

1 **Bird predation and defoliating insect abundance are greater on trees in urban forest**  
2 **fragments than ornamental landscapes**

3

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11

12 **Abstract**

13 Predation by natural enemies is important for regulating herbivore abundance and  
14 herbivory. Theory predicts that complex habitats support more natural enemies, which exert top-  
15 down control over arthropods and therefore can reduce herbivory. However, it is unclear if  
16 theory developed in other more natural systems similarly apply to predation by vertebrate and  
17 invertebrate natural enemies across urban habitats of varying complexity. We used plasticine  
18 caterpillar models to assess bird and insect predation, collected leaf-feeding arthropods, and  
19 measured herbivory in willow oak trees (*Quercus phellos*) in two seasons to determine how  
20 predation by birds and arthropods influenced herbivory across urban forest fragments, street trees  
21 planted near forest fragments, and downtown street trees. Predation by birds and abundance of  
22 chewing folivores were greater on trees growing in urban forest fragments than trees growing in  
23 downtown landscapes. Bird predation and herbivory levels were inconsistent for near-forest

24 trees. Arthropod predation did not statistically vary among the three urban tree habitats. Contrary  
25 to expectations based on theory, chewing folivore abundance and herbivory were generally  
26 highest on trees growing in urban forests, the most complex habitat we studied, and the habitat  
27 where predation by birds was greatest. We suggest that urban forests provide better habitat than  
28 ornamental landscapes for both urban birds and chewing folivores by having greater habitat  
29 complexity. Therefore, basal resources, such as availability of suitable habitat, mediate top-down  
30 effects on herbivores in cities.

31

32 **Keywords:** forest fragments, urban birds, defoliators, ornamental landscapes, top-down control

33

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## 45 **Introduction**

46           Urban trees provide ecosystem services for people and habitat for species. Unfortunately,  
47 urban street trees often have greater arthropod pest densities and herbivory than trees in rural  
48 forests which can reduce these services (Frankie & Ehler 1978; Dreistadt, Dahlsten & Frankie  
49 1990; Lunney & Burgin 2004; Christie & Hochuli 2005; Raupp, Shrewsbury & Herms 2010;  
50 Dale & Frank 2014). However, Kozlov et al. (2017) found lower herbivory in European cities  
51 than rural forests due to predation by birds and ants suggesting that while common, the pattern of  
52 elevated herbivory in urban ecosystems is not universal (Hochuli & Threlfall 2017). Urban trees  
53 grow in many different locations, such as along streets and in parking lots, in managed  
54 ornamental landscapes, and in forest fragments. Trees in each location likely encounter different  
55 herbivore communities which inflict different amounts of herbivory (Hanks & Denno 1993;  
56 Long, D'Amico & Frank 2019). Trees in forest fragments are often surrounded by many types of  
57 vegetation, including other trees and shrubs. Vegetation diversity and density could protect trees  
58 from herbivory through multiple ecological mechanisms, such as enhanced natural enemy  
59 abundance (Hanks & Denno 1993; Shrewsbury & Raupp 2000; Tooker & Hanks 2000) or  
60 associational resistance (Barbosa *et al.* 2009) where nearby plants help obscure host plants from  
61 their herbivores (Root 1973; Feeny 1976; Frank 2014). On the other hand, forest trees may be  
62 exposed to greater herbivore abundance and diversity and thus more herbivory than trees  
63 surrounded by pavement due to greater plant richness and abundance (Haddad *et al.* 2001;  
64 Vehviläinen, Koricheva & Ruohomäki 2007; Borer, Seabloom & Tilman 2012; Meyer *et al.*  
65 2017). Trees growing in a downtown sidewalk pit or the median of a busy street are isolated  
66 from other vegetation and exposed to abiotic stresses which can increase herbivore abundance  
67 and herbivory in some cases (Mattson & Haack 1987; Thomas & Hodkinson 1991; Cobb *et al.*

68 1997; Cregg & Dix 2001; Herms 2002; Huberty & Denno 2004) but not others (Craig *et al.*  
69 1991; Mopper & Whitham 1992; Nuckols & Connor 1995; Floater 1997; Herms 2002). Thus,  
70 urbanization can influence patterns of herbivory through biotic and abiotic mechanisms that  
71 differ based on the habitat in which a tree is growing.

72         Predation is important for regulating herbivore abundance and herbivory (Price *et al.*  
73 1980). Depauperate arthropod natural enemy communities have been blamed for damaging  
74 plant-pest densities in urban ecosystems (Hanks & Denno 1993; Shrewsbury & Raupp 2006).  
75 Urban habitats, such as those in which street trees are planted, are often characterized by low  
76 vegetation complexity and diversity (Aronson *et al.* 2017), and can negatively affect arthropod  
77 predators due to lack of refuge from intraguild predation (Finke & Denno 2002), fewer  
78 alternative resources (Lys, Zimmermann & Nentwig 1994; White *et al.* 1995), and scarcity of  
79 refuge from abiotic stress (Riechert & Bishop 1990; Grostal & O'Dowd 1994; Langellotto &  
80 Denno 2004). Birds are also important natural enemies of arthropods including defoliating  
81 herbivores like caterpillars (Holmes, Schultz & Nothnagle 1979; Woronecki & Dolbeer 1980;  
82 Moorman *et al.* 2007; Pagani-Núñez *et al.* 2017), sawflies (Buckner & Turnock 1965), katydids  
83 and grasshoppers (Bock, Bock & Grant 1992; Poulin & Lefebvre 1996; Sekercioglu *et al.* 2002;  
84 Moorman *et al.* 2007), and beetles (Sekercioglu *et al.* 2002; Moorman *et al.* 2007; Gilroy *et al.*  
85 2009). Predation by birds can decrease herbivory and increase growth in some deciduous trees  
86 (Marquis & Whelan 1994; Sipura 1999) and tropical agroforestry settings (Maas, Clough &  
87 Tschardtke 2013).

88         Bird communities in downtown urban areas, where hardscapes predominate, tend to be  
89 less diverse than those in rural areas (Germaine *et al.* 1998; Crooks, Suarez & Bolger 2004; Blair  
90 2004; La Sorte *et al.* 2018) and are largely comprised of omnivorous and granivorous species

91 (Beissinger & Osborne 1982) which may consume arthropods opportunistically but do not  
92 wholly subsist upon them (Rodewald 2015). Some urban birds have even adapted to feeding  
93 largely on human food waste and refuse (Auman, Meathrel & Richardson 2008). In contrast,  
94 rural forest bird communities are more diverse, with greater density of species (Aronson *et al.*  
95 2014), many of which are specialist insectivores (Beissinger & Osborne 1982; Marzluff 1997),  
96 that actively forage for, and subsist upon, arthropods. Thus, downtown urban bird communities  
97 might be predicted to have less potential for regulating herbivores than bird communities in  
98 urban forest fragments but there is little research on this subject (Lunney & Burgin 2004).  
99 Instead, most studies focus on rural-urban gradients and demonstrate a hump-shaped distribution  
100 where bird diversity peaks at intermediate levels of urbanization (Gaston 2010; La Sorte *et al.*  
101 2018). Therefore, it is unknown whether urban forest fragments support birds and predation  
102 services better than managed ornamental landscapes where trees may be more isolated from  
103 other vegetation.

104         The vertical distribution of vegetation varies greatly among different urban habitats (Frey  
105 *et al.* 2018) and vegetationally complex habitats support greater predation by insectivorous birds  
106 (Poch & Simonetti 2013; Muiruri, Rainio & Koricheva 2016) and greater abundance of predatory  
107 arthropods (Langellotto & Denno 2004). For example, city streets are often lined with a single  
108 species of evenly trimmed trees growing in similarly planted sidewalk medians that are subject to  
109 regular management, whereas urban forest fragments are patches of comparatively undisturbed  
110 vegetation having multiple strata made up of woody plants and herbaceous vegetation (Loram,  
111 Warren & Gaston 2008). Therefore, we hypothesize that predation of insect folivores by birds  
112 and arthropods is greater on trees growing in urban forest fragments and on near-fragment street  
113 trees than on street trees growing in downtown landscapes that are distant from forest fragments.

114 We included near-fragment street trees to determine if predation spills-over from forests into  
115 nearby ornamental landscapes. We addressed this hypothesis by measuring predation attempts on  
116 artificial plasticine larvae (Posa, Sodhi & Koh 2007) and comparing vegetation complexity  
117 among different urban habitats. Drawing from frequent observations that herbivorous arthropods  
118 attain greatest abundance in urban landscapes (reviewed by Raupp, Shrewsbury & Herms 2010)  
119 our second hypothesis is that, due to release from top-down control, herbivorous arthropods and  
120 herbivory are greatest on downtown street trees compared to street trees adjacent to forest  
121 fragments or trees actually growing in urban forest fragments. To address this hypothesis, we  
122 collected herbivorous arthropods and measured herbivory in the form of total leaf area  
123 consumed. This research will deepen our understanding about how different urban habitats  
124 support predators such as insectivorous birds and arthropods.

