance as the  
117 proportion of each species compared to the total number of individuals at each site. To examine  
118 changes over the summer season in carrion beetle diversity and relative abundance at the Louis  
119 Calder Center (a suburban site), we conducted three separate trapping surveys, from 22-29 June,  
120 14-21 July, and 22-29 July 2015. Only data collected from the third survey were used in the main  
121 urban-to-rural analysis to more accurately compare to samples taken during the same time period  
122 as sampling at the other sites (mid to late July 2016). We calculated the relative proportion of  
123 each species for each of the three surveys at the Louis Calder Center to examine changes  
124 throughout the study period.

125

126 *Historical comparison of carrion beetle presence and abundance*

127 Pirone and Sullivan (1980) performed carrion beetle sampling at the Louis Calder Center  
128 in Armonk, NY for an 8-month period (April-November) in 1974. They collected 4,300 silphid  
129 beetles in 6 pitfall traps. Although the current study is only a snapshot (3 weeks of sampling) of  
130 the current community assembly at this site, the current data collected in 2015 from all three  
131 surveys at the Louis Calder Center (June to July) were used to compare the current carrion beetle  
132 species (2015) with the species observed in the historical study (1974). A student's t-test was  
133 conducted to compare total relative abundance in 1974 to 2015.

134

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

136 To determine whether our sample size was robust enough for running subsequent  
137 statistical analyses we performed a rarefaction analysis for all sites in R v.3.2.3 (R Core Team



138 2015) using the vegan package. For the analysis along the urban-to-rural gradient we used two  
139 different measures; species richness and species diversity. To compare species diversity across  
140 sites, we calculated the Simpson's reciprocal index ( $1/D$ ; Simpson 1949) of diversity. We also  
141 calculated other diversity indices for comparison (equations; Jost 2006; Table S1). These results  
142 showed similar trends across sites for all indices, therefore we chose to use the very commonly  
143 used Simpson's reciprocal index for statistical analyses. We then calculated community  
144 similarity using the Jaccard Index of community similarity (Jaccard, 1901):

$$145 \quad CC_J = S_J = a / (a + b + c),$$

146 where  $S_J$  is the Jaccard similarity coefficient,  $a$  is the number of species shared by all sites,  $b$  is  
147 the number of species unique to the first site, and  $c$  is the number of species unique to the second  
148 site. Then we calculated the Jaccard coefficient of community similarity for all the data pooled  
149 across sites classes (urban, suburban and rural) to analyze overall carrion beetle community  
150 assemblages. Lastly, we conducted a hierarchical cluster analysis using the betapart package in R  
151 (Baselga & Orme, 2012) to explore patterns of beta diversity partitioning this diversity measure  
152 into the nestedness and the turnover components.

153 To examine the influence of urbanization on species richness and diversity, we calculated  
154 general linear regressions of mean percent impervious cover versus species richness and species  
155 diversity at each site using R. We also calculated a general linear regression to explore the  
156 difference in relative abundance of the most abundant species; *Nicrophorus tomentosus* versus  
157 mean percent impervious surface at all sites. Additionally, we performed a gradient analysis by  
158 creating a Non-metric Multidimensional Scaling (NMDS) plot using the Vegan package  
159 (Oksanen, et al. 2016) in R to investigate population dissimilarity based on site class (urban,  
160 suburban, and rural). NMDS compares species changes from one community to the next by using

161 rank order comparison and calculates the pairwise dissimilarity of points in low-dimensional  
162 space (Buttigieg and Ramette 2014). Thus, NMDS allows us to robustly estimate dissimilarity  
163 between site locations based on the type of site and the species located in each site.

164

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

166 Many studies on beetles have focused on specific characteristics that may underlie  
167 differences in species richness and diversity within sites and across studies (Davies, et al. 2000).  
168 We conducted a factorial ANOVA to examine the interaction effect of species body size (small <  
169 5 mm, medium = 5-6.5 mm, large > 6.5 mm; estimations and groupings based on data from  
170 Gibbs and Stanton 2001) and site classification (urban suburban, rural) based on relative  
171 abundance. We also used a Student's t-test to examine relative abundance when species are  
172 classified as habitat generalists versus habitat specialists (Gibbs and Stanton 2001). Lastly, we  
173 performed a general linear regression to explore if a relationship exists between species richness  
174 or species diversity and the forest area (%) existing at each site. At each site the forest area was  
175 calculated using the Tabulate area tool from the ArcGIS 10.3 (ESRI 2014) Toolbox to calculate  
176 the forest area within the same 2km buffers surrounding each site as was used to calculate  
177 percent impervious surface. We then calculated the relative proportion of forest area compared to  
178 the total area within the buffer. We used forest area data from the USGS National Landcover  
179 Dataset (Homer et al. 2011).

180

## 181 **Results**

182 *Relative abundance at urban, suburban and rural sites*

183 We collected a total of 2,170 carrion beetles comprising eight silphid species (Table 2)  
184 across all sites (Table 1, Figure 1). *Nicrophorus tomentosus* was the most abundant at all sites,  
185 accounting for 56.8% of all beetles captured (Figure 2), yet there was no significant relationship  
186 between *Ni. tomentosus* relative abundance and percent mean impervious surface of each site  
187 ( $F(2,10)=1.16, p>0.05$ ). Other species also varied in presence or abundance between urban,  
188 suburban and rural forests (Figure 2); specifically, *Oiceoptoma noveboracense* was captured  
189 more often in suburban areas (23.5%) and urban areas (21.9%) than at rural sites (1.6%),  
190 whereas *Nicrophorus defodiens* was captured predominantly in rural areas (7.1%) versus urban  
191 areas (0.3%) and suburban areas (0.2%). Similarly, *Necrophila americana* was recorded in  
192 suburban (8.4%) and rural areas (4.3%) but was not found in any urban sites. *Nicrophorus sayi*  
193 was only recorded at one rural park, accounting for 1.4% of the total number of beetles captured  
194 at rural sites (Table, 1, 2, and Figure 2).

