

Habitat usage of breeding songbirds in urban Columbus, Ohio

Thesis

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Abstract

Urbanization can have profound influences shaping patterns of songbird diversity. For many species, urbanization poses considerable challenges, yet in many instances urban areas provide important habitat for songbirds, most notably riparian urban areas. With renewed interest to maintain functioning urban forests, understanding the interactions between songbirds and their urban environments is critical to making informed land management decisions.

My research addresses habitat usage of breeding urban songbirds in Columbus, Ohio, focusing on the relationship between urban songbird presence and behavior and the vegetation in urban riparian forests. Previous songbird studies have been conducted in the Columbus metropolitan area since 2001 and have focused primarily on the impacts of urbanization on abundance, nesting, and survival. My goals for this study were to add to this knowledge base by examining potential correlations between songbird territory density and structural vegetative characteristics in urban forests and to investigate the foraging strategies of urban songbirds.

The first component of my study examines the relationship between the breeding territory densities of individual songbird species and the vegetation structure of urban sites. Given that vegetation structure has been linked to urban songbird abundance and survival, the number of trees, the size of trees, and the density of exotic or native stems in

a site may influence the territory density of certain species. I tested the hypotheses that overall songbird territory density will be greater in areas with fewer exotic stems and Neotropical territory density will increase with structural diversity. I conducted spot maps in urban riparian forests in Columbus, Ohio from late April to August in 2019 and compared these data to spot maps conducted by my colleagues in 2007 and 2011 to determine territory densities for the most common species, which included the Blue-gray Gnatcatcher, Blue Jay, Carolina Chickadee, Carolina wren, Gray Catbird, and the Northern Cardinal. We also conducted vegetation surveys during each year to quantify vegetation structure and composition changes. I developed models for each common species to predict territory density based on the measured vegetation variables. I found that large trees and year, with 2007 as the reference year were positive predictors of Blue-gray Gnatcatcher territory density and, contrary to my hypothesis, invasive exotic stems were not a negative predictor. I also found that exotic stems were a positive predictor of Northern Cardinal territory density and that medium trees were a negative predictor. My results suggest that preserving large trees is important to maintaining breeding habitat for Blue-gray Gnatcatchers in urban areas.

The second component of my study investigates the foraging strategies of breeding songbirds in urban riparian forests. Previous studies in different study systems have shown that songbirds exhibit tree-species specific foraging preferences, which may explain the avian community structure of those habitats. Given that plant species composition varies across urban forests and includes greater numbers of exotic shrubs than natural forests, identifying how songbirds use resources for foraging is important to

informing restoration efforts in regards to their conservation. I hypothesized that songbird species, such as Neotropical migrants, that have been historically more sensitive to urbanization would exhibit the strongest tree-species foraging preferences. I tested this hypothesis by comparing the tree species foraging choices of four songbird foraging guilds with the availability of each tree species. I conducted songbird foraging surveys from April to August in 2018 and 2019 and vegetation surveys to determine the tree and shrub species composition at urban riparian sites in Columbus, Ohio. I found that out of aerial insectivores, bark foragers, ground foragers, and foliage gleaners, ground foragers exhibited the strongest foraging preferences. Ground foragers showed the highest foraging preference for black cherry and the highest aversion to honey locust, osage-orange, pawpaw, and sugar maple. Considering that all four foraging guilds exhibited preferences for or did not exhibit aversions to American elm, black cherry, and silver maple, restoration efforts should consider the potential of these species (along with other goals and feasibility) to support the greatest diversity of urban songbirds.

My research shows that the structural and floristic aspects of vegetation in urban forests influence songbird foraging strategies. While territory density differences were less systematic, they do reinforce the importance that vegetation structure can have on bird assemblage. This study increases the knowledge of how breeding songbirds respond to urbanization in their territory and foraging choices, and thus, adds to the understanding of how urban forests can be restored to benefit songbirds.

In memory of my parents, Reggie and Rita Milbern, who encouraged my interests in wildlife and nature, and supported me in my pursuit of higher learning.

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Chapter 1: Introduction

Across the globe, people are increasingly moving away from rural areas and into urban environments. By 2050, 66% of the human population is expected to reside in urban areas (United Nations 2014). In the United States, developed land area is expected to increase by 50-80% between 2010 and 2100 (Sleeter et al. 2018). In light of this rapid increase in development, the impact of urbanization on biodiversity has been the focus of a large volume of research but gaps remain. We still do not understand the full extent to which urbanization alters the diet, reproduction, population dynamics, and life history of wildlife near cities (Shochat et al. 2010). Urbanization is linked to a global decrease in biodiversity, especially songbird diversity (Shochat et al. 2010, Chace & Walsh 2006). Songbirds play a critical role in urban environments by controlling pests, dispersing seeds, cycling nutrients, building nests used by other species, and providing recreational opportunities through bird watching (Whelan et al. 2008; Wenny et al. 2011). Aside from offering ecological benefits, maintaining diverse vegetation and wildlife populations in urban environments increases the wellbeing of its human inhabitants by increasing the appeal of visiting urban green spaces (Fuller et al. 2007; Hedblom et al. 2014; Wu 2014). However, therefore, ensuring the conservation of songbirds in urban environments is of great importance to urban inhabitants.

Abundance and Diversity of Songbirds in Urban Environments

Urbanization has greatly been shown to have a negative impact on songbird diversity. Most studies have supported a negative relationship between bird species

diversity and urbanization (Batten 1972; Blair 1996; Catterall et al. 2010; Fidino & Magle 2017; Goldstein et al. 1986; Hennings & Edge 2003; Pidgeon et al. 2014; Tratalos et al. 2007), with species richness occasionally highest in areas with medium urbanization levels (Marzluff 2005; Catterall et al. 2010). Therefore, identifying factors that lead to decreased diversity is important to inform songbird conservation efforts in urban areas.

Although most studies involving Neotropical migrants in urbanizing landscapes have shown a decrease in breeding abundance in relation to increasing urbanization (Friesen, Eagles, & Mackay 1995; Rodewald & Bakermans 2006; Hennings & Edge 2003), urban environments may serve as important stopover habitat for migrants. For example, Rodewald & Matthews (2005) found no correlation between Neotropical migrant abundance at stopover sites and the amount of urbanization within 1 km of the study sites in central Ohio.

Non-native songbird species are typically successful in urban environments (Blair 1996; Lussier et al. 2006; Sol et al. 2017). Blair (1996) and Lussier et al. (2006) both found an increased number of non-native and invasive songbirds in urban areas as opposed to less developed areas, which were dominated by native songbirds. Similarly, Shochat et al. (2010) found that house sparrows, European starlings, and rock pigeons made up 51% of the songbird community in urban Baltimore. Non-native songbird species may outcompete native species for resources, which may cause a decrease in urban songbird diversity (Shochat et al. 2010).