125

## 126 **Methods**

### 127 *Study Design:*

128 This study was conducted in Raleigh, NC USA (35.77°N, 78.64°W) which has a humid  
129 subtropical climate. Willow oak (*Quercus phellos* L., Family: Fagaceae) was the focal tree  
130 species for this study. *Quercus* hosts a wide diversity of specialist and generalist herbivores  
131 (Southwood 1961; Southwood, Moran & Kennedy 1982; Tallamy & Shropshire 2009). *Quercus*  
132 *phellos* is among the most common tree species planted in urban landscapes and growing in  
133 forests across the southeastern USA (USDA, [https://plants.usda.gov/factsheet/pdf/fs\\_quph.pdf](https://plants.usda.gov/factsheet/pdf/fs_quph.pdf)).

134 We identified 20 study trees in each of three urban habitat types: urban forest fragments,  
135 street trees planted in close proximity to urban forest fragments, and street trees planted in highly  
136 urbanized downtown landscapes which were situated far from forest fragments. The three urban

137 tree habitats will henceforth be referenced as ‘forest fragment’, ‘near-fragment’, and ‘downtown’  
138 respectively. Using maps provided by the Raleigh Department of Parks, Recreation and Cultural  
139 Resources and the North Carolina State University Office of the University Architect as  
140 references, we located forest fragments and surveyed them on foot for *Q. phellos* trees. We  
141 defined forest fragments as any space within the urban landscape which contains trees and an  
142 intact understory, shrub, groundcover, and litter layer (i.e. not being mowed, raked etc.). Forest  
143 fragment trees were always surrounded by other woody and herbaceous plants and therefore  
144 were in the most vegetationally complex habitats we studied (Figure 1A). Then, we searched the  
145 landscape surrounding each forest fragment to find the nearest planted *Q. phellos*. These trees  
146 were found growing in ornamental settings such as sidewalk and roadway medians, parking lot  
147 islands, and lawns. These near-fragment landscape trees were surrounded by a mix of grass,  
148 mulch, other woody and herbaceous ornamental plants, and impervious surface, and therefore  
149 could be considered intermediate in complexity and accessible to forest birds (Figure 1B). We  
150 also surveyed downtown Raleigh on foot to find planted *Q. phellos* growing in highly urbanized  
151 areas which were much more isolated from urban forest fragments. These downtown trees were  
152 planted near a road or sidewalk, often in narrow tree lawns or tree pits and surrounded by  
153 impervious surface, mulch, or grass and were simplest in terms of nearby vegetation complexity  
154 (Figure 1C). Fragment trees were all located in separate forest fragments and were separated by a  
155 minimum average distance of  $977.2 \pm 324.7$  (SEM) meters. All downtown trees were  $436.9 \pm$   
156  $56.1$  meters away from each other and  $2249.5 \pm 215.7$  meters from the nearest forest fragment  
157 tree. Near-fragment trees were closer, at  $36.3 \pm 3.9$  meters from the edge of the nearest forest  
158 fragment, and  $110.2 \pm 22.3$  meters from the nearest forest fragment tree, due to the nature of our  
159 question that bird and arthropod attacks spill over from forest fragments to near-fragment trees.

160 Near fragment trees were  $943.1 \pm 321.9$  meters from the closest other near-fragment tree,  $932.9 \pm$   
161  $323.4$  meters from the nearest other forest fragment tree, and  $2192.9 \pm 420.2$  meters from the  
162 nearest downtown tree.

163 We assessed local vegetation structural complexity, a measure of how densely different  
164 layers of vegetation fill a space (Parsons & Frank 2019), by adapting methods from (Schulz,  
165 Bechtold & Zarnoch 2009). We estimated percent cover of vegetation in the groundcover (0-  
166 0.61m), shrub (0.61-1.83m), understory (1.83-4.88m), and canopy (>4.88m) layers to the nearest  
167 10 percent in 5, 7-meter radius plots surrounding each tree. Plots which had less than 10 percent  
168 of cover in any layer were estimated as either 0 (no vegetation at all in the given cover layer), 1  
169 (presence of vegetation), or 5 percent. The study tree marked the location of the center plot and  
170 the four other plots were centered at 20 meters in each cardinal direction. We added the average  
171 percent cover of each layer to create a structural complexity index for habitat surrounding each  
172 tree similar to (Shrewsbury & Raupp 2000). Therefore, the maximum hypothetical index value  
173 possible would be 400 in a site where all plots had 100 percent coverage in each vegetation  
174 strata. We determined how habitat structural complexity varied among sites by specifying the  
175 structural complexity index score as the response variable and tree habitat (forest fragment, near-  
176 fragment, downtown) as categorical predictors in a Kruskal-Wallis test. We used the Steel-  
177 Dwass multiple comparisons test to evaluate pairwise differences among groups. These and all  
178 other statistical analyses were conducted using JMP ('JMP® Pro, Version 13.0.0. SAS Institute  
179 Inc., Cary, NC, 1987-2007').

180 As the percent of impervious surfaces such as buildings, roads, parking lots, and  
181 sidewalks increases, vegetation decreases (Tratalos *et al.* 2007) and across large spatial extents,  
182 means that the amount of suitable habitat for birds and predatory arthropods decreases. To obtain



183 an estimate of landscape-level vegetation coverage we used ArcGIS software to conduct an Iso-  
184 Cluster Unsupervised Classification on a 1-meter resolution raster image of the study region in  
185 which we masked out water and classified everything else as either vegetation or impervious  
186 surface. We then overlaid the coordinate points for each tree and calculated the proportion of  
187 vegetation within a 250-meter radius. Using a Kruskal-Wallis test we compared the proportion of  
188 vegetation coverage among each of the urban habitat types to substantiate that our tree selection  
189 resulted in differences in vegetation coverage among treatments.

190 *Bird and Arthropod Predation:*

191 Model caterpillars (approx. 40mm long, 5mm in diameter, and 2 grams) were constructed  
192 from green plasticine clay (Plastilina, Sargent Art, Hazelton, PA USA) a non-toxic, non-  
193 hardening, mineral-based modeling clay. When a bird or insect attacks the caterpillar model it  
194 leaves beak or mandible impressions in the soft clay. We glued one caterpillar model to a branch  
195 in each study tree between 1.5 and 3.5 meters above the ground (Figure 2A) on July 17, July 24,  
196 July 31, August 7, 2017 (henceforth called ‘summer’) and 7, 14, 21, 28 May 2018 (henceforth  
197 called ‘spring’). Each caterpillar was left for one week, but the number of bird (Figure 2B) and  
198 insect attacks (Figure 2C, 2D) were recorded on the 3rd and 7th day after placement. It was  
199 necessary to examine each model twice per week to minimize the frequency at which older  
200 attacks were obscured by more recent attacks. Multiple marks by the same type of predator were  
201 considered a single attack unless it could be discerned that the imprints were from different  
202 species (differences in size, shape, depth) or individuals attacking at different times (dirt or  
203 debris had settled onto older attacks). When imprints overlapped and the number of attacks could  
204 not be discerned, we counted it as a single bird or arthropod attack. Damaged caterpillars were  
205 repaired, by smoothing marks from the clay, or replaced as necessary. We removed the

206 caterpillar models on the seventh day after placement and glued a new caterpillar onto a different  
207 branch in the same tree, which initiated the next seven-day observation interval. We calculated  
208 the total number of attacks by birds and arthropods per tree for both summer and spring. To  
209 determine how attacks on model caterpillars differed among urban tree habitats we specified the  
210 number of attacks by birds or arthropods as separate response variables and the tree habitat as  
211 categorical predictors using a Kruskal-Wallis test. We used the Steel-Dwass multiple  
212 comparisons test to evaluate pairwise differences among groups.

213

#### 214 *Leaf-Chewing Herbivore Abundance and Richness:*

215         Arthropods were collected on August 15-16, 2017 and May 28-June 1, 2018 using a  
216 funnel beat sampler constructed of a 30.5 cm diameter funnel fixed to a 2.5 m pole (Sperry *et al.*  
217 2001; Meineke *et al.* 2016). The funnel is mounted to a telescoping pole and covered by a hinged  
218 lid which is attached to a rope that allows the user to beat leaves and branches over the funnel  
219 thus dislodging arthropods. The arthropods fall into a 50 ml. vial attached to the bottom of the  
220 funnel and are fixed in 70% ethanol. The standard sampling method was to place the open funnel  
221 beneath a branch with the lid above it and beat the same leaves 5 times. This process was  
222 repeated in six places around the lower portion (below 5.5 meters) of each tree's canopy. Since  
223 our questions focus on herbivory in which leaf area is removed by chewing insects, we identified  
224 arthropods to the family level and included any families having folivorous species in abundance  
225 and richness calculations. We specified herbivore abundance or richness as the response variable  
226 to test for differences among tree locations using a Kruskal-Wallis test.