195

#### 196 *Historical comparison of carrion beetle presence and abundance*

197 We captured 358 individuals cumulatively across three surveys at the Louis Calder  
198 Center throughout summer 2015. Five carrion beetle species were observed at Louis Calder  
199 Center with the absence of *Ni. defodiens*, *Ni. sayi* and *Oiceoptoma inaequale* found at other  
200 suburban and rural sites. *Nicrophorus pustulatus* and *Necrophila americana* were absent from  
201 the first surveys and appeared in later surveys. *Ni. tomentosus* became more prevalent (34.4%,  
202 54.5%, 74.0%) throughout the summer and *O. noveboracense* decreased in relative abundance  
203 (34.4%, 28.3%, 3.1%; Figure 3).

204 Results of carrion beetle observations at the Louis Calder Center site show a small  
205 reduction in species richness; 7 species in 1974 to 5 species in 2015 (Figure 3). *Ni. defodiens*, *Ni.*

206 *sayi*, and *O. inaequale* were absent both historically and currently at this site yet were present at  
207 other suburban sites. The two species not observed in 2015 that were already low in relative  
208 abundance in 1974 were *Necrodes surinamensis* (0.2%) and *Necrophilus pettiti* (0.3%; Figure 4).  
209 There was no significant difference in the relative abundance of species in 1974 to 2015  
210 ( $t(9)=0.546$ ,  $p=0.599$ ). The 2015 data show an increasing trend in the relative abundance of *Ni.*  
211 *tomentosus* (5.8% to 54.3%) in 1974 versus 2015, and a decreasing trend in the relative  
212 abundance of *Necrophila americana* (41.8% to 6.7%) and *O. noveboracense* (38% to 21.9%)  
213 since 1974 (Figure 4).

214

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

216 Across the urban-to-rural gradient there was no significant relationship between mean  
217 percent impervious surface of a site and carrion beetle species richness ( $R^2 = 0.028$ ,  $p > 0.05$ ) or  
218 species diversity ( $R^2 = 0.0213$ ,  $p > 0.05$ ). However, NMDS ordination plots exhibit dissimilarity  
219 in carrion beetle assemblages in rural and urban sites. NMDS also showed that beetle  
220 assemblages in suburban sites were more similar to those in the urban sites. Based on the size of  
221 the convex hulls, heterogeneity of carrion beetle species composition was the greatest for  
222 suburban sites and least for urban sites (Figure 5).

223 We observed relatively high community similarity indices across most pairwise  
224 comparisons ( $CC_j = 0.333-1.000$ ; Table 3). Several pairs of nearby sites had very high  
225 community similarity, such as two urban sites: Inwood Hill Park and New York Botanical  
226 Garden ( $CC_j = 1.000$ ); and two suburban sites: Convent of the Sacred Heart School and Louis  
227 Calder Center ( $CC_j = 1.000$ ). The most distant pairs of sites were less similar, most notably  
228 between highly urbanized Central Park and rural Clarence Fahnestock State Park ( $CC_j = 0.333$ ).

229 The pooled urban carrion beetle community was more similar to the pooled suburban community  
230 ( $CC_j = 0.857$ ) than to the pooled rural community ( $CC_j = 0.750$ ), as also demonstrated in the  
231 NMDS ordination (Figure 5). The pooled rural community was equally similar to both the  
232 pooled urban and suburban communities ( $CC_j = 0.750$ ). The nestedness component of beta  
233 diversity in the hierarchical cluster analysis clustered sites based on species richness trends, not  
234 based on site classifications (Figure 6A). Alternatively, the hierarchical clustering of the turnover  
235 component clusters all urban sites together with a few suburban sites in one branch and all rural  
236 sites and the other suburban sites in another cluster (Figure 6B) as reflected by the results of the  
237 NMDS plot (Figure 5).

238

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

240 We found no significant effect between beetle body size and site class (urban, suburban,  
241 rural) for relative abundance of carrion beetle species in this study. Additionally, when focusing  
242 on habitat specialization, we also found no significant difference in habitat specialization  
243 between urban, suburban, and rural sites (Table S1). Lastly, we found no trend in species  
244 richness (Figure S1A) or species diversity (Figure S1B) across increasing continuous forest areas  
245 throughout sampled sites.

246

## 247 **Discussion**

248 Contrary to our predictions, we observed few differences in beetle diversity or richness  
249 along an urban-to-rural gradient in the NYC metropolitan area. Along this gradient, urban and  
250 suburban sites were nearly equally diverse and species-rich as rural sites. We also detected little  
251 to no influence of urbanization (measured by mean percent impervious surface) on relative

252 species abundance, species diversity or species richness of carrion beetles throughout these sites.  
253 Although species richness is not very high, we observed relatively high carrion beetle  
254 community similarity values between most pairs of sites in this study regardless of their  
255 urbanization status (Jaccard Index= 0.333-1.000; Table 3). When partitioning beta diversity,  
256 nestedness follows species richness trends, further strengthening the result that there is no  
257 difference in carrion beetle communities between urban, suburban and rural classified sites.  
258 Alternatively, turnover may be driven by site class based on urbanization to some extent.