Differences in Response to Urbanization among Songbird Species

Some studies have noted a correlation between the diets of songbirds and their sensitivity to urbanization. Insectivores are especially sensitive to urbanization; their numbers have been repeatedly shown to decline with increases in urban land use (DeGraaf & Wentworth 1986; Lussier et al. 2006; Trollope et al. 2009). Conversely, Lussier et al. (2006) et al. showed that granivores responded positively to residential land use. The sensitivity difference between urban insectivores and granivores may be due to a preference for native plants among insectivores (Tallamy 2004), as supported by evidence that native plants may support higher insect densities and diversity than invasive plants (Lussier et al. 2006; Rottenborn 1999; Tallamy & Shropshire 2009). The presence of birdfeeders in highly developed areas may also increase survivorship among granivorous birds (Doherty & Grubb 2002). Likewise, there is evidence that response to urbanization differs among foraging guilds. Lussier et al. (2006) suggested that ground-gleaning bird populations increased significantly with residential land use, while bark-gleaning birds decreased with residential land use and foliage-gleaning bird populations showed no change. Similarly, Schneider & Miller (2014) found that aerial salliers responded negatively to exotic plant invasion. Additional studies are required to elucidate the factors that create this difference in response to urbanization among foraging guilds.

Predictably, songbird species that vary in their tolerance of human disturbance are also known to vary in their response to factors associated with urbanization. For example, Lussier et al. (2006) found that residential land use and impervious surface cover were negatively related to the abundance of intolerant species, such as the Acadian flycatcher

(*Empidonex virescens*), in riparian areas of Rhode Island. Tolerant species such as the Gray Catbird (*Dumetella carolinensis*), on the other hand, were positively related to urban-associated factors, including impervious surface cover, edge-to-area ratio, and invasive species cover (Lussier et al. 2006). Likewise, Evans et al. (2015) found that habitat generalists, species that can adapt to a wide variety of habitats such as the American Robin (*Turdus migratorius*), the Gray Catbird (*Dumetella carolinensis*), the Northern Cardinal (*Cardinalis cardinalis*), and the Song Sparrow (*Melospiza melodia*), experienced an increase in adult annual survivorship under moderate to high levels of urbanization, whereas obligate cavity-nesters including the Carolina Chickadee (*Poecile carolinensis*), the House Wren (*Troglodytes aedon*), and the Carolina Wren (*Thyrothorus ludovicianus*), experienced the highest annual survivorship in rural areas. This effect may be explained by a lack of tree cavities, avoidance of open area, or small forest sizes characteristic of urban environments (Blewett and Marzluff 2005; Robbins et al. 1989; Medley et al. 1995). Therefore, urbanization may harm some species of songbirds while benefiting others.

The Relationships between Urban Vegetation and Songbirds

Non-native plant species have been shown to respond positively to residential development and habitat fragmentation (Lussier et al. 2006; Schmidt & Whelan 1999). Considering that in North America, an average 35% of plant species are non-native (Clemants & Moore 2003), the relationship between non-native plants and urban songbirds is crucial to understanding the influence of urbanization on songbirds.

Non-native invasive shrubs are widely believed to act as ecological traps for nesting songbirds via higher rates of nest predation. This may be due to lower nest height and higher shrub volume surrounding nests in non-native invasive shrubs, which increases search efficiency and prey accessibility for mammalian nest predators (Borgmann & Rodewald 2004; Schmidt & Whelan 1999). Borgmann & Rodewald (2004) found that predation of Northern cardinal (*Cardinalis cardinalis*) and American Robin (*Turdus migratorius*) nests increased in invasive exotic shrubs (*Lonicera spp.* and *Rosa multiflora*) in urban landscapes but not rural landscapes. Since Northern cardinals (*Cardinalis cardinalis*) may prefer invasive exotic shrubs for nesting, exotic shrubs may act as ecological traps (Leston & Rodewald 2006). Furthermore, Rodewald, Shustack, & Hitchcock (2010) indicated that Northern cardinals (*Cardinalis cardinalis*) that nested in invasive exotic shrubs early in the breeding season fledged 20% fewer offspring than those that nested in native shrubs, but the correlation disappeared with nests attempted later in the breeding season. This may be due to the fact that more than 70% of the Northern Cardinal (*Cardinalis cardinalis*) nests were located in invasive exotic shrubs early in the breeding season and thus, predators may search invasive exotic shrubs for prey more extensively during that time (Rodewald, Shustack, & Hitchcock 2010). However, Ausprey & Rodewald (2011) reported that survival rates for Northern Cardinal (*Cardinalis cardinalis*) and Acadian flycatcher (*Empidonex virescens*) fledglings were not impacted by the percentage of Amur Honeysuckle (*Lonicera maackii*) cover. These results suggest that the effect of invasive exotic shrubs on juvenile songbird mortality in urban environments is limited to the pre-fledgling stage.

The food resources provided by non-native plants in urban habitats may also influence songbird fitness. Given the lack of evolutionary history that exists between non-native plants and native songbirds, it is widely believed that non-native plants are undesirable to native songbirds (Gleditsch 2017). However, Reichard et al. (2001) showed that non-native shrubs may provide important food resources for migrating and overwintering passerines via fruit production. Likewise, Gleditsch & Carlo (2014) suggested that the abundance of honeysuckle fruits may have been responsible for the healthy physiology they observed in gray catbird (*Dumetella carolinensis*) fledglings in honeysuckle-dominated areas. However, there are a lack of studies concerning the nutritional value of exotic shrub fruits (Lussier et al. 2006) and some songbird species, including migrants, seem to prefer native fruits (Smith et al. 2013). In sum, an abundance of food resources provided by non-native plants is preferable to a lack of food resources altogether; however, native plant species provide the best quality food for native songbirds overall.

The altered vegetation structure of urban areas may also affect songbird survival and diversity. With fewer native plants and greater numbers of exotic, ornamental plants, urban areas are not generally structured to support biodiversity since many native birds have not adapted to use nonnative vegetation (Gleditsch 2017; Lussier et al. 2006). Native songbirds typically live in structurally complex habitats dominated by native plants that vary in height and width (Hennings & Edge 2003). Woody vegetation volume, which tends to be decreased in urban environments dominated by lawn and impervious surface, has been found to have a positive relationship with songbird diversity (Goldstein

et al. 1986). Considering that urban areas tend to have simpler vegetative structure with few large plants and large areas of mowed grass or concrete, urban environments may not be able to support some songbird species due to their lack of complexity (Lussier et al. 2006).

Importance of Urban Riparian Forests for Songbirds

Despite the negative impacts of urbanization on some songbird species, urban environments, notably suburbs and remnant forests, can still support diverse songbird communities and serve as stopover habitat for migrants (Hedblom & Söderström 2010; Rodewald & Matthews 2005). Urban remnant riparian forests in particular host a high diversity of songbirds (Bennett et al. 2014), which may be due to their relatively high levels of structural vegetative complexity, tall trees, and thick vegetation characteristic of riparian forests (Sanders & Edge 1998). Bennett et al. (2014) found that riparian areas were not only inhabited by species that occupied non-riparian areas, but also by additional unique species. This may be due to the high availability of water in riparian zones, which results in more complex vegetation structure and increases the reliability and abundance of food resources, including seeds and invertebrates who often rely on water bodies for reproduction (Woinarski et al. 2000; Palmer & Bennett 2006). In addition, large older trees often occupy riparian forests, which provide shelter to songbirds via cavities and food resources via woody debris (Bennett et al. 2014). Due to the importance of riparian areas for songbird conservation, I have chosen to examine songbird use of urban riparian forest sites for my study. Songbirds have exhibited foraging preferences for certain tree species in remote riparian forests (Gabbe et al.