#### 227 *Herbivory:*

228 We collected two branches approximately 0.5 m long from opposite sides of each tree on  
229 August 15-16, 2017 and May 28-June 1, 2018. *Quercus* have semi-determinant growth and flush  
230 new leaves periodically throughout the growing season (Hanson *et al.* 1986; Sloan & Jacobs  
231 2016). To ensure that all the leaves were roughly the same age, and thus were exposed to  
232 herbivores for the same length of time, we examined the cut branches for evidence of second-  
233 flush foliage. If branches exhibited the presence of small, tender, lightly colored, or highly  
234 pubescent foliage apical to dark, fully expanded foliage it was deemed to be from a second flush  
235 and was removed during the summer sampling. In spring, no trees exhibited a second flush. After  
236 discarding second flush foliage we then removed all leaves from each branch and placed them  
237 into a container, which was shaken to mix the leaves. After mixing we selected 5 leaves at  
238 random from the container. We repeated this process, without replacing previously selected  
239 leaves, until 30 total leaves had been removed from the container. We then scanned these 30  
240 leaves using a desktop scanner (Epson Perfection V500 Photo) and the image was analyzed using  
241 Easy Leaf Area software (Plant Image Analysis – Department of Plant Sciences – University of  
242 California, 2013-2018) to estimate the area in cm<sup>2</sup> of each leaf. To determine the area of each  
243 leaf that was consumed by herbivores the images were imported to ImageJ 1.x software  
244 (Schneider, Rasband & Eliceiri 2012) and the missing leaf area was filled-in using the draw and  
245 fill tools. *Quercus phellos* leaves are simple ellipses, 5-12 cm long and 1-2.5 cm wide with an  
246 entire margin (Nelson *et al.* 2014), making it possible to estimate the entire leaf silhouette. We  
247 next analyzed the corrected image using Easy Leaf Area to obtain an estimate of intact leaf area.  
248 We subtracted the uncorrected leaf area from the corrected area of each leaf to obtain the area in  
249 cm<sup>2</sup> that had been consumed by chewing folivores. To test for differences in herbivory among  
250 tree locations we used one-way ANOVA and specified the leaf area consumed by herbivores as

251 the response variable. We used Tukey's HSD to test for pairwise differences among tree  
252 locations. For continuity, one technician estimated the missing area of all leaves.

253

## 254 **Results**

### 255 *Local Habitat Complexity and Landscape Vegetation Cover:*

256 Structural complexity index scores for habitats surrounding each tree ranged from a low  
257 of 2.4 in one downtown site to 306 in one forest fragment. The overall test of structural  
258 complexity was significant ( $X_2=46.78$ ,  $P<0.001$ ). Forest fragment trees were surrounded by  
259 greater structural complexity than either near-fragment ( $Z=5.39$ ,  $P<0.001$ ) or downtown trees  
260 ( $Z=5.40$ ,  $P<0.001$ ). Near-fragment trees also had greater structural complexity than downtown  
261 trees ( $Z=4.06$ ,  $P<0.001$ ). Landscape-level vegetation coverage ranged from a minimum of 24.7%  
262 to 90.1%. The overall test of vegetation coverage was significant ( $X_2=13.49$ ,  $P=0.001$ ). Forest  
263 fragment trees had more vegetation coverage within a 250-meter radius than downtown trees  
264 ( $Z=3.18$ ,  $P<0.004$ ). There was no significant difference between vegetation coverage  
265 surrounding forest fragment and near-fragment trees ( $Z=0.50$ ,  $P=0.871$ ). Near-fragment trees  
266 also had more vegetation coverage within 250 meters than downtown trees ( $Z=3.09$ ,  $P<0.006$ ).

### 267 *Bird and Arthropod Predation:*

268 Across both seasons of the study, birds made 20.6% more predation attempts in forest  
269 fragments than arthropods. In near-fragment trees arthropods made 15.3% more attacks than  
270 birds. Downtown, arthropods made 30.0% more attacks than birds (Online Resource 1). In  
271 summer, the overall test of bird predation was significant ( $X_2=8.47$ ,  $P=0.015$ ) (Figure 3A) such  
272 that there were more bird attacks on caterpillar models in forest fragments than downtown trees  
273 ( $Z=2.83$ ,  $P<0.013$ ). There was no difference in the number of attacks between forest fragment

274 and near-fragment trees ( $Z=1.36$ ,  $P=0.36$ ) or near-fragment and downtown trees ( $Z=1.64$ ,  
275  $P=0.23$ ). In spring, the overall test of bird predation was significant ( $X_2=23.51$ ,  $P<0.001$ ) (Figure  
276 3B) such that there were more bird attacks on caterpillar models in forest fragments than near-  
277 fragment or downtown trees ( $Z=3.78$ ,  $P<0.001$  and  $Z=4.35$ ,  $P<0.001$  respectively). There was no  
278 difference in the number of attacks between near-fragment and downtown trees ( $Z=1.03$ ,  
279  $P=0.56$ ). The overall test of arthropod predation was not significant during summer ( $X_2=2.36$ ,  
280  $P=0.31$ ) or spring ( $X_2=0.91$ ,  $P=0.63$ ) (Figures 4A, 4B respectively).

### 281 *Chewing Folivore Abundance and Richness:*

282 In summer, lepidopteran larvae from six taxa represented 50% of folivores caught. In  
283 spring, lepidopteran larvae represented 18% of the catch and chrysomelids accounted for 49%  
284 (Online Resource 2). In summer, the overall test of leaf feeding herbivore abundance was  
285 significant ( $X_2=15.30$ ,  $P<0.001$ ) (Figure 5A) with fewer herbivores in downtown and near-  
286 fragment trees ( $Z=-3.90$ ,  $P<0.001$  and  $Z=-2.59$ ,  $P=0.03$  respectively) than forest fragment trees.  
287 There was no difference in the abundance of herbivores between near-fragment and forest  
288 fragment trees ( $Z=-1.36$ ,  $P=0.36$ ). The model of herbivore abundance was also significant the  
289 following spring ( $X_2=9.12$ ,  $P=0.01$ ) (Figure 5B) with leaf-chewing herbivores less abundant on  
290 near-fragment ( $Z=-2.63$ ,  $P=0.02$ ) and downtown trees ( $Z=-2.46$ ,  $P=0.04$ ) than forest fragment  
291 trees. There was no difference in chewing folivore abundance between downtown and near-  
292 fragment trees ( $Z=0.30$ ,  $P=0.95$ ). The overall model for chewing folivore richness was  
293 significant in summer ( $X_2=16.88$ ,  $P<0.001$ ) (Figure 5C) with downtown trees having lower  
294 richness than forest fragment or near-fragment trees ( $Z=-4.11$ ,  $P<0.001$  and  $Z=-2.74$ ,  $P=0.01$   
295 respectively). Herbivore richness did not differ among near-fragment and forest fragment trees  
296 ( $Z=-1.36$ ,  $P=0.36$ ). The overall model for chewing folivore richness was significant in spring as

297 well ( $X_2=8.97$ ,  $P=0.01$ ) (Figure 5D) with downtown and near-fragment trees having lower  
298 richness than forest fragment trees ( $Z=-2.63$ ,  $P=0.02$  and  $Z=-2.43$ ,  $P=0.04$  respectively). There  
299 was no difference in richness between downtown and near-fragment trees ( $Z=0.09$ ,  $P=0.99$ ).

### 300 *Herbivory:*

301 By summer, leaf-chewing herbivores had consumed 22.3% of the leaf area across all  
302 habitats. But in spring they had consumed 11.2% of leaf area across habitats. In summer, the  
303 overall model for herbivory was significant ( $F_{2,57}=21.70$ ,  $P<0.001$ ) (Figure 6A) with *Q. phellos*  
304 growing in urban forest fragments having more of their leaf area consumed by chewing folivores  
305 than near-fragment ( $t=4.43$ ,  $P<0.001$ ) or downtown trees ( $t=6.44$ ,  $P<0.001$ ). There was no  
306 difference in the leaf area consumed between near-fragment and downtown trees ( $t=2.01$ ,  
307  $P=0.12$ ). Herbivory was also significant in the spring ( $F_{2,57}=3.49$ ,  $P=0.04$ ) (Figure 6B). Leaf area  
308 consumed by herbivores on *Q. phellos* growing in forest fragments did not differ from near-  
309 fragment ( $t=1.75$ ,  $P=0.19$ ) or downtown trees ( $t=-0.84$ ,  $P=0.68$ ). However, downtown *Q. phellos*  
310 had more leaf area consumed than near-fragment trees ( $t=-2.59$ ,  $P=0.03$ ).

311

### 312 **Discussion**

313 Ecological theory predicts that biological control by natural enemies should be high in  
314 landscapes with high vegetational diversity or structural complexity (Root 1973) but theory  
315 developed in natural or agricultural systems may not always translate to urban ecosystems  
316 (McDonnell & Pickett 1990; Grimm *et al.* 2008; Dale & Frank 2018) due to the nature of species  
317 present, distribution of habitat, and novelty of communities found there (Sattler *et al.* 2011;  
318 Braaker *et al.* 2014; Aronson *et al.* 2014). For example, urban areas are often planted with native  
319 and many exotic ornamental trees and shrubs and therefore the plant community can be quite

320 speciose. However, non-native plants support fewer primary consumers and subsequently fewer  
321 natural enemies (Burghardt, Tallamy & Shriver 2009; Burghardt *et al.* 2010) compared to a  
322 similarly diverse forest fragment. In line with theory, we found that predation by birds was more  
323 than four times greater on trees growing in urban forest fragments than trees growing in  
324 downtown landscapes. Contrary to theory and our hypothesis, predation by arthropods did not  
325 differ among the three urban habitat types. This suggests that birds and predatory arthropods  
326 utilize different habitats for foraging (Frey *et al.* 2018). For example, coccinellid beetles forage  
327 with greater efficiency in small, relatively simple habitats (Kareiva & Sahakian 1990) but at  
328 larger scales, greater habitat complexity disrupts their searching behavior and dispersal (Andow  
329 & Risch 1985; Kareiva 1987). Even a single tree may be all that is required to support some  
330 predatory arthropods (Grostal & O'Dowd 1994; Agrawal 1997; Roda *et al.* 2000). But  
331 insectivorous birds require greater heterogeneity across larger spatial extents to meet their  
332 foraging and nesting needs (MacArthur & MacArthur 1961; Blake 1983). Therefore, forest  
333 fragments are a valuable resource for insectivorous urban birds, but downtown landscape trees  
334 are more isolated from other vegetation meaning they offer fewer resources needed by birds and  
335 are less attractive to them. While we saw a strong and consistent response of bird predation in  
336 forest fragment and downtown trees, the pattern of bird predation in near-fragment trees, with  
337 respect to forest fragment and downtown trees, varied between summer and spring. Therefore,  
338 spillover of top-down control by birds from forest fragments into nearby street trees cannot be  
339 easily predicted and further suggests that increasing isolation of urban trees could reduce the  
340 abundance of insectivorous birds. We suspect that forest fragments support more insectivorous  
341 birds than other urban habitats due to our own predation findings as well as other literature which  
342 demonstrates that abundance of insectivorous birds is positively correlated with vegetation

343 diversity and habitat complexity (Bonifacio 2008). Thus, highlighting the value of forest  
344 fragments within urban landscapes and reinforcing positive effects of diverse urban habitat for  
345 natural enemies.