259 Overall, even with limited sampling, this study demonstrates that a diverse community of  
260 carrion beetles are able to thrive in rural, suburban and urban forests in and around New York  
261 City. Gibbs and Stanton (2001) and Wolf and Gibbs (2004) reported that carrion beetle diversity  
262 is significantly reduced around Syracuse, NY and Baltimore, MD due to forest fragmentation  
263 associated with urbanization, but our results indicate that forested city parks in the most  
264 urbanized areas of North America (i.e. Manhattan and the Bronx, NYC) do harbor substantial  
265 carrion beetle diversity compared to surrounding rural areas. We did not directly examine  
266 variation in fragment size within urban, suburban, and rural areas, but the discrepancy between  
267 these earlier results and ours may be due to the fact that urban forests in NYC parks are relatively  
268 large compared to other cities.

269 Arthropods have exhibited highly variable, even dichotomous, responses to urbanization  
270 around the world (Lessard and Buddle 2005; Sattler, et al., 2010). Other studies show that the  
271 influence of urbanization varies based on taxonomic group, geographic location, climate and  
272 spatial scale (McKinney 2008; Kotze, et al. 2011, Martinson and Raupp 2013). Carabid beetles  
273 are the most well-studied arthropod group: carabid species richness has been found to decrease  
274 (Gaublomme, et al. 2008) or not change (Dieschel 2006) in urban areas. In a review of carabids

275 and urbanization, Magura et al. (2010) argued that this variation was due to site-specific effects  
276 operating in each study. Urbanization did not homogenize carabid assemblages in cities in  
277 England, Denmark, and Helsinki, Finland, but urbanization did affect species assemblages in  
278 other Finnish cities, Hungary, Japan and Bulgaria (Kotze, et al. 2011). Other than location,  
279 discrepancies across studies may be related to the choice of variables for analysis. Differing  
280 climates, different measures of urbanization (e.g. human population density, economics, housing  
281 density, or impervious surface), different times of the year studies were conducted, and spatial  
282 scale (Faeth, et al. 2011) all could affect species presence, richness, and diversity results in urban  
283 areas. Although carrion beetles are may not be representative of all arthropod species, these same  
284 factors may also explain some of the differences between the NYC results presented here, and  
285 those of Gibbs and Stanton (2001) and Wolf and Gibbs (2004) for Syracuse, NY and Baltimore,  
286 MD.

287       When quantifying and classifying urbanization, many studies use measures based on  
288 forest fragmentation, extent of forest cover, isolation caused by human-induced disturbance,  
289 impervious surface, or human population density (Macdonnell and Hahs 2008). The use of a  
290 common index to represent urbanization is necessary to compare results across studies, but there  
291 are no common indices currently in wide use. Macdonnell and Hahs (2008) and Kotze, et al.  
292 (2011) stress the need for such common measures to examine the generality the influence of  
293 urbanization on biodiversity patterns. Comparing our study to other carrion beetle studies, we  
294 used mean percent impervious surface to quantify urbanization, whereas Gibbs and Stanton  
295 (2001), Wolf and Gibbs (2004) and Klein (1989) utilized continuous forest cover and  
296 fragmentation to classify the level of urbanization at each site. Our study specifically quantified  
297 urbanization with mean percent impervious surface using 2 km buffers as was previously

298 reported by Munshi-South, et al. (2016) for many of the same study sites. Although many  
299 metrics can be employed to measure urbanization, we believe that impervious surface cover is  
300 particularly useful for urban-to-rural gradient studies because it is measurable for nearly any  
301 terrestrial area and directly related to urban landscape modification.

302 We also examined species relative abundance changes over three sampling periods at a  
303 suburban site: the Louis Calder Center in Westchester County, NY. Despite no significant  
304 change in total abundance across samples throughout the summer season, we did see slight  
305 changes in species abundance over different collection periods (Figure 3). In comparison to Wolf  
306 and Gibbs (2004) our study showed opposite trends in species presence across the collection  
307 period. This difference could be due to difference in climate and temperature across June, July,  
308 and August in NYC versus the more southern Baltimore, MD. In Armonk, NY, *Ni. tomentosus*,  
309 *O. noveboracense*, and *O. inaequale* were more abundant later in the summer, and *Ni. orbicollis*  
310 was more abundant earlier in the summer. Scott (1998) describes *Ni. tomentosus* as a late  
311 summer / early fall breeder, which was corroborated by our observation that *Ni. tomentosus* was  
312 most abundant in the latest summer survey. *Ni. orbicollis* begins breeding in late spring  
313 (Ratcliffe 1996), and was the most abundant in our first sample session at this site. *Ni. sayi* is  
314 most active in very early spring, which may explain the absence of this species at this site during  
315 the summer. Lastly, the absence of *Ni. pustulatus* may be due to their habitat preference for  
316 wetlands (Gibbs and Stanton 2001), which were not very extensive around our trap sites in this  
317 study.

