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

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Abstract

Predation by natural enemies is important for regulating herbivore abundance and herbivory. Theory predicts that complex habitats support more natural enemies, which exert top-down control over arthropods and therefore can reduce herbivory. However, it is unclear if theory developed in other more natural systems similarly apply to predation by vertebrate and invertebrate natural enemies across urban habitats of varying complexity. We used plasticine caterpillar models to assess bird and insect predation, collected leaf-feeding arthropods, and measured herbivory in willow oak trees (Quercus phellos) in two seasons to determine how predation by birds and arthropods influenced herbivory across urban forest fragments, street trees planted near forest fragments, and downtown street trees. Predation by birds and abundance of chewing folivores were greater on trees growing in urban forest fragments than trees growing in downtown landscapes. Bird predation and herbivory levels were inconsistent for near-forest
trees. Arthropod predation did not statistically vary among the three urban tree habitats. Contrary to expectations based on theory, chewing folivore abundance and herbivory were generally highest on trees growing in urban forests, the most complex habitat we studied, and the habitat where predation by birds was greatest. We suggest that urban forests provide better habitat than ornamental landscapes for both urban birds and chewing folivores by having greater habitat complexity. Therefore, basal resources, such as availability of suitable habitat, mediate top-down effects on herbivores in cities.

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

**Acknowledgements:**

This project was supported by Cooperative Agreement no. G15AP00153 from the United States Geological Survey. Its contents are solely the responsibility of the authors and do not necessarily represent the views of the Department of the Interior Southeast Climate Adaptation Science Center or the USGS. Funding for this work was also provided by a Southeast Climate Adaptation Science Center graduate fellowship awarded to L.C.L. This study was funded by an Agricultural and Food Research Initiative Competitive grant no. (2013-02476) and an ARDP grant no. (2016-70006-25827 from the USDA National Institute of Food and Agriculture to S.D.F.). The North Carolina State University Department of Entomology also contributed support for this research. We thank Michael Reiskind, Barbara Fair, Vince D’Amico, Rob Dunn, Michael Just and two anonymous reviewers for providing valuable comments on the manuscript.
Introduction

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

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

Bird communities in downtown urban areas, where hardscapes predominate, tend to be less diverse than those in rural areas (Germaine et al. 1998; Crooks, Suarez & Bolger 2004; Blair 2004; La Sorte et al. 2018) and are largely comprised of omnivorous and granivorous species...
which may consume arthropods opportunistically but do not wholly subsist upon them (Rodewald 2015). Some urban birds have even adapted to feeding largely on human food waste and refuse (Auman, Meathrel & Richardson 2008). In contrast, rural forest bird communities are more diverse, with greater density of species (Aronson et al. 2014), many of which are specialist insectivores (Beissinger & Osborne 1982; Marzluff 1997), that actively forage for, and subsist upon, arthropods. Thus, downtown urban bird communities might be predicted to have less potential for regulating herbivores than bird communities in urban forest fragments but there is little research on this subject (Lunney & Burgin 2004).

Instead, most studies focus on rural-urban gradients and demonstrate a hump-shaped distribution where bird diversity peaks at intermediate levels of urbanization (Gaston 2010; La Sorte et al. 2018). Therefore, it is unknown whether urban forest fragments support birds and predation services better than managed ornamental landscapes where trees may be more isolated from other vegetation.