346         Trees growing in vegetationally complex or diverse habitats are predicted to have fewer  
347 herbivores and less herbivory due, in part, to greater biological control from arthropod and bird  
348 natural enemies (Shrewsbury & Raupp 2000; Langellotto & Denno 2004; Raupp, Shrewsbury &  
349 Herms 2010; Gámez-Virués *et al.* 2010). However, we found that urban forest fragments, the  
350 most complex of the three urban tree habitats we studied, had more herbivores and more  
351 herbivory than trees isolated in downtown urban landscapes in summer. Our findings corroborate  
352 those of Nuckols & Connor (1995) who found damage from leaf-chewing insects to be  
353 consistently higher on trees in natural forests than those planted in ornamental settings. They  
354 posited that reduced leaf herbivory may arise from lower rates of dispersal, higher levels of plant  
355 resistance, or lower survival of chewing herbivores in urban environments. Had predation by  
356 natural enemies been the only factor driving herbivore abundance, downtown trees would have  
357 had more herbivores and thus greater herbivory due to the differential natural control that we  
358 observed in the predation experiment. Gámez-Virués *et al.* (2010) also found that herbivory  
359 generally increased with complexity of habitats surrounding their study trees both with and  
360 without bird exclusion. Habitat complexity and diversity is known to increase available niches  
361 which favors arthropod abundance and diversity (Raupp *et al.* 2001; Araujo *et al.* 2006) while  
362 increasing searching time and decreasing predator efficiency (Baudry & Burel 2004; Sanders *et*  
363 *al.* 2008). Therefore, we suggest that top-down control does not solely mediate herbivory in this  
364 system but instead that habitat mediates top-down effects on herbivores and herbivory.



365           In this study, downtown trees supported fewer herbivores than trees in forest fragments  
366 and the pattern of herbivore abundance among downtown and forest trees matched the pattern of  
367 bird predation that we found in the predation study. Top-down control of herbivorous insects by  
368 birds has been well-documented using exclusion studies (Holmes, Schultz & Nothnagle 1979;  
369 Atlegrim 1989; Bock, Bock & Grant 1992; Marquis & Whelan 1994; Gunnarsson 1996;  
370 Tremblay, Mineau & Stewart 2001; Gámez-Virués *et al.* 2010; Karp *et al.* 2013) and many  
371 studies also demonstrate reductions in herbivory (Atlegrim 1989; Greenberg *et al.* 2000; Van  
372 Bael & Brawn 2005; Bael *et al.* 2008; Böhm, Wells & Kalko 2011). However, each of these  
373 studies also acknowledge that other factors such as plant diversity, complexity of habitat, or plant  
374 defense also contribute to herbivore abundance and herbivory.

375           The herbivory we observed in summer followed the same pattern as bird predation and  
376 herbivore abundance by decreasing from greatest in forest fragment trees to lowest in downtown  
377 trees. However, in spring, herbivory between forest and downtown trees did not differ even  
378 though defoliating arthropods were nearly three times less abundant on downtown than forest  
379 trees. The inconsistency we observed between herbivore abundance and herbivory during spring  
380 could be due to short-lived insect outbreaks, which are common among urban trees. For  
381 example, *Q. phellos* in urban areas of the southeastern and mid-Atlantic USA are subject to  
382 outbreaks of the defoliating pests spring cankerworm, fall cankerworm (Noukoun, Bryant &  
383 Frank 2014; Asaro & Chamberlin 2015), and orange-striped oakworm (Coffelt & Schultz 1990).  
384 In the event of an outbreak, trees in vegetationally simple landscapes, such as sidewalk medians  
385 or parking lot islands suffer greater defoliation than trees in complex landscapes (Frank 2014).  
386 Although Frank (2014) did not test it, predation by birds in complex habitats is put forth as a  
387 possible contributing factor. We expect that under outbreak conditions downtown trees would

388 likely suffer greater defoliation than forest trees because of lower top-down control by  
389 insectivorous birds.

390         Measuring arthropod predation with plasticine caterpillars is probably limited to detecting  
391 roaming generalist predators such as ants, carabid and rove beetles, assassin bugs, and predatory  
392 wasps and does not assess contributions from parasitoids, specialist predators that rely on  
393 olfactory cues to locate prey or sit-and-wait predators like jumping spiders. Furthermore, our  
394 research focused only on leaf-chewing herbivore abundance and herbivory but other feeding  
395 guilds such as sap-feeders and leaf galls may show different patterns (Raupp, Shrewsbury &  
396 Herms 2010). Future research considering the entire natural enemy community as well as other  
397 herbivorous feeding guilds would provide an even clearer picture of how tree habitat affects  
398 natural pest control and herbivory. Future work should also address more specific questions such  
399 as how overall diversity of vegetation influences predation services in cities or how forest  
400 fragments contribute to biodiversity by quantifying bird community composition among urban  
401 habitat types. Several studies document shifts from diverse, largely insectivorous bird  
402 communities in rural forests to more homogeneous, granivorous communities in urban areas  
403 (reviewed by Chace & Walsh 2006), which should indicate lower insect predation by birds.  
404 However, Kozlov *et al.* (2017) found more bird predation in urban than rural forests which  
405 suggests that bird predation is likely not linear and can be affected by both local habitat  
406 complexity and the overall amount of habitat at the landscape-level (Frey *et al.* 2018). Other  
407 authors have demonstrated that predation rates increase in remnant habitat patches compared to  
408 continuous forests (González-Gómez, Estades & Simonetti 2006; Tscharntke *et al.* 2012;  
409 Ferrante, Lo Cacciato & Lövei 2014; Turrini, Sanders & Knop 2016; Philpott & Bichier 2017).  
410 Our research suggests a similar pattern in urban habitats, where forest fragments are habitat

411 patches which support greater bird predation, and probably greater insectivore abundance, than  
412 other urban habitats. It is important to know how various urban habitats differ in terms of  
413 insectivore community composition compared to rural forests.

414         The results of this study demonstrate that trees growing in urban forests support more  
415 chewing folivores than trees growing in downtown habitats, but also greater predation of  
416 herbivorous arthropods by birds. We suggest this is likely due to urban forests having greater  
417 vegetational complexity, and likely more insectivorous birds, which supports theory that basal  
418 resources mediate top-down effects on herbivores (Langellotto & Denno 2004). Landscape  
419 designers could take these results into consideration by adapting designs which increase woody  
420 plant heterogeneity and therefore, also increase insectivorous birds and arthropods. For example,  
421 increasing the frequency with which urban forest fragments occur on the landscape would  
422 preserve biodiversity, including insectivorous birds, and increase overall landscape  
423 heterogeneity. Urban forest fragments are a unique natural habitat occurring within highly  
424 contrived urban areas and their influence on bird predation and herbivore abundance should be  
425 considered when the aim is to promote insectivore abundance and biodiversity.

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429 **References**

- 430 Agrawal, A. (1997) Do leaf domatia mediate a plant-mite mutualism? An experimental test of  
431 the effects on predators and herbivores. *Ecological Entomology*, **22**, 371–376.
- 432 Andow, D.A. & Risch, S.J. (1985) Predation in Diversified Agroecosystems: Relations Between  
433 a Coccinellid Predator *Coleomegilla maculata* and Its Food. *The Journal of Applied*  
434 *Ecology*, **22**, 357.
- 435 Araujo, A.P.A., De Paula, J.D., Carneiro, M.A.A. & Schoereder, J.H. (2006) Effects of host plant  
436 architecture on colonization by galling insects. *Austral Ecology*, **31**, 343–348.
- 437 Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Nilon,  
438 C.H. & Vargo, T. (2017) Biodiversity in the city: key challenges for urban green space  
439 management. *Frontiers in Ecology and the Environment*, **15**, 189–196.
- 440 Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren,  
441 P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M.,  
442 Klotz, S., Kooijmans, J.L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U.,  
443 Pyšek, P., Siebert, S., Sushinsky, J., Werner, P. & Winter, M. (2014) A global analysis of  
444 the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers.  
445 *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133330.
- 446 Asaro, C. & Chamberlin, L.A. (2015) Outbreak History (1953-2014) of Spring Defoliators  
447 Impacting Oak-Dominated Forests in Virginia, with Emphasis on Gypsy Moth ( *Lymantria*  
448 *dispar* L.) and Fall Cankerworm ( *Alsophila pometaria* Harris). *American Entomologist*, **61**,  
449 174–185.
- 450 Atlegrim, O. (1989) Exclusion of birds from bilberry stands: impact on insect larval density and  
451 damage to the bilberry. *Oecologia*, **79**, 136–139.