318 Species richness of carrion beetles did not differ greatly between 1974 and 2015 at the  
319 Louis Calder Center site. However, we did record pronounced species-specific differences in  
320 abundance between the past study (Pirone and Sullivan, 1980) and this current study in 2015



321 (Figure 4). Species differences over time could be due to anthropogenic modification of the  
322 landscape in and around the Louis Calder Center site since the early 1970s. There was an  
323 increase in human population density in the town of North Castle, NY in Westchester County  
324 from 9,591 (1970) to 11,841 (2010) according to the Decennial Census 1950-2010 (U.S Census  
325 Bureau, 2010). An increase in population density often results in construction of more housing  
326 and roads and subsequent fragmentation of forests, which could alter current species  
327 assemblages. We identified the most drastic change in relative abundance over time for 3  
328 species; *Ni. tomentosus*, *O. noveboracense* and *Necrophila americana* (Figure 4). In contrast,  
329 relative abundance of *Ni. tomentosus* increased, which could be due to the fact that this species is  
330 an ecological generalist that becomes more common after habitat degradation. There was a  
331 substantial decrease in *O. noveboracense* since 1974. Since univoltine arthropod species are  
332 more affected by habitat loss, (Kotze et al. 2011) the reduction in *O. noveboracense* may be due  
333 to their inability to effectively compete with multivoltine species, as well as their limited  
334 dispersal ability in warmer temperatures (Ratcliffe 1996). Lastly, the most drastic decline was in  
335 *Necrophila americana*, which is perhaps due to its large body size (smaller bodied generalists  
336 can survive in more disturbed/urban habitat; Gibbs and Stanton 2001; Elek and Lovei, 2007) and  
337 its preference for field habitat (Ratcliffe 1996), which may be more limited in the area in 2015  
338 due to fragmentation and the reduction in agriculture. Two previously-observed species,  
339 *Necrodes surinamensis* and *Necrophilus pettiti*, were completely absent in our contemporary  
340 sample. *Necrodes surinamensis* is nocturnal and highly attracted to artificial lights, causing  
341 Ratcliffe (1998) to state concern for this species in cities where increased nocturnal lighting is  
342 common. This may be the reason for the decrease or even the extirpation of this species at this  
343 site. As for *Necrophilus pettiti*, it is a flightless carrion beetle species (Peck 1991), possibly

344 limiting its dispersal and survivability in increasingly urbanized areas. Alternatively, our use of  
345 hanging traps rather than pitfall traps as in Pirone and Sullivan (1980) may explain the absence  
346 of this flightless species in our study.

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

356 Competition with scavengers may also limit carrion beetle abundance and diversity.  
357 Competitors for carrion include other invertebrates (flies and mites- Gibbs and Stanton 2001)  
358 and many vertebrate mesopredators that are abundant in cities (raccoons, opossums, coyotes,  
359 skunks- DeVault, et al. 2011). However, Suguira, et al. (2013) recently reported that resource  
360 competition between invertebrates and vertebrates for carrion was less prevalent than previously  
361 thought. Vertebrate competitors are likely present at all of our study sites but may not  
362 substantially influence carrion beetle abundance, particularly if they are utilizing food resources  
363 provided by humans in cities. As for intraspecific competition with other carrion beetle species,  
364 Scott (1998) found there to be competition between *Ni. orbicollis* and *Ni. defodiens* based on  
365 temperature. Trumbo & Bloch (2002) found that *Ni. defodiens* can locate carcasses sooner than  
366 other species, but *Ni. orbicollis* uses cues from *Ni. defodiens* to locate and subsequently

367 dominate carrion. We identified a higher abundance of *Ni. orbicollis* than *Ni. defodiens*,  
368 especially in urban and suburban sites (Figure 2). Greater abundance of *Ni. orbicollis* in our sites  
369 could be due to these competitive abilities that aid *Ni. orbicollis* in locating and dominating prey  
370 more effectively. Lastly, intraspecific invertebrate competitors such as flies are often very  
371 prevalent in human altered landscapes (Kavazos and Wallman 2012). Flies are known to quickly  
372 locate carcasses and may outcompete beetles on carrion (Scott, 1987; Scott & Traniello 1990;  
373 Trumbo 1990; Gibbs and Stanton 2001). If there is fly abundance in NYC parks, our study  
374 indicates that this intraspecific competition is not restricting beetle abundance in urban forests  
375 compared to suburban and rural forests. Some carrion beetles have also evolved adaptations to  
376 thwart fly competition. For example, *Ni. tomentosus* was the most abundant carrion beetle in  
377 urban forests in this study, and may be thriving partially due to its cooperative burying behavior  
378 rapidly conceals carcasses from flies during times of day when flies are most active (Scott, et al.  
379 1987).

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

390 We found no trend in body size (as classified via Scott 1998 & Gibbs and Stanton 2001),  
391 across habitat specialization (from Gibbs and Stanton, 2001), or with continuous forest habitat  
392 area compared to abundance of species found in urban, suburban and rural sites (Supplementary  
393 Fig. 3,4,5). Our results of body size and habitat specialization were again contradictory to past  
394 burying beetle literature where Ulrich, et al. (2007) found a negative association between body  
395 size of necrophagous beetles and distance from the city center in northern Poland. Gibbs and  
396 Stanton (2001) also reported that carrion beetles thriving in urban areas were often small-bodied  
397 and habitat generalists. Magura et al. 2006 used even more stringent statistical measures to assess  
398 carabid beetle body size across an urbanization gradient. These studies measured body length  
399 and / or biomass of each individual, whereas our study was limited by gross approximation of  
400 body sizes classes, which may have caused us to miss this effect. In a broader analysis of 69  
401 beetle species (Davies et al. 2000), body size was not correlated with fragmentation. The authors  
402 argued that the relationship between extinction risk and body size is very complex and  
403 influenced by other factors like spatial scale, population fluctuation, and longevity.

404 In general, our study shows that within NYC, urban parks are able to house nearly the  
405 same community as continuous forest tracts in the rural surrounding areas despite local  
406 impervious surface and ecological / life history variability across species. These results highlight  
407 the importance of maintaining and conserving large areas of forest throughout NYC within city  
408 parks commonly used for human recreation.