2002), so it is critical to evaluate how these patterns transfer to urban forests given the altered tree and shrub composition (Lussier et al. 2006; Schneider & Miller 2014).

Previous research in study area

My study is a continuation of a songbird research effort that has been conducted in urban riparian parks in Columbus, Ohio and in surrounding rural riparian areas for nearly two decades. In the summers from 2001 to 2004, songbird abundance was measured and Northern Cardinal (*Cardinalis cardinalis*) and American Robin (*Turdus migratorius*) nests were monitored along an urban-rural gradient to track nestling survival. The amount of urban development (percentage pavement, mowed lawn, etc.) within 1 km of the sites predicted greater than 94% of the variation between songbird communities, with residents and short-distance migrants being positively associated with urban development and Neotropical migrants being negatively associated (Rodewald & Bakermans 2006). Likewise, Leston & Rodewald (2006) reported that Northern Cardinals were 1.7-4x more abundant in urban sites (dependent on season) and were associated with dense understory vegetation characteristic of urban sites. They also found that Northern cardinals along the urban-rural gradient exhibited similar nesting success and survival rates. Daily mortality rates were increased for Northern Cardinal and American Robin nestlings in exotic shrubs in urban sites, which may have been due to lower nest heights and larger shrub volumes surrounding those nests (Rodewald & Borgmann 2004). Rodewald, Shustack, & Hitchcock (2010) found that Northern Cardinal nestling survival in exotic shrubs in these sites was dependent on seasonality rather than nest height, with Northern Cardinals fledging 20% fewer offspring in their first nesting attempt in an

exotic shrub than those that had first nested in native shrubs. These studies show that although the presence of exotic shrubs can have a negative effect on Northern Cardinal, urban sites can still provide sufficient breeding habitat to Northern Cardinals and that they do not act as ecological traps.

Meanwhile, in May to August from 2001 to 2006, Acadian flycatchers (*Empidonax virescens*) were banded and their nests were also monitored at the same sites surrounding Columbus, Ohio. Adult and nestling survival rates were unrelated to the degree of surrounding urbanization. However, reproductive productivity was lower in more urbanized areas; this may have been due to higher brood parasitism rates and fewer nesting attempts made in urban sites, effects that were not observed in other songbird species at these sites (Rodewald, Kearns, & Shustack 2013). Urban sites also exhibited higher rates of turnover in Acadian flycatcher occupancy (Rodewald & Shustack 2008). Brood parasitism rates were positively correlated with the number of understory stems surrounding the nest, which also increased with urbanization due to Amur honeysuckle invasion in urban sites (Rodewald 2009). These results suggest that the urban sites do not provide an optimal breeding habitat for Acadian Flycatchers.

Rodewald & Matthews (2005) examined migrant stopover usage of urban sites from 2001 to 2003 and found that the degree of surrounding urbanization was unrelated to Neotropical and temperate transient migrant abundance. From 2004 to 2007, they used radio telemetry data to investigate Swainson Thrush (*Catharus ustulatus*) stopover usage of the urban sites. Matthews & Rodewald (2010) concluded that Swainson Thrush stopover duration was also unrelated to the degree of surrounding urbanization. These

findings implicate that the study area offers important stopover habitat to migratory songbirds.

From 2004 to 2009, nest monitoring continued for five songbird species and surveys of nest predators were conducted at the Columbus sites. The number of avian and mammalian nest predators increased with the degree of surrounding urban development. However, nestling survival rates were unrelated to the number of nest predators at the urban sites, which suggests a decoupling of predator-prey relationships due to predator usage of anthropogenic resources (Rodewald, Kearns, & Shustack 2011). From 2008 to 2010, predator surveys and nest monitoring of Northern Cardinals and Acadian Flycatchers resumed to study the relationships between predator activity and nest distributions and survival (Kearns & Rodewald 2017). Similar to the previous predator study, nest survival rates were unrelated to the amount of surrounding urbanization. Predator activity predicted nest distribution and survival in that Northern Cardinals nested in areas of high avian predator usage, but nest survival only declined where mammalian predator usage was high; conversely, Acadian Flycatcher nest distribution was not associated with predator usage, but nest survival decreased in areas of high avian predator usage and low mammalian predator usage.

From 2006 to 2008, Northern Cardinal plumage coloration was studied at both the urban and rural sites (Jones, Rodewald, & Shustack 2010). They found that male plumage brightness was negatively correlated with the degree of urbanization and was not as strongly linked to body condition as the relationship observed in rural males. Likewise, Rodewald, Shustack, & Jones (2011) reported that plumage brightness in urban males

was not associated with reproductive success or the quality of their territories, which suggests that the presence of anthropogenic resources, namely birdfeeders, may have dissolved the usual link between male fitness and plumage coloration.

From 2008-2009, Acadian Flycatcher and Northern Cardinal fledglings were tracked with radio transmitters to observe the effect of Amur honeysuckle on fledgling survival and movement patterns along an urban-to-rural gradient. Ausprey & Rodewald (2011) reported that Northern Cardinal fledgling survivorship was positively associated with urbanization within the first 3 days after fledging, but there was no relationship observed for any other time post-fledging or for Acadian Flycatcher fledglings. Furthermore, there was no relationship observed between Northern Cardinal survivorship or Amur honeysuckle coverage, despite fledglings from Amur honeysuckle exhibiting lower natal ranges (Ausprey & Rodewald 2013). These results suggest that the urban forests can provide suitable breeding habitat for songbirds. Likewise, Padilla & Rodewald (2015) used spot map data from 2005 – 2011 and gathered radio telemetry data from tagged Acadian Flycatchers and Northern Cardinals to analyze the population dynamics of songbirds at the urban sites. Most of the songbird species exhibited high rates of population turnover with negative population growth rates for both Acadian Flycatchers and Northern Cardinals, which indicates that most of the urban populations function as sinks.

During the winter of 2007, honeysuckle was removed from 2 ha plots on several of the urban sites to examine interactions between songbirds and plants and to observe the effects of forest restoration on these interactions (Rodewald et al 2015). This study

built on the findings of Rodewald et al (2014), which reported that bird-plant interactions strengthened with increasing urbanization and that nest survival was decreased in areas dominated by these networks. Rodewald et al (2015) found that honeysuckle removal failed to restore natural bird-plant networks, which suggests a time lag in the effect of urban forest restoration on songbird floristic interactions.