452 Auman, H.J., Meathrel, C.E. & Richardson, A. (2008) Supersize Me: Does Anthropogenic Food  
453 Change the Body Condition of Silver Gulls? A Comparison Between Urbanized and  
454 Remote, Non-urbanized Areas. [https://doi.org/10.1675/1524-](https://doi.org/10.1675/1524-4695(2008)31[122:SMDAFC]2.0.CO;2)  
455 [4695\(2008\)31\[122:SMDAFC\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2008)31[122:SMDAFC]2.0.CO;2), **31**, 122–127.

456 Bael, S.A. Van, Philpott, S.M., Greenberg, R., Bichier, P., Barber, N.A., Mooney, K.A. &  
457 Gruner, D.S. (2008) Birds as predators in tropical agroforestry systems. *Ecology*, **89**, 928–  
458 934.

459 Van Bael, S.A. & Brawn, J.D. (2005) The direct and indirect effects of insectivory by birds in  
460 two contrasting Neotropical forests. *Oecologia*, **145**, 658–668.

461 Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009)  
462 Associational Resistance and Associational Susceptibility: Having Right or Wrong  
463 Neighbors. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 1–20.

464 Baudry, J. & Burel, F. (2004) Trophic Flows and Spatial Heterogeneity in Agricultural  
465 Landscapes. *Food Webs at the Landscape Level* (eds G.A. Polis, M.E. Power, & G.R.  
466 Huxel), pp. 317–322. University of Chicago Press, Chicago.

467 Beissinger, S.R. & Osborne, D.R. (1982) Effects of Urbanization on Avian Community  
468 Organization. *The Condor*, **84**, 75.

469 Blair, R. (2004) The Effects of Urban Sprawl on Birds at Multiple Levels of Biological  
470 Organization. *Ecology and Society*, **9**, art2.

471 Blake, J.G. (1983) Trophic Structure of Bird Communities in Forest Patches in East-Central  
472 Illinois on JSTOR. *The Wilson Bulletin*, **95**, 416–430.

473 Bock, C.E., Bock, J.H. & Grant, M.C. (1992) Effects of Bird Predation on Grasshopper Densities  
474 in an Arizona Grassland. *Ecology*, **73**, 1706–1717.

475 Böhmer, S.M., Wells, K. & Kalko, E.K. V. (2011) Top-Down Control of Herbivory by Birds and  
476 Bats in the Canopy of Temperate Broad-Leaved Oaks (*Quercus robur*) ed B. Fenton. *PLoS*  
477 *ONE*, **6**, e17857.

478 Bonifacio, R.S. (2008) *The Effects of Structural and Floristic Diversity of Shelterbelts on the*  
479 *Abundance and Diversity of Birds and Bats on Farms*. The University of Sydney, Australia.

480 Borer, E.T., Seabloom, E.W. & Tilman, D. (2012) Plant diversity controls arthropod biomass and  
481 temporal stability. *Ecology Letters*, **15**, 1457–1464.

482 Braaker, S., Ghazoul, J., Obrist, M.K. & Moretti, M. (2014) Habitat connectivity shapes urban  
483 arthropod communities: the key role of green roofs. *Ecology*, **95**, 1010–1021.

484 Buckner, C.H. & Turnock, W.J. (1965) Avian Predation on the Larch Sawfly, *Pristiphora*  
485 *Erichsonii* (HTG.), (Hymenoptera: Tenthredinidae). *Ecology*, **46**, 223–236.

486 Burghardt, K.T., Tallamy, D.W., Philips, C. & Shropshire, K.J. (2010) Non-native plants reduce  
487 abundance, richness, and host specialization in lepidopteran communities. *Ecosphere*, **1**,  
488 art11.

489 Burghardt, K.T., Tallamy, D.W. & Shriver, G.W. (2009) Impact of Native Plants on Bird and  
490 Butterfly Biodiversity in Suburban Landscapes. *Conservation Biology*, **23**, 219–224.

491 Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and*  
492 *Urban Planning*, **74**, 46–69.

493 Christie, F. & Hochuli, D. (2005) Elevated levels of herbivory in urban landscapes: Are declines  
494 in tree health more than an edge effect? *ECOLOGY AND SOCIETY*, **10**.

495 Cobb, N.S., Mopper, S., Gehring, C.A., Caouette, M., Christensen, K.M. & Whitham, T.G.  
496 (1997) Increased moth herbivory associated with environmental stress of pinyon pine at  
497 local and regional levels. *Oecologia*, **109**, 389–397.

498 Coffelt, M.A. & Schultz, P.B. (1990) Development of an Aesthetic Injury Level to Decrease  
499 Pesticide Use Against Orange striped Oakworm (Lepidoptera: Saturniidae) in an Urban Pest  
500 Management Project. *Journal of Economic Entomology*, **83**, 2044–2049.

501 Craig, T.P., Wagner, M.R., McCullough, D.G. & Frantz, D.P. (1991) Effects of experimentally  
502 altered plant moisture stress on the performance of Neodiprion sawflies. *Forest Ecology  
503 and Management*, **39**, 247–261.

504 Cregg, B.M. & Dix, M.E. (2001) Tree moisture stress and insect damage in urban areas in  
505 relation to heat island effects. *Journal of Arboriculture*, **27**.

506 Crooks, K.R., Suarez, A. V & Bolger, D.T. (2004) Avian assemblages along a gradient of  
507 urbanization in a highly fragmented landscape. *Biological Conservation*, **115**, 451–462.

508 Dale, A.G. & Frank, S.D. (2014) The effects of urban warming on herbivore abundance and  
509 street tree condition. *PloS one*, **9**, e102996.

510 Dale, A.G. & Frank, S.D. (2018) Urban plants and climate drive unique arthropod interactions  
511 with unpredictable consequences. *Current Opinion in Insect Science*, **29**, 27–33.

512 Dreistadt, S.H., Dahlsten, D.L. & Frankie, G.W. (1990) Urban Forests and Insect Ecology.  
513 *BioScience*, **40**, 192–198.

514 Feeny, P. (1976) Plant Apparency and Chemical Defense. *Biochemical Interaction Between  
515 Plants and Insects*, pp. 1–40. Springer US, Boston, MA.

516 Ferrante, M., Lo Cacciato, A. & Lövei, G.L. (2014) Quantifying predation pressure along an  
517 urbanisation gradient in Denmark using artificial caterpillars. *European Journal of  
518 Entomology*, **111**, 649–654.

519 Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex structured  
520 vegetation: Implications for prey suppression. *Ecology*, **83**, 643–652.

521 Floater, G. (1997) Rainfall, nitrogen and host plant condition: consequences for the  
522 processionary caterpillar, *Ochrogaster lunifer*. *Ecological Entomology*, **22**, 247–255.

523 Frank, S.D. (2014) Bad neighbors: urban habitats increase cankerworm damage to non-host  
524 understory plants. *Urban Ecosystems*, **17**, 1135–1145.

525 Frankie, G.W. & Ehler, L.E. (1978) Ecology of Insects in Urban Environments. *Annual Review*  
526 *of Entomology*, **23**, 367–387.

527 Frey, D., Vega, K., Zellweger, F., Ghazoul, J., Hansen, D. & Moretti, M. (2018) Predation risk  
528 shaped by habitat and landscape complexity in urban environments ed M. Stanley. *Journal*  
529 *of Applied Ecology*, **55**, 2343–2353.

530 Gámez-Virués, S., Gurr, G.M., Raman, A. & Nicol, H.I. (2010) Plant diversity and habitat  
531 structure affect tree growth, herbivory and natural enemies in shelterbelts. *Basic and*  
532 *Applied Ecology*, **11**, 542–549.

533 Gaston, K.J. (2010) *Urban Ecology*. Cambridge University Press.

534 Germaine, S.S., Rosenstock, S.S., Schweinsburg, R.E. & Richardson, W.S. (1998) Relationships  
535 among breeding birds, habitat, and residential development in greater Tucson, Arizona.  
536 *Ecological Applications*, **8**, 680–691.

537 Gilroy, J.J., Anderson, G.Q.A., Grice, P. V., Vickery, J.A., Watts, P.N. & Sutherland, W.J.  
538 (2009) Foraging habitat selection, diet and nestling condition in Yellow Wagtails *Motacilla*  
539 *flava* breeding on arable farmland. *Bird Study*, **56**, 221–232.

540 González-Gómez, P.L., Estades, C.F. & Simonetti, J.A. (2006) Strengthened insectivory in a  
541 temperate fragmented forest. *Oecologia*, **148**, 137–143.

542 Greenberg, R., Bichier, P., Angon, A.C., MacVean, C., Perez, R. & Cano, E. (2000) The impact  
543 of avian insectory on arthropods and leaf damage in some Guatemalan coffee plantations.



544 *Ecology*, **81**, 1750–1755.