409

#### 410 **Conclusions:**

411 Urban parks have the potential to house diverse habitats rich in biodiversity (Kotze, et al.  
412 2011) of both plants and animals (Angold, et al. 2006). Even highly modified landscapes

413 containing small reserves comprising ample green space have the potential to house large beetle  
414 diversity (Watts and Lariviere 2004) and high abundance of other arthropod species (Bolger,  
415 2008; Faeth, et al. 2011). The maintenance of arthropod biodiversity in urban parks may  
416 ultimately be mediated by human influence on plant communities (Faeth, et al. 2011).  
417 Alternatively, arthropod species thriving in urban habitats may be preadapted for tolerance to  
418 fragmentation and high colonization potential (Sattler, et. al 2010). A current review on  
419 biodiversity in cities suggests that patch area and corridors have the strongest positive effect on  
420 biodiversity and that we need to maintain sites with larger than 50 hectares to prevent rapid loss  
421 of sensitive species (Beninde, et al. 2015). Maintenance of carrion beetle diversity in NYC will  
422 stabilize the interconnectedness of urban food webs, aid in nutrient cycling, and promote natural  
423 decomposition of carcasses (Beasley, et al. 2015) in our urban parks. Sustaining the ecosystem  
424 services provided by carrion beetles will require conservation of large, continuous forest tracts in  
425 urban parks. Greater connectivity between small green areas, and connectivity between the  
426 urban core and surrounding forested areas will promote the biodiversity potential of small  
427 patches (Doo and Joo, 2011). A “land sparing city” approach is one way to maintain essential  
428 ecosystem services (Stott, et al. 2015) provided by carrion beetles in the New York City area.

429  
430 **Acknowledgements:** We thank Matthew Combs and Jane Park for photographing carrion  
431 beetles, and Elizabeth Carlen, Carol Henger, and Emily Puckett for helpful comments on the  
432 manuscript. Gabor Lovei and two anonymous reviewers also provided very thorough and  
433 constructive suggestions for improving the manuscripts.

434  
435 **Funding Statement:** A. Zhao’s work on this project was supported in part by a National Science  
436 Foundation REU Site grant (No. 1063076) to Fordham University and the Louis Calder Center

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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

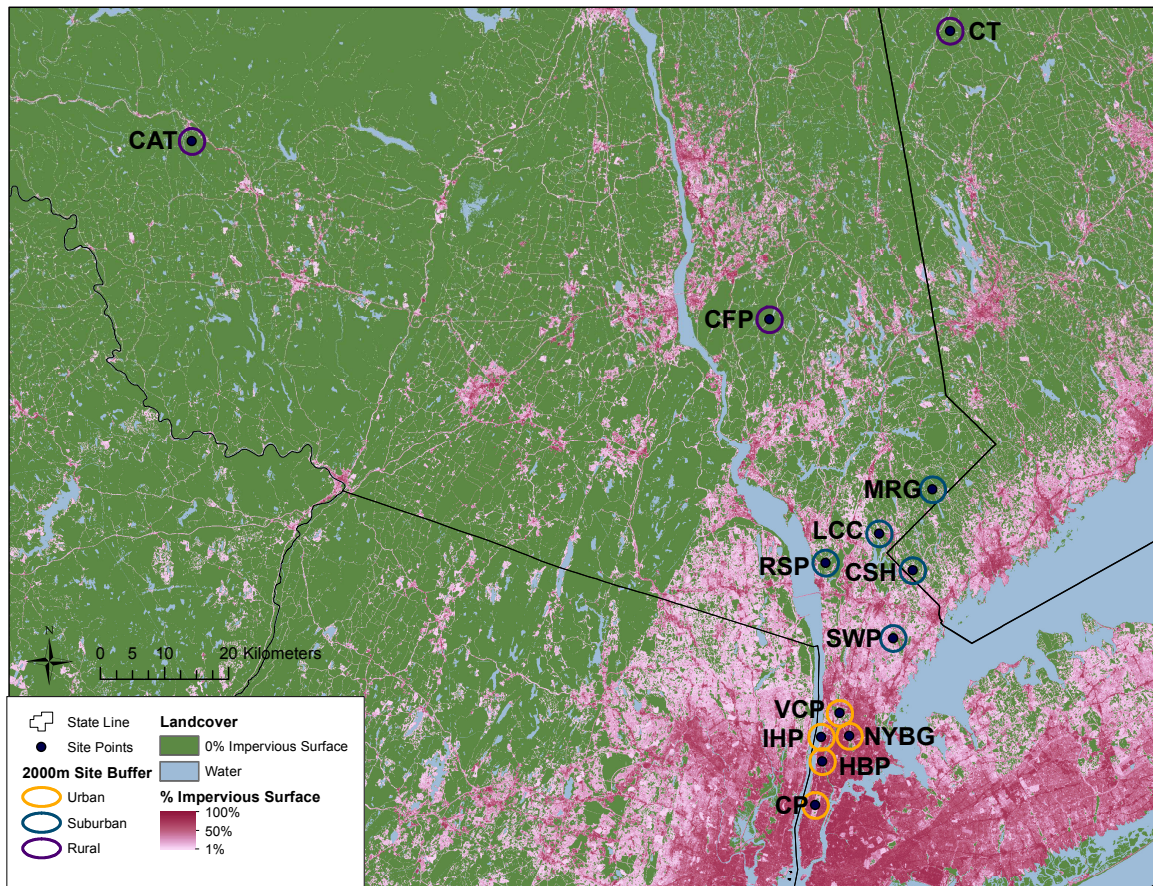
**Table 2.** Abundance data for eight carrion beetle (Family: Silphidae) species at all site locations (site abbreviations and classification found in Table 1).