The vertical distribution of vegetation varies greatly among different urban habitats (Frey et al. 2018) and vegetationally complex habitats support greater predation by insectivorous birds (Poch & Simonetti 2013; Muiruri, Rainio & Koricheva 2016) and greater abundance of predatory arthropods (Langellotto & Denno 2004). For example, city streets are often lined with a single species of evenly trimmed trees growing in similarly planted sidewalk medians that are subject to regular management, whereas urban forest fragments are patches of comparatively undisturbed vegetation having multiple strata made up of woody plants and herbaceous vegetation (Loram, Warren & Gaston 2008). Therefore, we hypothesize that predation of insect folivores by birds and arthropods is greater on trees growing in urban forest fragments and on near-fragment street trees than on street trees growing in downtown landscapes that are distant from forest fragments.
We included near-fragment street trees to determine if predation spills-over from forests into nearby ornamental landscapes. We addressed this hypothesis by measuring predation attempts on artificial plasticine larvae (Posa, Sodhi & Koh 2007) and comparing vegetation complexity among different urban habitats. Drawing from frequent observations that herbivorous arthropods attain greatest abundance in urban landscapes (reviewed by Raupp, Shrewsbury & Herms 2010) our second hypothesis is that, due to release from top-down control, herbivorous arthropods and herbivory are greatest on downtown street trees compared to street trees adjacent to forest fragments or trees actually growing in urban forest fragments. To address this hypothesis, we collected herbivorous arthropods and measured herbivory in the form of total leaf area consumed. This research will deepen our understanding about how different urban habitats support predators such as insectivorous birds and arthropods.

Methods

Study Design:

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

We identified 20 study trees in each of three urban habitat types: urban forest fragments, street trees planted in close proximity to urban forest fragments, and street trees planted in highly urbanized downtown landscapes which were situated far from forest fragments. The three urban
tree habitats will henceforth be referenced as ‘forest fragment’, ‘near-fragment’, and ‘downtown’ respectively. Using maps provided by the Raleigh Department of Parks, Recreation and Cultural Resources and the North Carolina State University Office of the University Architect as references, we located forest fragments and surveyed them on foot for *Q. phellos* trees. We defined forest fragments as any space within the urban landscape which contains trees and an intact understory, shrub, groundcover, and litter layer (i.e. not being mowed, raked etc.). Forest fragment trees were always surrounded by other woody and herbaceous plants and therefore were in the most vegetationally complex habitats we studied (Figure 1A). Then, we searched the landscape surrounding each forest fragment to find the nearest planted *Q. phellos*. These trees were found growing in ornamental settings such as sidewalk and roadway medians, parking lot islands, and lawns. These near-fragment landscape trees were surrounded by a mix of grass, mulch, other woody and herbaceous ornamental plants, and impervious surface, and therefore could be considered intermediate in complexity and accessible to forest birds (Figure 1B). We also surveyed downtown Raleigh on foot to find planted *Q. phellos* growing in highly urbanized areas which were much more isolated from urban forest fragments. These downtown trees were planted near a road or sidewalk, often in narrow tree lawns or tree pits and surrounded by impervious surface, mulch, or grass and were simplest in terms of nearby vegetation complexity (Figure 1C). Fragment trees were all located in separate forest fragments and were separated by a minimum average distance of $977.2 \pm 324.7$ (SEM) meters. All downtown trees were $436.9 \pm 56.1$ meters away from each other and $2249.5 \pm 215.7$ meters from the nearest forest fragment tree. Near-fragment trees were closer, at $36.3 \pm 3.9$ meters from the edge of the nearest forest fragment, and $110.2 \pm 22.3$ meters from the nearest forest fragment tree, due to the nature of our question that bird and arthropod attacks spill over from forest fragments to near-fragment trees.
Near fragment trees were 943.1 ± 321.9 meters from the closest other near-fragment tree, 932.9 ± 323.4 meters from the nearest other forest fragment tree, and 2192.9 ± 420.2 meters from the nearest downtown tree.

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

As the percent of impervious surfaces such as buildings, roads, parking lots, and sidewalks increases, vegetation decreases (Tratalos et al. 2007) and across large spatial extents, means that the amount of suitable habitat for birds and predatory arthropods decreases. To obtain
an estimate of landscape-level vegetation coverage we used ArcGIS software to conduct an Iso-
Cluster Unsupervised Classification on a 1-meter resolution raster image of the study region in
which we masked out water and classified everything else as either vegetation or impervious
surface. We then overlaid the coordinate points for each tree and calculated the proportion of
vegetation within a 250-meter radius. Using a Kruskal-Wallis test we compared the proportion of
vegetation coverage among each of the urban habitat types to substantiate that our tree selection
resulted in differences in vegetation coverage among treatments.