Research Goals

Although the effects of vegetation structure on reproductive output for urban songbirds have been investigated in this study system, the relationship between vegetation structure and breeding territory density has yet to be examined (Figure 1.1). Studying breeding territory density could help elucidate how breeding urban songbirds respond to the altered vegetation structure of urban forests. For example, since understory stem density is linked to brood parasitism, do Acadian flycatchers set up fewer breeding territories at sites with greater understory stem density? Investigating the connection between breeding territory density and vegetation structure could help to inform urban restoration efforts to support breeding songbirds.

Food resources for urban songbirds have also yet to be examined in my study system. Studying the foraging behaviors and preferences of urban songbirds could help to reveal factors which may affect songbird abundance or reproductive output (Figure 1.1). For example, songbirds that are more selective in their tree-species foraging preferences may not be abundant in urban areas where their preferred foraging substrate is not as available.

My research focused on songbird habitat use and the tree-species preferences for foraging and foraging behaviors of songbirds in restored and unrestored sections of urban riparian forests in Columbus, Ohio USA. Given that tree composition in urban areas is different from natural forests, I hypothesized that the tree species on which songbirds choose to forage may also differ in urban areas. Understanding the foraging behaviors and tree-species preferences of urban songbirds may help to inform future restoration efforts in urban areas.

In my project, I will pursue the following two objectives:

1. Understand how songbird territory density is linked to the structural complexity of their habitat. I predict that songbird territory density is linked to the structural complexity of their habitat and, specifically, that songbird guilds historically more sensitive to urbanization (i.e. Neotropical migrants) will be more likely to form territories in more areas with structurally diverse trees and shrubs. I also predict that songbird diversity will have increased since invasive plant removal in 2007 (Rodewald et al 2015).
2. Understand how urban songbirds utilize their floristic environment for foraging. I aim to discover whether songbirds that breed on urban riparian forest sites have foraging preferences for certain tree species and if so, whether certain tree species play a greater role in the overall foraging ecology of the urban songbird community. I predict that songbirds will be more likely to forage on native tree and shrub species in comparison to non-native tree and shrub species.

Significance

By further examining the relationships between urban songbirds and their floristic and structural environment, I aim to contribute to the large body of research for previous urban study in this system. Specifically, the long-term effects of the previous restoration efforts on songbird communities remains unclear, and my research will help to inform future urban forest restoration. For example, understanding songbird territory traits and foraging preferences in urban forests may elucidate the factors that influence urban sites to function as population sinks (Padilla & Rodewald 2015), drive decreases in Neotropical migrant abundance (Rodewald & Bakermans 2006), or result in some species of songbirds to experience lower reproductive success in urban environments (Chamberlain et al 2009). With a better understanding of how urban songbirds interact with their environment, we can improve urban restoration efforts in regards to songbird conservation.

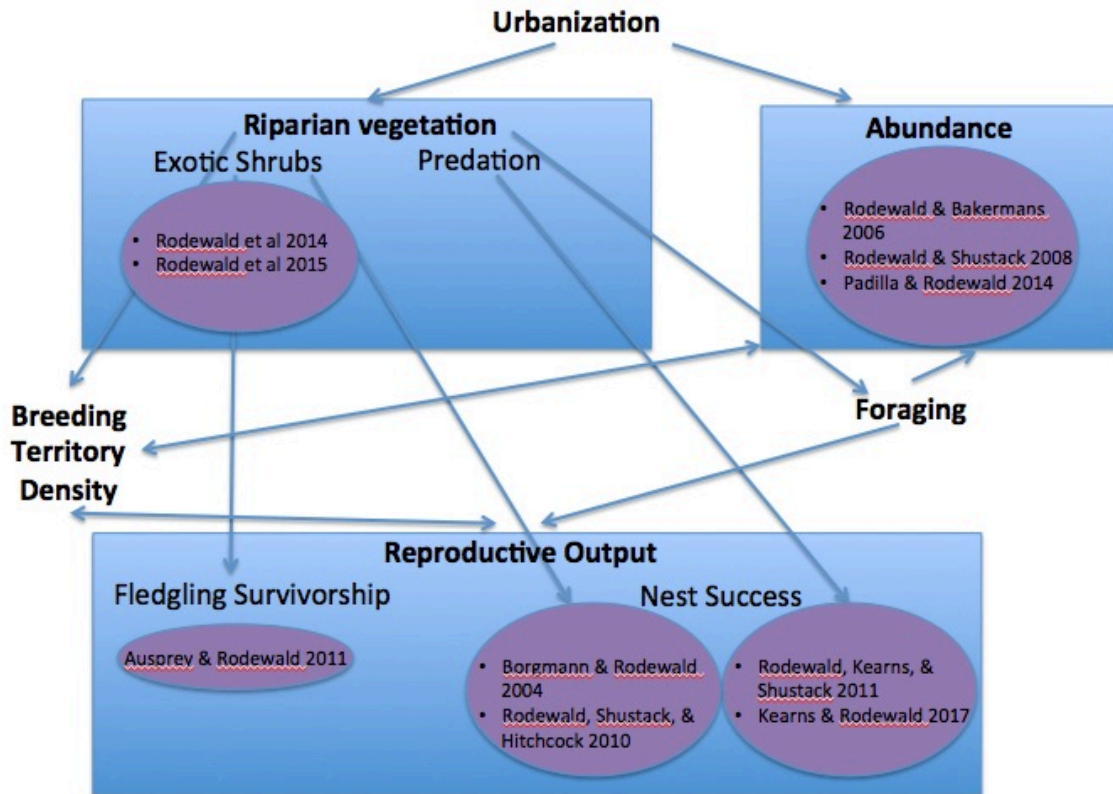


Figure 1.1. The relationships between the previous work in my study system and my current work investigating urban songbird breeding territory density and foraging behavior.

Chapter 2: Songbird territory density in relation to vegetation structure in urban forests

Introduction

Urban forests are often characterized by non-native plant invasion and decreased native plant diversity (Cadotte et al. 2017, Aronson et al. 2014). Therefore, it is important to understand how breeding songbirds respond to the altered vegetation structure and composition in urban areas (Lussier et al. 2006, Schneider & Miller 2014). Most existing literature focuses on the effects of urbanization and exotic plant invasion on songbird abundance. For example, Pennington & Blair (2011) investigated songbird abundance in relation to landscape scale and local scale vegetation characteristics in riparian forests surrounding metropolitan Cincinnati and found that native tree and understory stem frequency within the sites best explained bird distributions at a local scale, while both landscape variables and vegetation characteristics best explained the majority of species abundance patterns. The effect of vegetation structure on urban songbird abundance varies with species. For instance, resident and short-distance migrants tend to be more abundant in urban areas with dense understory vegetation and closed canopies, whereas Neotropical migrants tend to be more abundant in less developed areas with open canopies (Hennings & Edge 2003; Leston & Rodewald 2006).

Urbanization may post reproductive consequences for breeding songbirds. Breeding urban songbirds often exhibit earlier egg lay dates, lower nestling weights, smaller clutch sizes, and fewer fledglings per nesting attempt (Chamberlain et al. 2009). The dense understory vegetation and high densities of exotic shrubs typical of urban forests may pose a challenge for breeding songbirds by making it easier for predators to

search for and access nests. For example, American Robin and Northern Cardinal nestlings in exotic shrubs suffered higher daily mortality rates than those in native trees and shrubs (Borgmann & Rodewald 2004). Likewise, Acadian Flycatcher nests that were surrounded by high numbers of understory stems suffered higher rates of brood parasitism in the same study system (Rodewald 2009).