Species	<i>Nicrophorus orbicollis</i>	<i>Nicrophorus tomentosus</i>	<i>Nicrophorus defodiens</i>	<i>Nicrophorus pustulatus</i>	<i>Nicrophorus sayi</i>	<i>Oiceoptoma inaequale</i>	<i>Oiceoptoma noveboracense</i>	<i>Necrophila americana</i>
								
NYBG	50	165	1	8	0	25	77	0
HBP	3	28	0	0	0	1	7	0
CP	0	6	0	0	0	0	19	0
IHP	61	70	1	1	0	1	20	0
VCP	22	75	0	1	0	3	75	0
SWP	7	87	0	15	0	1	125	0
LCC	39	257	0	3	0	0	55	41
LCC1	8	54	0	0	0	0	28	9
LCC2	26	168	0	1	0	0	7	25
LCC3	5	35	0	2	0	0	20	7
CSH	50	182	2	0	0	0	11	53
RSP	17	90	0	0	0	0	74	0
MRG	26	221	35	0	0	0	6	4
CT	1	97	0	0	0	0	15	20
CAT	63	106	0	5	7	0	2	17
CFP	50	165	1	8	0	25	77	0

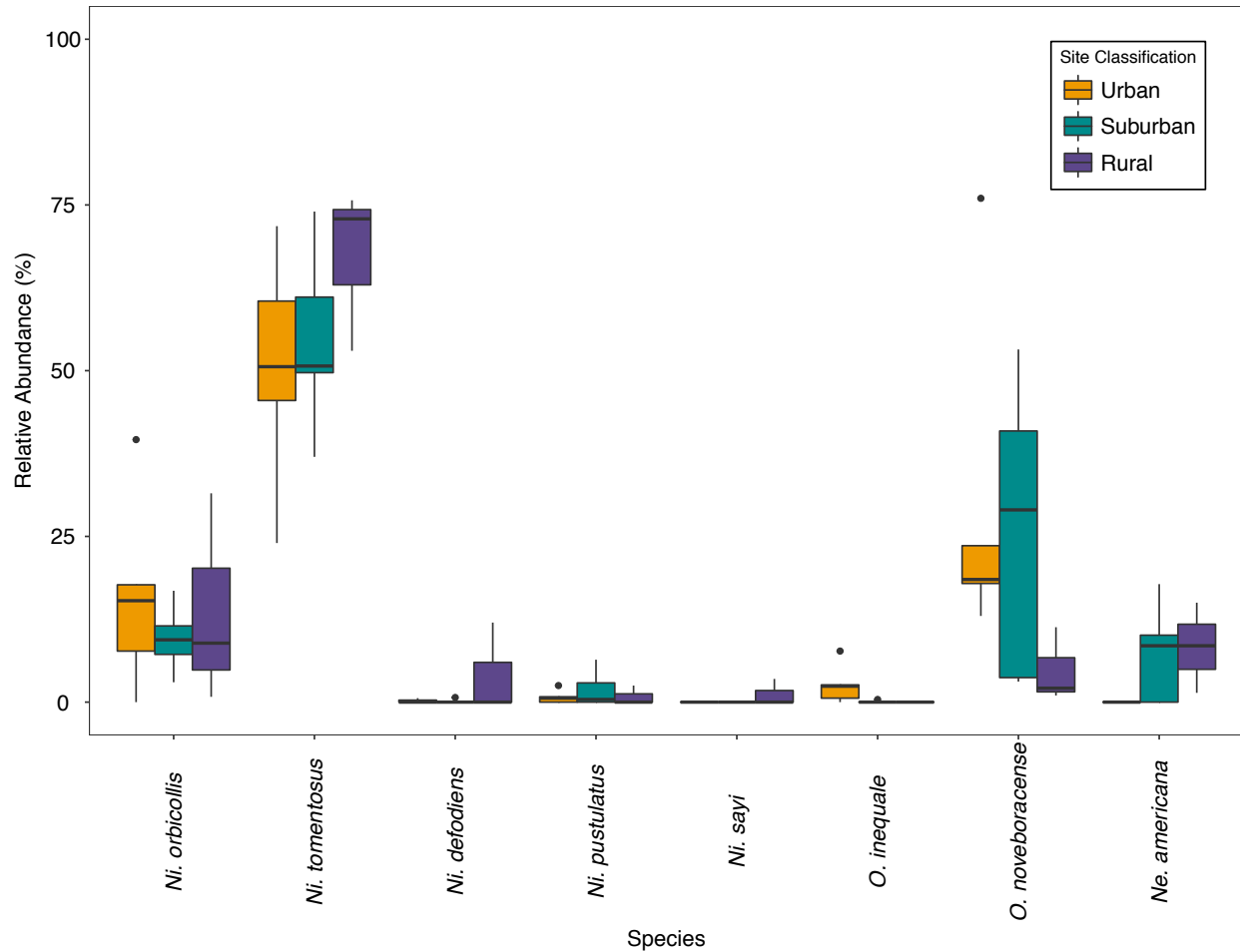
**Table 3.** Pairwise Jaccard community similarity index values calculated between all sample sites (site abbreviations and classification located in Table 1).