545 Grostal, R. & O’Dowd, D.J. (1994) Plants, mites and mutualism: leaf domatia and the abundance  
546 and reproduction of mites on *Viburnum tinus* (Caprifoliaceae). *Oecologia*, **97**, 308–315.

547 Gunnarsson, B. (1996) Bird Predation and Vegetation Structure Affecting Spruce-Living  
548 Arthropods in a Temperate Forest. *The Journal of Animal Ecology*, **65**, 389.

549 Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J.M. (2001) Contrasting effects of  
550 plant richness and composition on insect communities: a field experiment. *The American*  
551 *naturalist*, **158**, 17–35.

552 Hanks, L.M. & Denno, R.F. (1993) Natural enemies and plant water relations influence the  
553 distribution of an armored scale insect. *Ecology*, **74**, 1081–1091.

554 Hanson, P.J., Dickson, R.E., Isebrands, J.G., Crow, T.R. & Dixon, R.K. (1986) A morphological  
555 index of *Quercus* seedling ontogeny for use in studies of physiology and growth. *Tree*  
556 *Physiology*, **2**, 273–281.

557 Herms, D.A. (2002) Strategies for Deployment of Insect Resistant Ornamental Plants.  
558 *Mechanisms and Deployment of Resistance in Trees to Insects*, pp. 217–237. Kluwer  
559 Academic Publishers, Dordrecht.

560 Hochuli, D.F. & Threlfall, C.G. (2017) Planning for protection : Promoting pest suppressing  
561 urban landscapes through habitat management. *Urban Biodiversity From Research to*  
562 *Practice* (eds O. Alessandra & N. Jari), pp. 54–70. Routledge.

563 Holmes, R.T., Schultz, J.C. & Nothnagle, P. (1979) Bird Predation on Forest Insects: An  
564 Exclosure Experiment. *Science*, **206**, 462–463.

565 Huberty, A.F. & Denno, R.F. (2004) Plant water stress and its consequences for herbivorous  
566 insects: A new synthesis. *Ecology*, **85**, 1383–1398.

567 JMP® Pro, Version 13.0.0. SAS Institute Inc., Cary, NC, 1987-2007.

568 Kareiva, P. (1987) Habitat fragmentation and the stability of predator–prey interactions. *Nature*,  
569 **326**, 388–390.

570 Kareiva, P. & Sahakian, R. (1990) Tritrophic effects of a simple architectural mutation in pea  
571 plants. *Nature*, **345**, 433–434.

572 Karp, D.S., Mendenhall, C.D., Sandí, R.F., Chaumont, N., Ehrlich, P.R., Hadly, E.A. & Daily,  
573 G.C. (2013) Forest bolsters bird abundance, pest control and coffee yield ed J. Lawler.  
574 *Ecology Letters*, **16**, 1339–1347.

575 Kozlov, M. V., Lanta, V., Zverev, V., Rainio, K., Kunavin, M.A. & Zvereva, E.L. (2017)  
576 Decreased losses of woody plant foliage to insects in large urban areas are explained by bird  
577 predation. *Global Change Biology*, **23**, 4354–4364.

578 Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-  
579 structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

580 Long, L.C., D’Amico, V. & Frank, S.D. (2019) Urban forest fragments buffer trees from  
581 warming and pests. *Science of The Total Environment*, **658**, 1523–1530.

582 Loram, A., Warren, P.H. & Gaston, K.J. (2008) Urban Domestic Gardens (XIV): The  
583 Characteristics of Gardens in Five Cities. *Environmental Management*, **42**, 361–376.

584 Lunney, D. & Burgin, S. (2004) Ecology of Sydney’s urban fragments: has fragmentation taken  
585 the sting out of insect herbivory? *Forum on Urban Wildlife - More than meets the Eye*.  
586 *Royal Zoological Society of New South Wales.*, pp. 63–69. Royal Zoological Society of  
587 New South Wales, Mosman, AUSTRALIA.

588 Lys, J.-A., Zimmermann, M. & Nentwig, W. (1994) Increase in activity density and species  
589 number of carabid beetles in cereals as a result of strip-management. *Entomologia*

590 *Experimentalis et Applicata*, **73**, 1–9.

591 Maas, B., Clough, Y. & Tschardtke, T. (2013) Bats and birds increase crop yield in tropical  
592 agroforestry landscapes ed F. Courchamp. *Ecology Letters*, **16**, 1480–1487.

593 MacArthur, R.H. & MacArthur, J.W. (1961) On Bird Species Diversity. *Ecology*, **42**, 594–598.

594 Marquis, R.J. & Whelan, C.J. (1994) Insectivorous Birds Increase Growth of White Oak through  
595 Consumption of Leaf-Chewing Insects. *Ecology*, **75**, 2007–2014.

596 Marzluff, J.M. (1997) *Effects of Urbanization and Recreation on Songbirds. In: Songbird*  
597 *Ecology in Southwestern Ponderosa Pine Forests: A Literature Review. Gen. Tech. Re RM-*  
598 *GTR-292. US Department of Agriculture, Forest Service.*

599 Mattson, W.J. & Haack, R.A. (1987) The role of drought stress in provoking outbreaks of  
600 phytophagous insects. *Insect Outbreaks* (eds P. Barbosa & J. Schultz), pp. 365–407.  
601 Academic Press, San Diego, CA.

602 Meineke, E., Youngsteadt, E., Dunn, R.R. & Frank, S.D. (2016) Urban warming reduces  
603 aboveground carbon storage. *Proceedings of the Royal Society B: Biological Sciences*, **283**,  
604 20161574.

605 Meyer, S.T., Scheithe, L., Hertzog, L., Ebeling, A., Wagg, C., Roscher, C. & Weisser, W.W.  
606 (2017) Consistent increase in herbivory along two experimental plant diversity gradients  
607 over multiple years. *Ecosphere*, **8**, e01876.

608 Moorman, C.E., Bowen, L.T., Kilgo, J.C., Sorenson, C.E., Hanula, J.L., Horn, S. & Ulyshen,  
609 M.D. (2007) Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest.  
610 *Journal of Field Ornithology*, **78**, 11–20.

611 Mopper, S. & Whitham, T.G. (1992) The Plant Stress Paradox: Effects on Pinyon Sawfly Sex  
612 Ratios and Fecundity. *Ecology*, **73**, 515–525.

613 Muiruri, E.W., Rainio, K. & Koricheva, J. (2016) Do birds see the forest for the trees? Scale-  
614 dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia*, **180**,  
615 619–630.

616 Nelson, G., Earle, C.J., Spellenberg, R., More, D. & Hughes, A.K. (2014) *Trees of Eastern North*  
617 *America* (ed A.K. Hughes). Princeton University Press.

618 Noukoun, C., Bryant, G. & Frank, S.D. (2014) The Effect of Sticky Bands on Cankerworm  
619 Abundance and Defoliation in Urban Trees, Discovery Service for North Carolina State  
620 Univ Libraries. *Arboriculture & Urban Forestry*, **40**, 135–142.

621 Nuckols, M.S. & Connor, E.F. (1995) Do trees in urban or ornamental plantings receive more  
622 damage by insects than trees in natural forests? *Ecological Entomology*, **20**, 253–260.

623 Pagani-Núñez, E., Renom, M., Mateos-Gonzalez, F., Cotín, J. & Senar, J.C. (2017) The diet of  
624 great tit nestlings: Comparing observation records and stable isotope analyses. *Basic and*  
625 *Applied Ecology*, **18**, 57–66.

626 Parsons, S.E. & Frank, S.D. (2019) Urban tree pests and natural enemies respond to habitat at  
627 different spatial scales. *Journal of Urban Ecology*, **5**.

628 Philpott, S.M. & Bichier, P. (2017) Local and landscape drivers of predation services in urban  
629 gardens. *Ecological Applications*, **27**, 966–976.

630 Poch, T.J. & Simonetti, J.A. (2013) Insectivory in *Pinus radiata* plantations with different degree  
631 of structural complexity. *Forest Ecology and Management*, **304**, 132–136.

632 Posa, M.R.C., Sodhi, N.S. & Koh, L.P. (2007) Predation on artificial nests and caterpillar models  
633 across a disturbance gradient in Subic Bay, Philippines. *Journal of Tropical Ecology*, **23**,  
634 27–33.

635 Poulin, B. & Lefebvre, G. (1996) Dietary Relationships of Migrant and Resident Birds from a

636 Humid Forest in Central Panama. *The Auk*, **113**, 277–287.

637 Price, P.W., Bouton, C.E., Gross, P., McPherson, B.A., Thompson, J.N. & Weis, A.E. (1980)  
638 Interactions among three trophic levels: Influence of plants on interactions between insect  
639 herbivores and Natural Enemies. *Annual review of Ecology and Systematics*, **11**, 41–65.

640 Raupp, M.J., Shrewsbury, P.M. & Herms, D.A. (2010) Ecology of Herbivorous Arthropods in  
641 Urban Landscapes. *Annual Review of Entomology*, **55**, 19–38.

642 Raupp, M.J., Shrewsbury, P.M., Holmes, J.J. & Davidson, J.A. (2001) Plant species diversity  
643 and abundance affects the number of arthropod pests in residential landscapes. *Journal of*  
644 *Arboriculture*, **27**.