Although many studies have examined the songbird abundance and nesting success in urban habitats, few have investigated breeding territory density in urban forests. Measuring territory density provides information in regards to the density of breeding songbirds in urban forests, whereas measuring abundance only examines the density of present songbirds, regardless of whether they are breeding there (Sutherland 2006). Abundance measurements from point counts may also have greater levels of error than territory density measurements (Newell et al. 2013). Spot maps, a method for measuring territory density, may not provide as much information about reproductive success as nest studies, but spot maps are not as time intensive as nest studies and therefore, allow for a focus on a greater number of species. Furthermore, given that breeding territory density has been linked to songbird fecundity, foraging rate, territory size, and access to food resources, measuring territory density can provide insight into the suitability of habitat for breeding (Rodenhouse et al. 2003).

Considering the potential impact of exotic shrub invasions on songbirds, I aimed to understand how urban songbird territory density is linked to exotic shrub presence, the structural characteristics of their habitat, and the degree of urbanization surrounding their habitat. Furthermore, I aimed to investigate the long-term effects of honeysuckle (*Lonicera maackii*) removal in urban parks on territory density. I predicted that (1)

Neotropical migrant territory density will be greater in more complex, less invaded areas with greater numbers of small, medium, and large trees (2) songbird territory densities will have increased since the years immediately following the invasive shrub removal, and (3) resident territory density will increase with urban index whereas Neotropical migrant territory density will decrease with urban index.

Methods

Study Sites

Our study sites consist of 4 urban riparian forest sites and 2 rural riparian forest sites in the Scioto River Watershed in central Ohio (ca. 40°, -83°) and are located in and around Columbus, Ohio, a city with an estimated population of 892,533 (US Census 2018; Figure 2.1). Tuttle Park North, an urban site, is located along the Olentangy River near the northern campus of Ohio State University. Casto Park, an urban site, is located along Alum Creek near Westerville, Ohio. The other two urban sites, Rush Run Park and Kenney Park, are located between Clintonville, Ohio and Worthington, Ohio along the Olentangy River. Our 2 rural riparian forest sites are located in Three Creeks Metro Park along Blacklick Creek near Groveport, Ohio and Battelle Darby Creek Metro Park located along Big Darby Creek near Darbydale, Ohio. The major tree species at the sites include boxelder (*Acer negundo*), American elm (*Ulmus americana*), silver maple (*A. saccharinum*), sugar maple (*A. saccharum*), hackberry (*Celtis occidentalis*), eastern cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), and black walnut (*Juglans nigra*). Understory vegetation includes Amur honeysuckle (*L. maackii*),

multiflora rose (*Rosa multiflora*), spicebush (*Lindera benzoin*), hawthorn (*Crataegus spp.*), and overstory tree saplings. Honeysuckle was removed from 2 ha plots on two of the urban sites, Kenney Park and Tuttle Park, during the winter of 2007 as a part of an invasive removal experiment (Rodewald et al. 2015).

Sites were classified as either urban or rural based on the percentage of developed land (ex: pavement, concrete, buildings) within a 1 km radius using thematic mapper imagery (Leston & Rodewald 2006; ESRI, ArcView). Urban sites all had greater than 13% development surrounding them, with Casto Park at 47% development and Rush Run at 21% development within 1 km. The rural sites were characterized as having less than 8% development within a 1 km radius.

Vegetation Surveys

Vegetation composition and structure were measured in 2007, 2011, and 2019 at 5-8, 11.3 m-radius plots at each site (Rodewald et al 2015; Appendix A). Within each plot, all woody plants greater than 3 cm at diameter breast height (dbh) were counted and identified and logs, stumps, and snags greater than 7.5 cm in circumference were also counted. Woody plants were measured to nearest 0.5 cm dbh and were binned according to size: saplings (3 – 8 cm dbh), small trees (8.5 – 23 cm dbh), medium trees (23.5 – 38 cm dbh), and large trees (greater than 38 cm dbh). All forb, exotic shrub, native shrub, and tree stem hits were recorded in 1 m increments up to 3 m using a vegetation pole every 2 m along 2, 22.6 m long transects, one running east-to-west and the other running north-to-south. Canopy cover was tallied (1 if standing directly under canopy, 0 if open

sky) every 2 m along both transects and reported as a sum between 0 and 10 and averaged between the two transects. All variables were averaged among plots to calculate an overall mean for each site per year, which were used in the statistical analyses.

Avian Surveys

I conducted spot maps at each site 5-8 times during each breeding season approximately every week from the end of April through mid-July in 2018 and 2019 between 15 minutes after sunrise and 11:00 AM to locate territories within plots following the protocol defined in Bibby et al. (2012). Briefly, I systematically searched plots at a rate of approximately 2-ha per hour and recorded the locations of observed songbirds and estimated the locations of all songbirds heard. I delineated territories if a songbird of the same species was seen or heard during three visits in a range determined by its typical territory range for that species reported in previous literature (Brewer 1955; Brewer 1963; Conner et al. 1986; Cox 1984; Haggerty & Morton 1995; Root 1969; Young 1951). A countersinging event, when two male songbirds of the same species are calling back and forth to each other, was also considered when delineating territories. I mapped the territories and determined territory densities for each species at each site after the end of each breeding season. Spot map data from 2007 and 2011 were also incorporated to build models relating territory density to vegetation variables (Rodewald et al. 2015). In 2007 and 2011, territory density was determined from 10 spot map surveys per site.

Statistical Analyses

I measured the correlation between territory density in 2018 and the urban index for common species using Spearman's method. The urban index for each site was taken from Shustack & Rodewald (2008), which was calculated analyzing disturbance metrics (proportion of pavement, mowed lawn, road, agriculture, etc.) within a 1 km radius of each site. The correlations with $p < 0.05$ were considered statistically significant.

The effects of the vegetation variables (see Table 2.1) and year on territory density were analyzed for the most common species separately with a mixed-model framework using Program R (v 3.6.1; R Core Development Team 2019). Each model included site as a random effect to account for effects specific to the location. I included the following parameters as fixed effects: year, mean canopy cover, mean exotic stem count, mean native stem count, mean tree stem count, mean sapling count, mean small tree count, mean medium tree count, and mean large tree count (see Table 2.1 for detailed descriptions of variables). All variables were screened for collinearity; the only variables that had high collinearity were medium trees and large trees, but they were not incorporated together in the top models (Table A.1). Since most species exhibited low average territory counts per site per year and the data appeared right-skewed, I first used the Poisson distribution to model the data (Ramsey & Schafer 2013). I used the AER package (Kleiber & Zeileis 2008) to check for over- and under-dispersion for each species model. Considering that the data was under-dispersed for every species model except for that of the American Robin, the Conway-Maxwell-Poisson distribution was used to model territory density using the spaMM package (Lynch et al. 2014; Rousset &

Ferdy 2014). I used stepwise regression and calculated the Akaike Information Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson 2002) to examine the relationship between territory density and the vegetation parameters for each species separately. I considered models with $\Delta\text{AIC}_c < 7$ as the models with the most support (Burnham, Anderson, & Huyvert 2011). I used Akaike weights (w_i , weight of evidence for each model) to express the relative strength for each model and the likelihood that any particular model was the best possible model. I considered the models with the fewest parameters and with $\Delta\text{AIC}_c < 7$ to be the strongest. I also approximated 95% confidence intervals based on student's t – distributions for the parameters of the model with the most support and considered parameters with confidence intervals that did not overlap 0 statistically significant. Models were not averaged due to small sample size.