	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													-

**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.

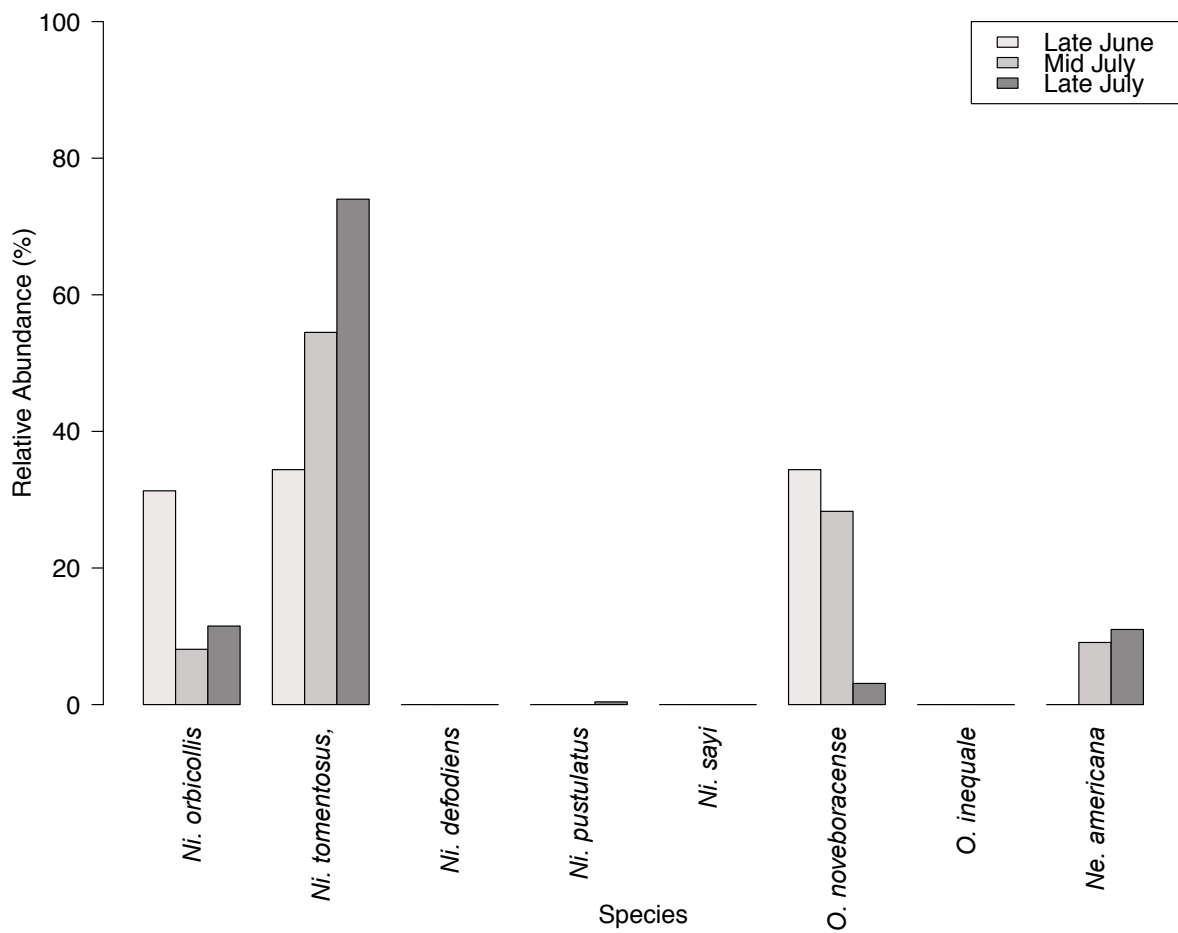


**Figure 2.** Relative abundance (%) of species across site classes; urban (orange), suburban (teal), rural (purple) sites. Bold lines within the boxes indicate the median value, the colored boxes represent the inter-quartile range (Quartile 1- Quartile 3), the whiskers extend 1.5 \* IQR, and the dots represent outlier values.