Bird and Arthropod Predation:

Model caterpillars (approx. 40mm long, 5mm in diameter, and 2 grams) were constructed
from green plasticine clay (Plastilina, Sargent Art, Hazelton, PA USA) a non-toxic, non-
hardening, mineral-based modeling clay. When a bird or insect attacks the caterpillar model it
leaves beak or mandible impressions in the soft clay. We glued one caterpillar model to a branch
in each study tree between 1.5 and 3.5 meters above the ground (Figure 2A) on July 17, July 24,
July 31, August 7, 2017 (henceforth called ‘summer’) and 7, 14, 21, 28 May 2018 (henceforth
called ‘spring’). Each caterpillar was left for one week, but the number of bird (Figure 2B) and
insect attacks (Figure 2C, 2D) were recorded on the 3rd and 7th day after placement. It was
necessary to examine each model twice per week to minimize the frequency at which older
attacks were obscured by more recent attacks. Multiple marks by the same type of predator were
considered a single attack unless it could be discerned that the imprints were from different
species (differences in size, shape, depth) or individuals attacking at different times (dirt or
debris had settled onto older attacks). When imprints overlapped and the number of attacks could
not be discerned, we counted it as a single bird or arthropod attack. Damaged caterpillars were
repaired, by smoothing marks from the clay, or replaced as necessary. We removed the
caterpillar models on the seventh day after placement and glued a new caterpillar onto a different
branch in the same tree, which initiated the next seven-day observation interval. We calculated
the total number of attacks by birds and arthropods per tree for both summer and spring. To
determine how attacks on model caterpillars differed among urban tree habitats we specified the
number of attacks by birds or arthropods as separate response variables and the tree habitat as
categorical predictors using a Kruskal-Wallis test. We used the Steel-Dwass multiple
comparisons test to evaluate pairwise differences among groups.

Leaf-Chewing Herbivore Abundance and Richness:

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

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

Results

Local Habitat Complexity and Landscape Vegetation Cover:

Structural complexity index scores for habitats surrounding each tree ranged from a low
of 2.4 in one downtown site to 306 in one forest fragment. The overall test of structural
complexity was significant ($X^2=46.78, P<0.001$). Forest fragment trees were surrounded by
greater structural complexity than either near-fragment ($Z=5.39, P<0.001$) or downtown trees
($Z=5.40, P<0.001$). Near-fragment trees also had greater structural complexity than downtown
trees ($Z=4.06, P<0.001$). Landscape-level vegetation coverage ranged from a minimum of 24.7%
to 90.1%. The overall test of vegetation coverage was significant ($X^2=13.49, P=0.001$). Forest
fragment trees had more vegetation coverage within a 250-meter radius than downtown trees
($Z=3.18, P<0.004$). There was no significant difference between vegetation coverage
surrounding forest fragment and near-fragment trees ($Z=0.50, P=0.871$). Near-fragment trees
also had more vegetation coverage within 250 meters than downtown trees ($Z=3.09, P<0.006$).