645 Riechert, S.E. & Bishop, L. (1990) Prey Control by an Assemblage of Generalist Predators:  
646 Spiders in Garden Test Systems. *Ecology*, **71**, 1441–1450.

647 Roda, A., Nyrop, J., Dicke, M. & English-Loeb, G. (2000) Trichomes and spider-mite webbing  
648 protect predatory mite eggs from intraguild predation. *Oecologia*, **125**, 428–435.

649 Rodewald, P. (ed). (2015) *The Birds of North America*. Cornell Laboratory of Ornithology,  
650 Ithaca, NY.

651 Root, R.B. (1973) Organization of a Plant-Arthropod Association in Simple and Diverse  
652 Habitats: The Fauna of Collards (*Brassica Oleracea*). *Ecological Monographs*, **43**, 95–124.

653 Sanders, D., Nickel, H., Grützner, T. & Platner, C. (2008) Habitat structure mediates top–down  
654 effects of spiders and ants on herbivores. *Basic and Applied Ecology*, **9**, 152–160.

655 Sattler, T., Obrist, M.K., Duelli, P. & Moretti, M. (2011) Urban arthropod communities: Added  
656 value or just a blend of surrounding biodiversity? *Landscape and Urban Planning*, **103**,  
657 347–361.

658 Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of

659 image analysis. *Nature methods*, **9**, 671–675.

660 Schulz, B.K., Bechtold, W.A. & Zarnoch, S.J. (2009) *Sampling and Estimation Procedures for*  
661 *the Vegetation Diversity and Structure Indicator*.

662 Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D. & Sandi, R.F. (2002)  
663 Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the*  
664 *National Academy of Sciences of the United States of America*, **99**, 263–7.

665 Shrewsbury, P.M. & Raupp, M.J. (2000) Evaluation of Components of Vegetational Texture for  
666 Predicting Azalea Lace Bug, *Stephanitis pyrioides* (Heteroptera: Tingidae), Abundance in  
667 Managed Landscapes. *Environmental Entomology*, **29**, 919–926.

668 Shrewsbury, P.M. & Raupp, M.J. (2006) Do Top-Down Or Bottom-Up Forces Determine  
669 *Stephanitis Pyrioides* Abundance In Urban Landscapes? *Ecological Applications*, **16**, 262–  
670 272.

671 Sipura, M. (1999) Tritrophic interactions: willows, herbivorous insects and insectivorous birds.  
672 *Oecologia*, **121**, 537–545.

673 Sloan, J.L. & Jacobs, D.F. (2016) Ontogeny influences developmental physiology of post-  
674 transplant *Quercus rubra* seedlings more than genotype. *Annals of Forest Science*, **73**, 987–  
675 993.

676 La Sorte, F.A., Lepczyk, C.A., Aronson, M.F.J., Goddard, M.A., Hedblom, M., Katti, M.,  
677 MacGregor-Fors, I., Mörtberg, U., Nilon, C.H., Warren, P.S., Williams, N.S.G. & Yang, J.  
678 (2018) The phylogenetic and functional diversity of regional breeding bird assemblages is  
679 reduced and constricted through urbanization. *Diversity and Distributions*, **24**, 928–938.

680 Southwood, T.R.E. (1961) The Number of Species of Insect Associated with Various Trees. *The*  
681 *Journal of Animal Ecology*, **30**, 1.

682 Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.J. (1982) The Richness, Abundance and  
683 Biomass of the Arthropod Communities on Trees. *The Journal of Animal Ecology*, **51**, 635.

684 Sperry, C.E., Chaney, W.R., Shao, G. & Sadof, C. (2001) Effects of tree density, tree species  
685 diversity, and percentage of hardscape on three insect pests of honeylocust. *Journal of*  
686 *Arboriculture*, **27**, 263–271.

687 Tallamy, D.W. & Shropshire, K.J. (2009) Ranking Lepidopteran Use of Native Versus  
688 Introduced Plants. *Conservation Biology*, **23**, 941–947.

689 Thomas, A.T. & Hodkinson, I.D. (1991) Nitrogen, Water Stress and the Feeding Efficiency of  
690 Lepidopteran Herbivores. *The Journal of Applied Ecology*, **28**, 703.

691 Tooker, J.F. & Hanks, L.M. (2000) Influence of Plant Community Structure on Natural Enemies  
692 of Pine Needle Scale (Homoptera: Diaspididae) in Urban Landscapes. *Environmental*  
693 *Entomology*, **29**, 1305–1311.

694 Tratalos, J., Fuller, R.A., Warren, P.H., Davies, R.G. & Gaston, K.J. (2007) Urban form,  
695 biodiversity potential and ecosystem services. *Landscape and Urban Planning*, **83**, 308–  
696 317.

697 Tremblay, A., Mineau, P. & Stewart, R.. (2001) Effects of bird predation on some pest insect  
698 populations in corn. *Agriculture, Ecosystems & Environment*, **83**, 143–152.

699 Tscharrntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J.,  
700 Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A.,  
701 Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D.,  
702 Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal,  
703 C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses.  
704 *Biological Reviews*, **87**, 661–685.

705 Turrini, T., Sanders, D. & Knop, E. (2016) Effects of urbanization on direct and indirect  
706 interactions in a tri-trophic system. *Ecological Applications*, **26**, 664–675.

707 Vehviläinen, H., Koricheva, J. & Ruohomäki, K. (2007) Tree species diversity influences  
708 herbivore abundance and damage: meta-analysis of long-term forest experiments.  
709 *Oecologia*, **152**, 287–298.

710 White, A.J., Wratten, S.D., Berry, N.A. & Weigmann, U. (1995) Habitat Manipulation to  
711 Enhance Biological Control of Brassica Pests by Hover Flies (Diptera: Syrphidae). *Journal*  
712 *of Economic Entomology*, **88**, 1171–1176.

713 Woronecki, P.P. & Dolbeer, R.A. (1980) The influence of insects in bird damage control.  
714 *Conference, Proceedings of the 9th Vertebrate Pest*, pp. 53–59.

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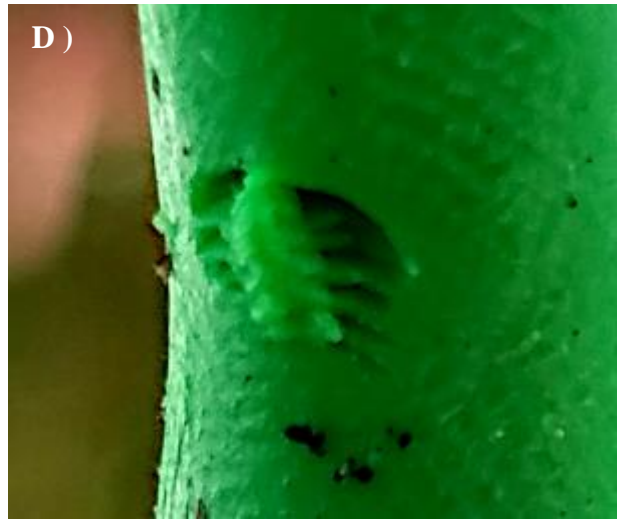


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718 Figure 1: Images showing typical habitat surrounding *Q. phellos* growing in: A) forest

719 fragments, B) near-fragments, and C) downtown.

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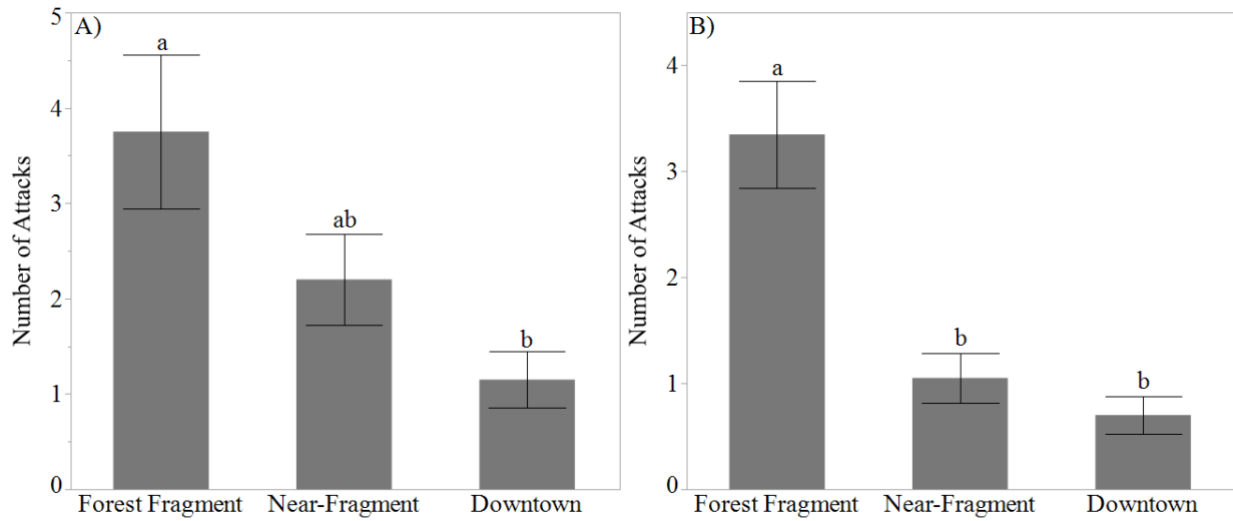
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**Figure 1:** Photos showing A) typical deployment of plasticine larva model, B) example of bird predation, C) ant predation, and D) wasp predation.