Results

Eastern Wood-Pewee and Blue Jay were the only species that exhibited ecologically significant correlations between territory density and degree of urbanization, with a strong negative correlation for the Eastern Wood-Pewee ($r = -0.99$, $p \sim 0$) and a marginally significant positive correlation for the Blue Jay ($r = 0.81$, $p = 0.05$; Figure 2.2). Although statistically insignificant, the Northern Cardinal and the Acadian Flycatcher also showed correlations of $r > 0.5$ between territory density and urbanization, with a positive correlation for the Northern Cardinal ($r = 0.54$, $p = 0.30$) and a negative correlation for the Acadian Flycatcher ($r = -0.70$, $p = 0.12$).

Of the 6 candidate models for Blue-gray Gnatcatchers, year + large trees was the model with the fewest parameters that best predicted territory density (Figure 2.3; Table 2.2). Three other models were within $\Delta AICc < 7$, which also included year as a predictor (Table 2.2). The top model had 36% of the total weight and predicted Blue-gray Gnatcatcher territory density as: $\log(\text{territory density}) = -0.83 + 8.29(\text{year}_{2011}) + 1.66(\text{year}_{2019}) + 0.33(\text{large trees}) + 1.36(\text{random effect})$, using year₂₀₀₇ as a reference category (Table 2.3). The 95% confidence intervals did not overlap 0 for year₂₀₁₁ and large trees (Table 2.3).

Of the 10 candidate models for Northern Cardinals, exotic stems + medium trees was the model with the most support (Figure 2.4; Figure 2.5; Table 2.4). Two other models were within $\Delta AICc < 7$, which both included exotic stems and medium trees. Since the variables medium trees and exotic stems had a correlation value of 0.25, the variables were not considered collinear and could both be incorporated into the model. The top model had 67% of the total weight and predicted Northern Cardinal territory density as: $\log(\text{territory density}) = 18.97 + 0.14(\text{exotic stems}) - 2.41(\text{medium trees}) + 1.44(\text{random effect})$ (Table 2.5). The 95% confidence intervals for exotic stems and medium trees did not overlap 0 (Table 2.5). The null models for the American Robin, Blue Jay, Carolina Chickadee, Carolina Wren, or Gray Catbird were within $\Delta AICc < 7$ of the top model and therefore were considered inconclusive.

Discussion

Songbird breeding territory density is known to fluctuate over time and can affect the reproductive performance, foraging rates, territory size, and consequently, access to food resources for individuals in the community (Rodenhause et al. 2003; Sillett et al. 2004). Territory density has been found to have a negative correlation between fecundity and a positive correlation between time spent foraging in breeding warblers (Rodenhause et al. 2003). Between breeding seasons, male songbirds may move to more desirable areas with greater food resources and fewer predators (Rodenhause et al. 2003). These results provide insights to density pattern in an urban environment where vegetation structure and time since invasive Amur honeysuckle removal appears to influence urban songbird breeding territories for some species.

Blue-gray Gnatcatcher territory density increased from 2007, the reference year, to 2011, but decreased in 2019 (Table 2.3). Contrary to my hypothesis, I found no significant negative relationship between Neotropical migrant territory density and mean exotic tree stem counts. This may have been due to small sample size for restored sites and low variation in mean exotic stem count between sites and years overall (Figure 2.6). Territory density may have been larger in 2011 in comparison to 2007 and 2019 due to territory-dependent population dynamics. Songbirds have been shown to fledge fewer offspring in breeding seasons with higher territory density due to increased competition and higher fecundity is positively related to the recruitment of yearlings in subsequent breeding seasons (Rodenhause et al. 2003). Likewise, male songbirds have been shown to choose breeding sites with greater food resources in subsequent breeding seasons

(Rodenhouse et al. 2003). The low territory density of Blue-gray Gnatcatchers in 2007 may have led to higher fecundity in the subsequent seasons, which may explain why territory density was higher in 2011. Conversely, the high territory density in 2011 could have led to increased competition for food resources and may have resulted in lower fecundity, which may have led to lower territory densities in following breeding seasons.

Large trees were also a predictor of Blue-gray Gnatcatcher territory density. Large tree count had a positive effect on territory density in the top model (Table 2.3). Given that Blue-gray Gnatcatchers nest tend to nest in the upper half of trees at an average height of 8.5 m, they may select territories that have greater numbers of large trees and therefore, greater numbers of suitable nesting sites (Kershner & Ellison 2012). However, mean large tree counts declined over time at four of the sites, Kenney North, Kenney South, Tuttle North, and Tuttle South. This may explain why temporal difference were important factor in capturing changes in density (Table 2.4; Figure 2.7; Figure A.2; Figure A.3; Figure A.5; Figure A.6). Although large trees declined, which was likely due to large ash trees dying due to emerald ash borer infestation, year was still a positive predictor of territory density, which suggests that there may have been another factor, such as Amur honeysuckle removal, that influenced an increase in territory density (Flower et al. 2013).

Exotic stem count was a predictor of small magnitude for Northern Cardinal territory density in the top model (Tables 2.4 & 2.5). My results coincide with those of previous studies in this system. Leston & Rodewald (2006) found that Northern Cardinals strongly selected habitat with dense understory vegetation characteristic of heavily

invaded, urban sites. Similarly, Ausprey & Rodewald (2011) found that post-fledgling Northern Cardinals selected habitat with complex understory vegetation, which was positively related to survivorship. In southwestern Ohio, Filiater et al. (1994) found that 65% of Northern Cardinal nests were located in Amur honeysuckle. Given Northern Cardinal preference for dense understory vegetation and the lack of evidence for decreased survivorship among fledglings in invaded areas, Northern Cardinals may select breeding territories with greater numbers of exotic stems (Ausprey & Rodewald 2011; Leston & Rodewald 2006;).

I also found that medium tree count had a large, significant effect on Northern Cardinal territory density. This negative relationship may be connected to Northern Cardinal survivorship, given that medium tree count was negatively correlated with survivorship among post-fledgling Northern Cardinals (Ausprey & Rodewald 2011). Alternatively, medium tree count may have a negative effect on territory density due to increased nest predation. Kearns & Rodewald (2017) found that Northern Cardinal nest survival was lower in areas frequently used by mammalian predators, such as squirrels. Given that Eastern Gray Squirrels are associated with trees greater than 22.8 cm dbh, Northern Cardinals may select territories with lower numbers of medium trees to avoid predation (Allen 1982).