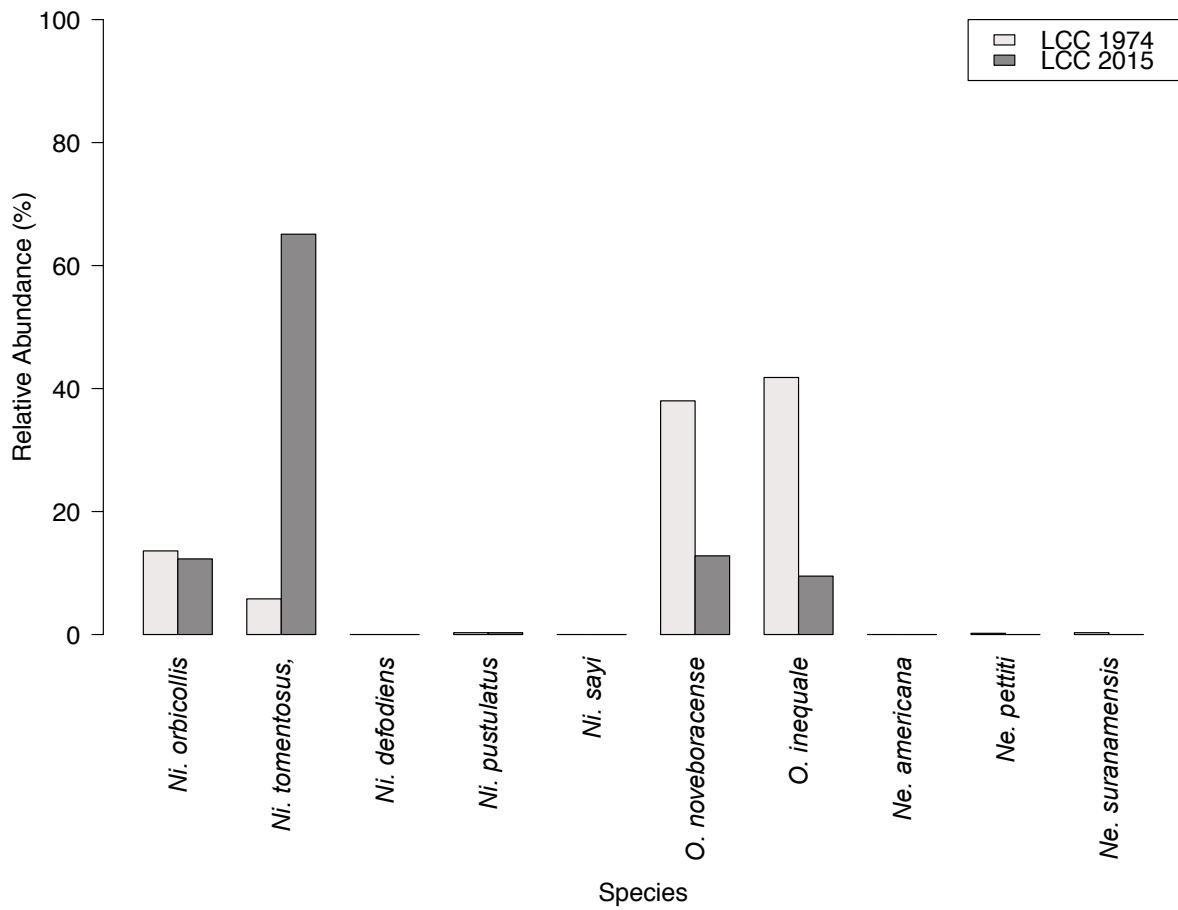




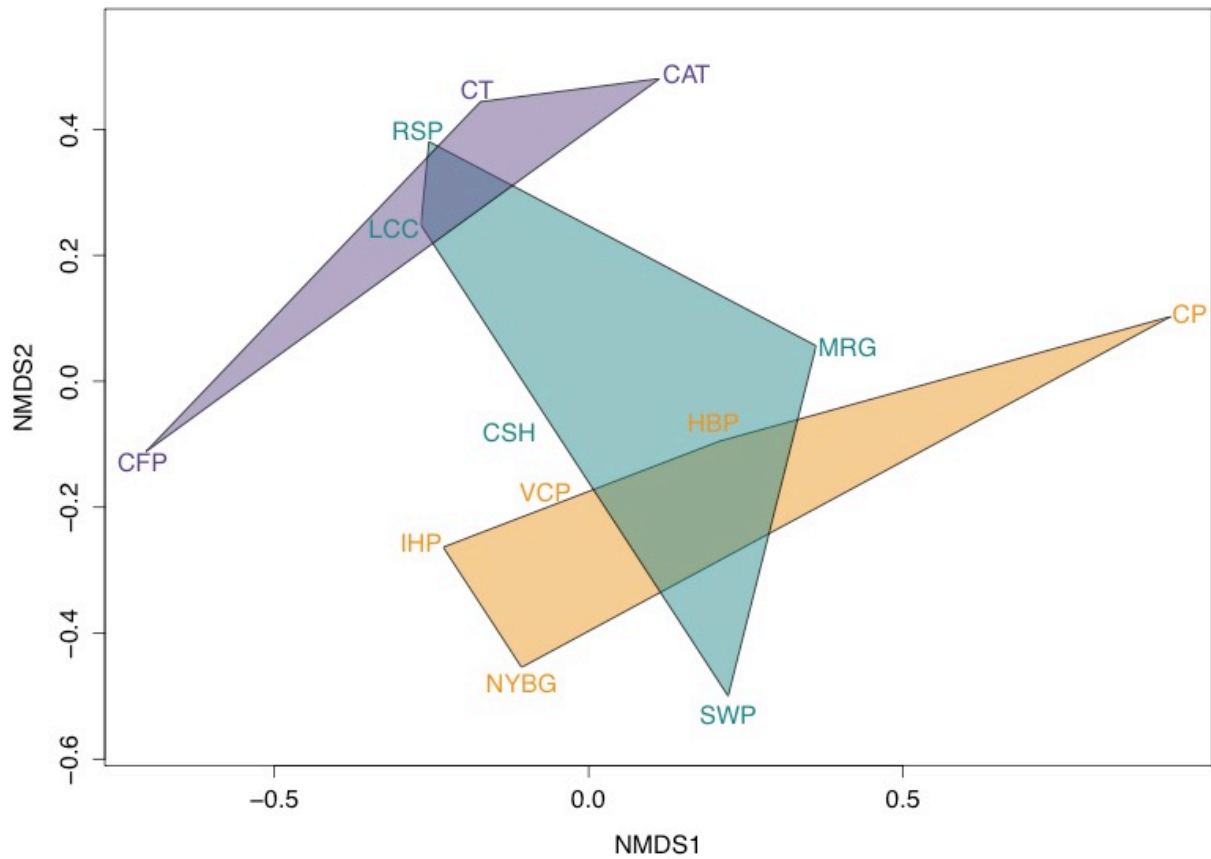
**Figure 3.** Relative abundance (%) of species across three sampling surveys (Late June, Mid July, Late July) at the Louis Calder Center site in Armonk, NY.



**Figure 4.** Relative abundance of species at the Louis Calder Center site in 1974 (Pirone and Sullivan, 1980) and in 2015.



**Figure 5.** Non-metric multidimensional scaling (NMDS) of abundance of carrion beetle species at each site grouped by site class as a convex hull.



**Figure 6.** Hierarchical cluster analysis of sites (abbreviations found in Table 1) based on (A) the nestedness component of the Jaccard Similarity Index for beta diversity ( $\beta_{JNE}$ ) and (B) the turnover component ( $\beta_{JTU}$ ).