Bird and Arthropod Predation:

Across both seasons of the study, birds made 20.6% more predation attempts in forest
fragments than arthropods. In near-fragment trees arthropods made 15.3% more attacks than
birds. Downtown, arthropods made 30.0% more attacks than birds (Online Resource 1). In
summer, the overall test of bird predation was significant ($X^2=8.47, P=0.015$) (Figure 3A) such
that there were more bird attacks on caterpillar models in forest fragments than downtown trees
($Z=2.83, P<0.013$). There was no difference in the number of attacks between forest fragment
and near-fragment trees ($Z=1.36$, $P=0.36$) or near-fragment and downtown trees ($Z=1.64$, $P=0.23$). In spring, the overall test of bird predation was significant ($X^2=23.51$, $P<0.001$) (Figure 3B) such that there were more bird attacks on caterpillar models in forest fragments than near-fragment or downtown trees ($Z=3.78$, $P<0.001$ and $Z=4.35$, $P<0.001$ respectively). There was no difference in the number of attacks between near-fragment and downtown trees ($Z=1.03$, $P=0.56$). The overall test of arthropod predation was not significant during summer ($X^2=2.36$, $P=0.31$) or spring ($X^2=0.91$, $P=0.63$) (Figures 4A, 4B respectively).

Chewing Folivore Abundance and Richness:

In summer, lepidopteran larvae from six taxa represented 50% of folivores caught. In spring, lepidopteran larvae represented 18% of the catch and chrysomelids accounted for 49% (Online Resource 2). In summer, the overall test of leaf feeding herbivore abundance was significant ($X^2=15.30$, $P<0.001$) (Figure 5A) with fewer herbivores in downtown and near-fragment trees ($Z=-3.90$, $P<0.001$ and $Z=-2.59$, $P=0.03$ respectively) than forest fragment trees. There was no difference in the abundance of herbivores between near-fragment and forest fragment trees ($Z=-1.36$, $P=0.36$). The model of herbivore abundance was also significant the following spring ($X^2=9.12$, $P=0.01$) (Figure 5B) with leaf-chewing herbivores less abundant on near-fragment ($Z=-2.63$, $P=0.02$) and downtown trees ($Z=-2.46$, $P=0.04$) than forest fragment trees. There was no difference in chewing folivore abundance between downtown and near-fragment trees ($Z=0.30$, $P=0.95$). The overall model for chewing folivore richness was significant in summer ($X^2=16.88$, $P<0.001$) (Figure 5C) with downtown trees having lower richness than forest fragment or near-fragment trees ($Z=-4.11$, $P<0.001$ and $Z=-2.74$, $P=0.01$ respectively). Herbivore richness did not differ among near-fragment and forest fragment trees ($Z=-1.36$, $P=0.36$). The overall model for chewing folivore richness was significant in spring as
well ($X^2=8.97, P=0.01$) (Figure 5D) with downtown and near-fragment trees having lower richness than forest fragment trees ($Z=-2.63, P=0.02$ and $Z=-2.43, P=0.04$ respectively). There was no difference in richness between downtown and near-fragment trees ($Z=0.09, P=0.99$).