Rodewald & Bakermans (2006) found that Neotropical migrant abundance was negatively-associated with degree of urbanization while resident abundance was positively-associated in the same study system. Similarly, my results supported this pattern with lower breeding territory densities of Neotropical migrants in urban sites.

However, I only found a significant correlation between territory density and degree of urbanization for one Neotropical migrant, the Eastern Wood-Pewee, and one resident species, the Blue Jay. Further study including a greater number of rural sites may be necessary to draw conclusions about the relationship between territory density and urbanization for other songbird species.

Limitations

Considering that only the Northern Cardinal and the Blue-gray Gnatcatcher exhibited significant relationships between territory density and the vegetation parameters, I am unable to draw any conclusions concerning the relationship between vegetation structure and the overall urban songbird community. One limitation of this study is that there were only 2 restored sites and 4 unrestored sites surveyed, and thus, there was insufficient data to measure the effect of urban forest restoration on territory density. Further study incorporating a larger sample size of restored and unrestored urban sites is necessary to form conclusions regarding the relationship between songbird species breeding territory density and urban forest structure and to elucidate the effect of restoration on songbird breeding populations.

Another limitation of this study is that 0.04 ha plots within the site were used to average the overall vegetation for the entire site. Due to variation within the site, the averages of the vegetation variables may differ from the vegetation characteristics within each territory.

Management Implications

Given that the resident species and Neotropical migrant species in this study responded differently to tree size and stem variables, maintaining structural vegetative diversity is likely important to support a diversity of breeding songbirds. Considering that Neotropical migrant populations are in decline, providing suitable habitat for them should be considered when managing and restoring urban forests (Donovan et al. 2002). Since large trees positively predicted territory density for Blue-gray Gnatcatchers, preserving older trees should be considered in urban forest management. Likewise, considering that Blue-gray Gnatcatcher territory density increased from the reference year, they may respond positively to restoration efforts that include removal of Amur honeysuckle and opening up the midstory, thus continuous treatment is likely need to prevent reinvasion of honeysuckle. Further study incorporating a larger sample size of sites throughout the urban to rural gradient would help to elucidate the effect of urbanization on the population dynamics of Neotropical migrants.

Table 2.1. Descriptions of parameters measured during vegetation surveys and used in territory density models. Vegetation surveys were conducted at 6 sites within the Columbus, Ohio metropolitan area in 2007, 2011, and 2019.

vegetation variable	Description
site	The site in which the data was collected, which was incorporated into the model as a random effect to account for site level dependencies.
year	The year in which the data was collected. 2007, the reference year, was the year of honeysuckle removal. 2011 was the last year honeysuckle was treated with herbicide.
saplings	The average number of trees in a 0.04 ha plot within site 3-8 cm dbh.
small trees	The average number of trees in a 0.04 ha plot within site 8.5-23 cm dbh.
medium trees	The average number of trees in a 0.04 ha plot within site 23.5-38 cm dbh
large trees	The average number of trees in a 0.04 ha plot within site >38 cm dbh
canopy	The average number of canopy hits in a 0.04 ha plot within site.
exotic stems	The average number of exotic stem hits in a 0.04 plot within site.
native stems	The average number of native shrub stem hits in a 0.04 plot within site.
tree stems	The average number of native tree stem hits in a 0.04 plot within site.

Table 2.2. Relative fit of models explaining Blue-Gray Gnatcatcher territory density using Akaike's Information Criterion corrected for small sample sizes (AIC_c). All models include site as a random effect. Models include year, canopy cover, and densities of exotic stems, native stems, tree stems, saplings, small trees, medium trees, and large trees (See Table 2.1 for detailed variable descriptions). Surveys were conducted at 6 sites within the Columbus, Ohio metropolitan area in 2007, 2011, and 2019. K , number of parameters; ΔAIC_c , distance from top model; w_i , model weight.

Model	LL	K	AIC_c	ΔAIC_c	w_i
year + canopy + exotic stems + native stems + tree stems	-30.04	7	45.45	0	0.36
year + large trees	-34.49	4	45.47	0.02	0.36
year + small trees + large trees	-32.98	5	46.64	1.19	0.20
year + small trees + medium trees + large trees	-31.66	6	48.47	3.02	0.08
year + sapling + small trees + medium trees + large trees	-27.19	7	53.69	8.24	0.01
null	-47.39	1	57.50	12.05	0

Table 2.3. Parameter estimates for the effect of site, year, and vegetation on Blue-gray Gnatcatcher territory density for three plausible models. Surveys were conducted at 6 sites within the Columbus, Ohio metropolitan area in 2007, 2011, and 2019.

Parameter	Estimate	SE	<i>t</i>	95% CI
Intercept	-0.83	1.50	-0.56	(-3.77, 2.11)
e _{site} (Intercept)	1.36	0.86		(0.25, 7.31)
2011*	8.29	1.45	5.72	(5.45, 11.13)
2019	1.66	1.55	1.07	(-1.38, 4.71)
large trees	0.33	0.08	4.10	(0.17, 0.49)

*2007, the year of honeysuckle removal, used as reference year.

Table 2.4. Relative fit of models explaining Northern Cardinal territory density using Akaike's Information Criterion corrected for small sample sizes (AIC_c). All models include site as a random effect. Models include year, canopy cover, and densities of exotic stems, native stems, tree stems, saplings, small trees, medium trees, and large trees (See table 1 for detailed variable descriptions). Surveys were conducted at 6 sites within the Columbus, Ohio metropolitan area in 2007, 2011, and 2019. LL, log likelihood; *K*, number of parameters; Δ AIC_c, distance from top model; *w_i*, model weight.

Model	LL	K	AIC _c	Δ AIC _c	<i>w_i</i>
exotic stems + medium trees	-24.20	4	58.51	0	0.67
year + exotic stems + medium trees	-22.56	5	60.44	1.93	0.26
year + exotic stems + small trees + medium trees	-22.28	6	63.50	4.99	0.06
year + exotic stems + small trees + medium trees + large trees	-21.66	7	66.32	7.81	0.01
year + exotic stems + saplings + small trees + medium trees	-21.38	8	70.36	11.85	0
+ large trees					
year + exotic stems	-30.11	4	72.34	13.83	0
year + exotic stems + tree stems	-29.60	5	74.54	16.03	0
year + exotic stems + native stems + tree stems	-29.80	6	78.54	20.03	0
year + canopy + exotic stems + native stems + tree stems	-30.04	7	83.07	24.56	0
null	-47.39	2	96.77	38.26	0

Table 2.5. Parameter estimates for the effect of site, year, and vegetation on Northern Cardinal territory density for two plausible models. Surveys were conducted at 6 sites within the Columbus, Ohio metropolitan area in 2007, 2011, and 2019.