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**Figure 3:** All pairwise differences in average bird predation among urban tree habitats from

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Steel-Dwass multiple comparisons test for A) summer 2017 and B) spring 2018. Bars sharing a

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letter are not significantly different ( $P < 0.05$ ).

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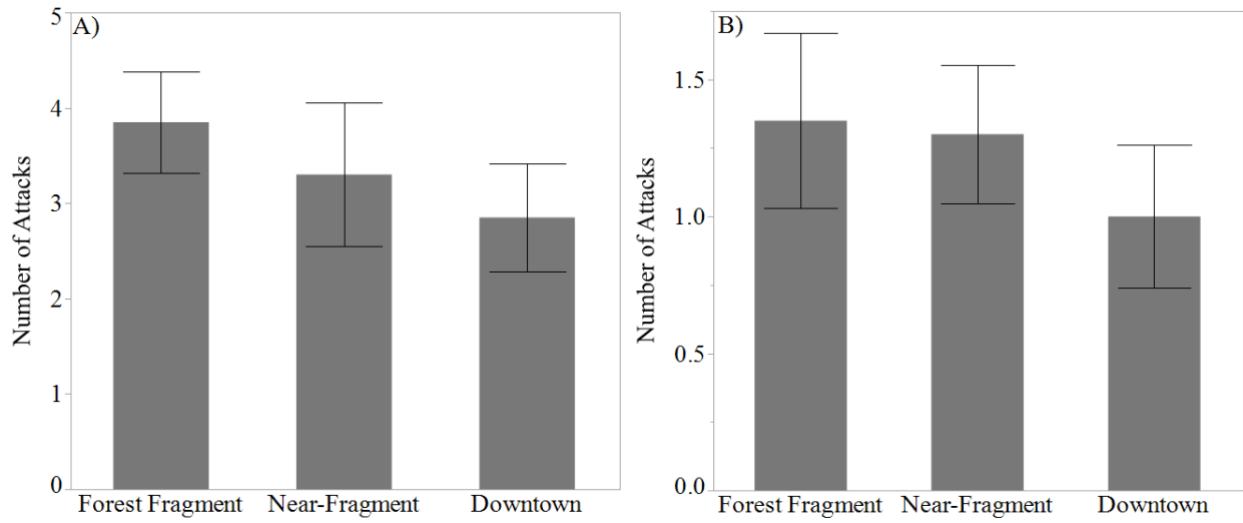
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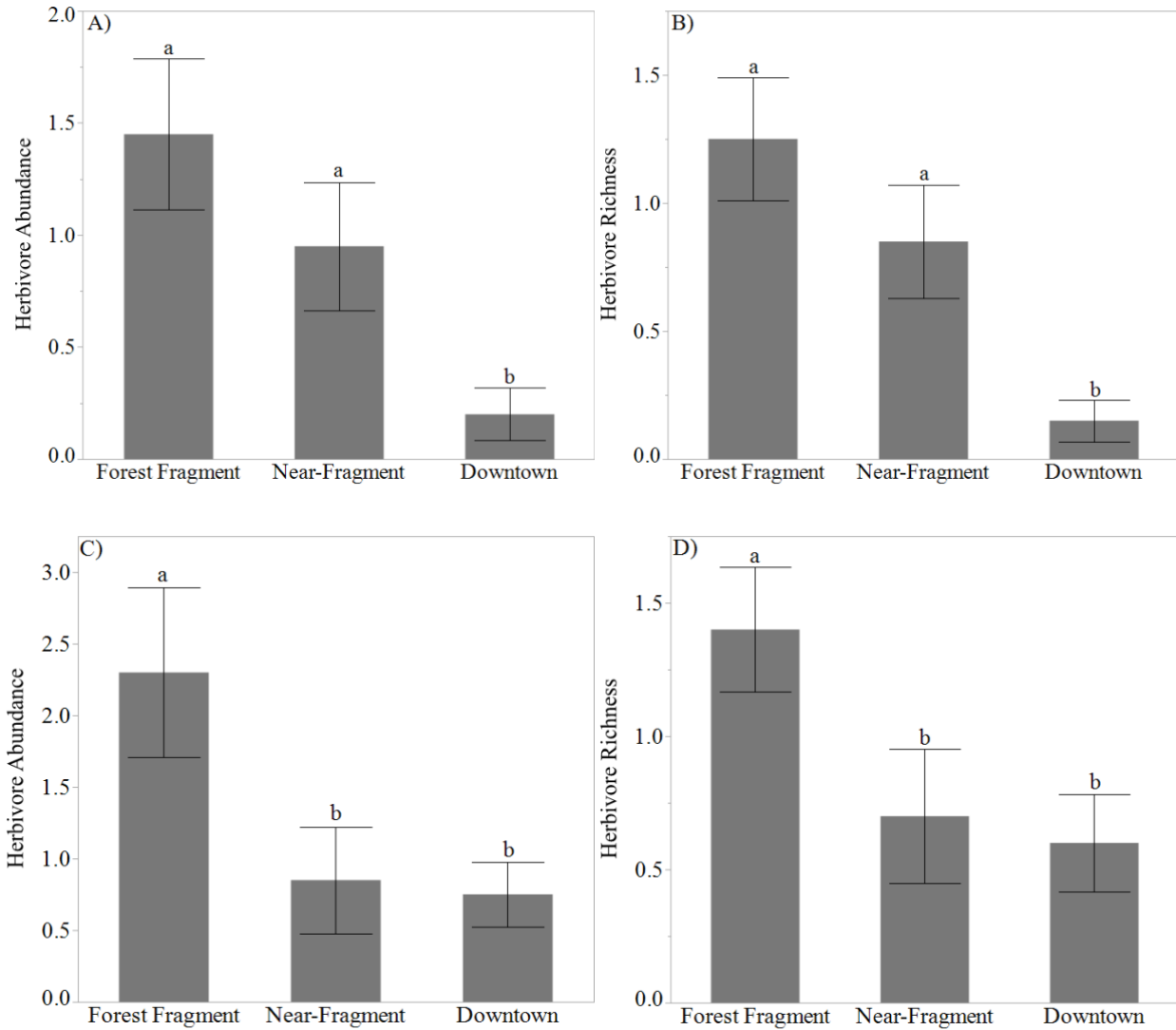
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736 **Figure 4:** All pairwise differences in average arthropod predation among urban tree habitats

737 from Steel-Dwass multiple comparisons test for A) summer 2017 and B) spring 2018.



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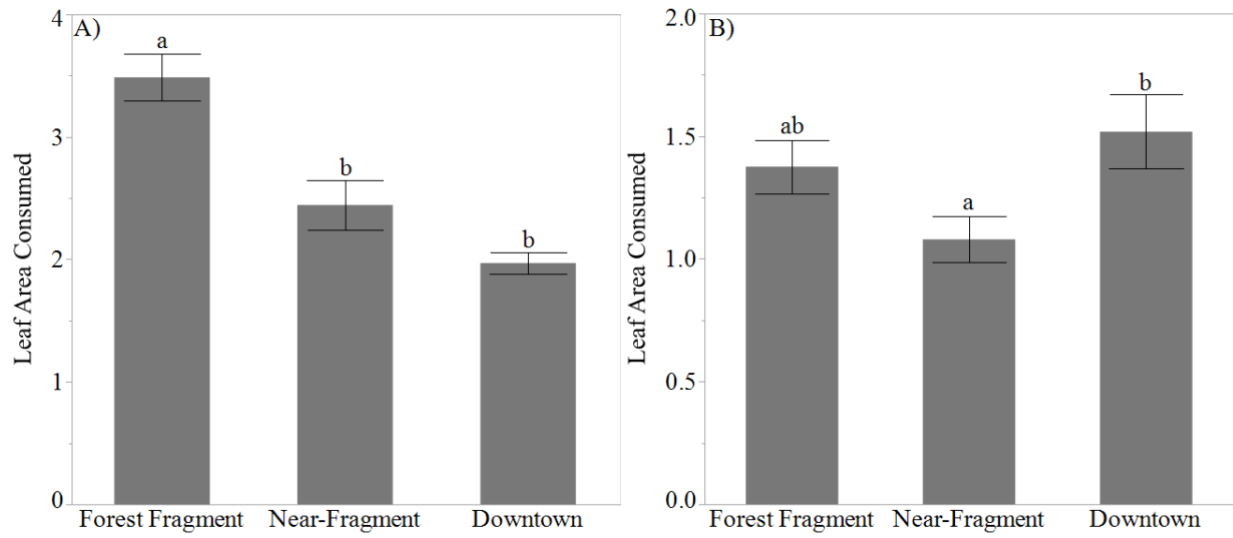
739 **Figure 5:** Pairwise differences in average leaf-chewing herbivore abundance and richness among

740 urban habitat types from Steel-Dwass method. A) summer 2017 abundance, B) summer 2017

741 richness, C) spring 2018 abundance, D) spring 2018 richness. Bars sharing a letter are not

742 significantly different ( $P < 0.05$ ).

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745 **Figure 6:** Pairwise differences in average leaf area consumed (cm<sup>2</sup>) among urban habitat types

746 from Tukey's HSD for A) summer 2017 and B) spring 2018. Bars sharing a letter are not

747 significantly different ( $P < 0.05$ ).