**Herbivory:**

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

**Discussion**

Ecological theory predicts that biological control by natural enemies should be high in landscapes with high vegetational diversity or structural complexity (Root 1973) but theory developed in natural or agricultural systems may not always translate to urban ecosystems (McDonnell & Pickett 1990; Grimm *et al.* 2008; Dale & Frank 2018) due to the nature of species present, distribution of habitat, and novelty of communities found there (Sattler *et al.* 2011; Braaker *et al.* 2014; Aronson *et al.* 2014). For example, urban areas are often planted with native and many exotic ornamental trees and shrubs and therefore the plant community can be quite
speciose. However, non-native plants support fewer primary consumers and subsequently fewer natural enemies (Burghardt, Tallamy & Shriver 2009; Burghardt et al. 2010) compared to a similarly diverse forest fragment. In line with theory, we found that predation by birds was more than four times greater on trees growing in urban forest fragments than trees growing in downtown landscapes. Contrary to theory and our hypothesis, predation by arthropods did not differ among the three urban habitat types. This suggests that birds and predatory arthropods utilize different habitats for foraging (Frey et al. 2018). For example, coccinellid beetles forage with greater efficiency in small, relatively simple habitats (Kareiva & Sahakian 1990) but at larger scales, greater habitat complexity disrupts their searching behavior and dispersal (Andow & Risch 1985; Kareiva 1987). Even a single tree may be all that is required to support some predatory arthropods (Groстал & O’Dowd 1994; Agrawal 1997; Roda et al. 2000). But insectivorous birds require greater heterogeneity across larger spatial extents to meet their foraging and nesting needs (MacArthur & MacArthur 1961; Blake 1983). Therefore, forest fragments are a valuable resource for insectivorous urban birds, but downtown landscape trees are more isolated from other vegetation meaning they offer fewer resources needed by birds and are less attractive to them. While we saw a strong and consistent response of bird predation in forest fragment and downtown trees, the pattern of bird predation in near-fragment trees, with respect to forest fragment and downtown trees, varied between summer and spring. Therefore, spillover of top-down control by birds from forest fragments into nearby street trees cannot be easily predicted and further suggests that increasing isolation of urban trees could reduce the abundance of insectivorous birds. We suspect that forest fragments support more insectivorous birds than other urban habitats due to our own predation findings as well as other literature which demonstrates that abundance of insectivorous birds is positively correlated with vegetation.
diversity and habitat complexity (Bonifacio 2008). Thus, highlighting the value of forest fragments within urban landscapes and reinforcing positive effects of diverse urban habitat for natural enemies.

Trees growing in vegetationally complex or diverse habitats are predicted to have fewer herbivores and less herbivory due, in part, to greater biological control from arthropod and bird natural enemies (Shrewsbury & Raupp 2000; Langellotto & Denno 2004; Raupp, Shrewsbury & Herms 2010; Gámez-Virués et al. 2010). However, we found that urban forest fragments, the most complex of the three urban tree habitats we studied, had more herbivores and more herbivory than trees isolated in downtown urban landscapes in summer. Our findings corroborate those of Nuckols & Connor (1995) who found damage from leaf-chewing insects to be consistently higher on trees in natural forests than those planted in ornamental settings. They posited that reduced leaf herbivory may arise from lower rates of dispersal, higher levels of plant resistance, or lower survival of chewing herbivores in urban environments. Had predation by natural enemies been the only factor driving herbivore abundance, downtown trees would have had more herbivores and thus greater herbivory due to the differential natural control that we observed in the predation experiment. Gámez-Virués et al. (2010) also found that herbivory generally increased with complexity of habitats surrounding their study trees both with and without bird exclusion. Habitat complexity and diversity is known to increase available niches which favors arthropod abundance and diversity (Raupp et al. 2001; Araujo et al. 2006) while increasing searching time and decreasing predator efficiency (Baudry & Burel 2004; Sanders et al. 2008). Therefore, we suggest that top-down control does not solely mediate herbivory in this system but instead that habitat mediates top-down effects on herbivores and herbivory.
In this study, downtown trees supported fewer herbivores than trees in forest fragments and the pattern of herbivore abundance among downtown and forest trees matched the pattern of bird predation that we found in the predation study. Top-down control of herbivorous insects by birds has been well-documented using exclusion studies (Holmes, Schultz & Nothnagle 1979; Atlegrim 1989; Bock, Bock & Grant 1992; Marquis & Whelan 1994; Gunnarsson 1996; Tremblay, Mineau & Stewart 2001; Gámez-Virués et al. 2010; Karp et al. 2013) and many studies also demonstrate reductions in herbivory (Atlegrim 1989; Greenberg et al. 2000; Van Bael & Brawn 2005; Bael et al. 2008; Böhm, Wells & Kalko 2011). However, each of these studies also acknowledge that other factors such as plant diversity, complexity of habitat, or plant defense also contribute to herbivore abundance and herbivory.

The herbivory we observed in summer followed the same pattern as bird predation and herbivore abundance by decreasing from greatest in forest fragment trees to lowest in downtown trees. However, in spring, herbivory between forest and downtown trees did not differ even though defoliating arthropods were nearly three times less abundant on downtown than forest trees. The inconsistency we observed between herbivore abundance and herbivory during spring could be due to short-lived insect outbreaks, which are common among urban trees. For example, *Q. phellos* in urban areas of the southeastern and mid-Atlantic USA are subject to outbreaks of the defoliating pests spring cankerworm, fall cankerworm (Noukoun, Bryant & Frank 2014; Asaro & Chamberlin 2015), and orange-striped oakworm (Coffelt & Schultz 1990). In the event of an outbreak, trees in vegetationally simple landscapes, such as sidewalk medians or parking lot islands suffer greater defoliation than trees in complex landscapes (Frank 2014). Although Frank (2014) did not test it, predation by birds in complex habitats is put forth as a possible contributing factor. We expect that under outbreak conditions downtown trees would
likely suffer greater defoliation than forest trees because of lower top-down control by insectivorous birds. Measuring arthropod predation with plasticine caterpillars is probably limited to detecting roaming generalist predators such as ants, carabid and rove beetles, assassin bugs, and predatory wasps and does not assess contributions from parasitoids, specialist predators that rely on olfactory cues to locate prey or sit-and-wait predators like jumping spiders. Furthermore, our research focused only on leaf-chewing herbivore abundance and herbivory but other feeding guilds such as sap-feeders and leaf gallers may show different patterns (Raupp, Shrewsbury & Herms 2010). Future research considering the entire natural enemy community as well as other herbivorous feeding guilds would provide an even clearer picture of how tree habitat affects natural pest control and herbivory. Future work should also address more specific questions such as how overall diversity of vegetation influences predation services in cities or how forest fragments contribute to biodiversity by quantifying bird community composition among urban habitat types. Several studies document shifts from diverse, largely insectivorous bird communities in rural forests to more homogeneous, granivorous communities in urban areas (reviewed by Chace & Walsh 2006), which should indicate lower insect predation by birds. However, Kozlov et al. (2017) found more bird predation in urban than rural forests which suggests that bird predation is likely not linear and can be affected by both local habitat complexity and the overall amount of habitat at the landscape-level (Frey et al. 2018). Other authors have demonstrated that predation rates increase in remnant habitat patches compared to continuous forests (González-Gómez, Estades & Simonetti 2006; Tscharntke et al. 2012; Ferrante, Lo Cacciatto & Lövei 2014; Turrini, Sanders & Knop 2016; Philpott & Bichier 2017). Our research suggests a similar pattern in urban habitats, where forest fragments are habitat
patches which support greater bird predation, and probably greater insectivore abundance, than other urban habitats. It is important to know how various urban habitats differ in terms of insectivore community composition compared to rural forests.

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


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Figure 1: Images showing typical habitat surrounding *Q. phellos* growing in: A) forest fragments, B) near-fragments, and C) downtown.
Figure 1: Photos showing A) typical deployment of plasticine larva model, B) example of bird predation, C) ant predation, and D) wasp predation.
Figure 3: All pairwise differences in average bird predation among urban tree habitats from Steel-Dwass multiple comparisons test for A) summer 2017 and B) spring 2018. Bars sharing a letter are not significantly different ($P<0.05$).
Figure 4: All pairwise differences in average arthropod predation among urban tree habitats from Steel-Dwass multiple comparisons test for A) summer 2017 and B) spring 2018.
Figure 5: Pairwise differences in average leaf-chewing herbivore abundance and richness among urban habitat types from Steel-Dwass method. A) summer 2017 abundance, B) summer 2017 richness, C) spring 2018 abundance, D) spring 2018 richness. Bars sharing a letter are not significantly different ($P<0.05$).
**Figure 6:** Pairwise differences in average leaf area consumed (cm$^2$) among urban habitat types from Tukey’s HSD for A) summer 2017 and B) spring 2018. Bars sharing a letter are not significantly different ($P<0.05$).