Parameter	Estimate	SE	<i>T</i>	95% CI
(Intercept)	18.97	1.18	16.04	(16.65, 21.29)
$e^{\text{site (Intercept)}}$	4.22	0.69		(1.09, 16.32)
exotic stems	0.14	0.03	-6.10	(0.08, 0.19)
medium trees	-2.41	0.39	4.88	(-3.18, -1.63)

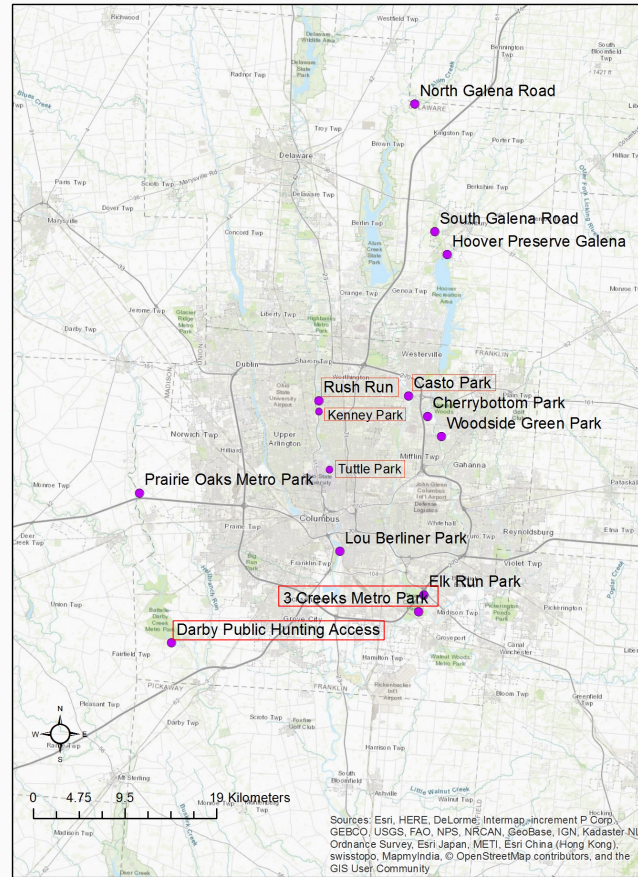


Figure 2.1. Location and names of sites used in study surrounding Columbus, Ohio. Sites used are highlighted in red.

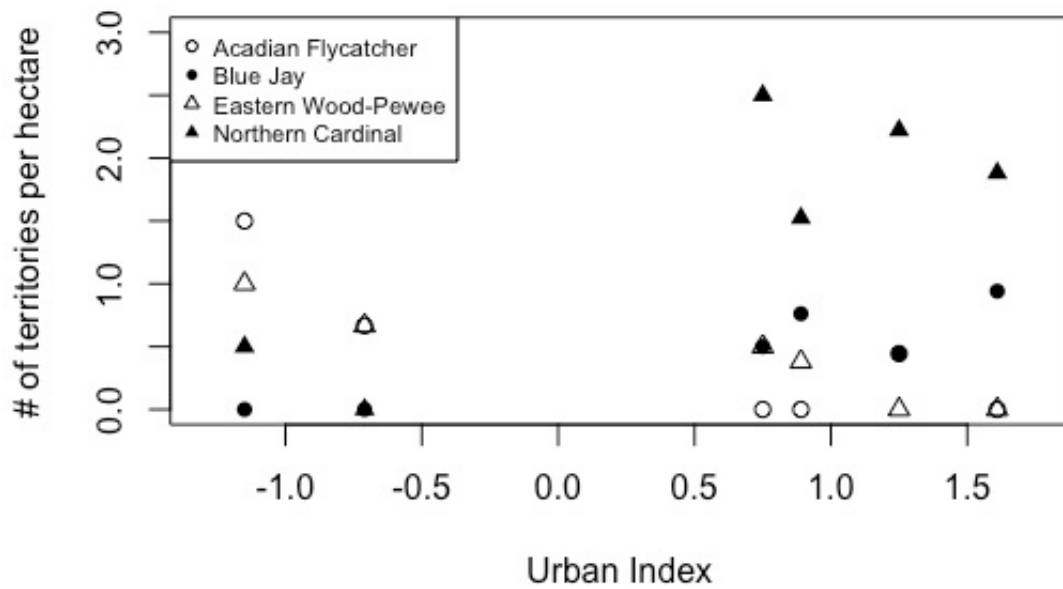


Figure 2.2. The territory density plotted against the urban index for the Northern Cardinal ($r = 0.54$, $p = .30$), Blue Jay ($r = 0.81$, $p = .05$), Acadian Flycatcher ($r = -0.70$, $p = .12$), and Eastern Wood-Pewee ($r = -0.99$, $p \sim 0$) among urban and rural sites near Columbus, Ohio in 2018. Correlation values were calculated using the Spearman's method.

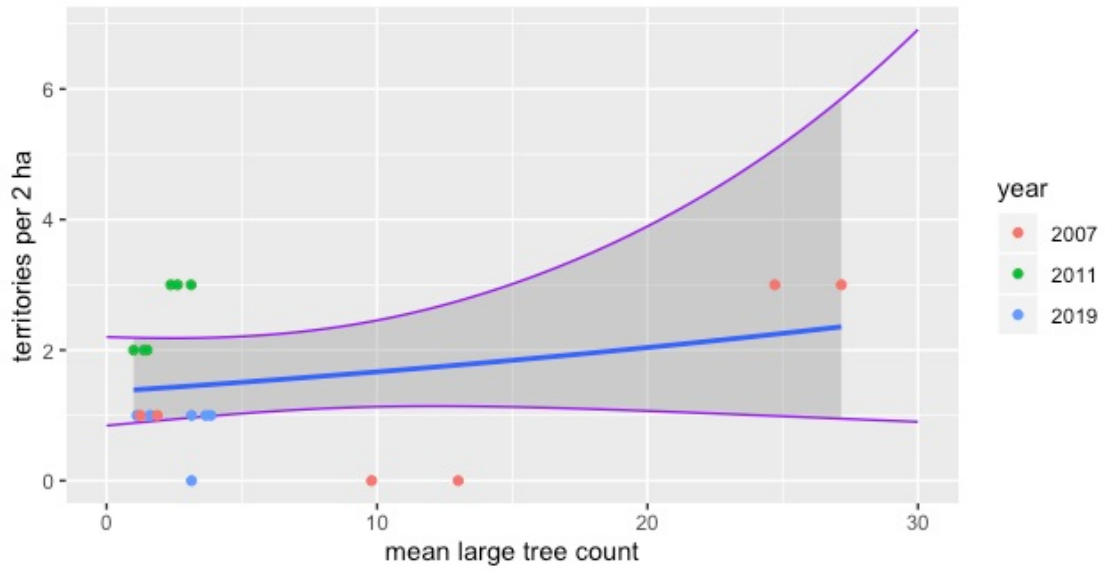


Figure 2.3. The relationship between Blue-Gray gnatcatcher territory density and mean large tree count color-coded for year in urban Columbus, Ohio. Shaded area represents approximated 95% confidence interval.

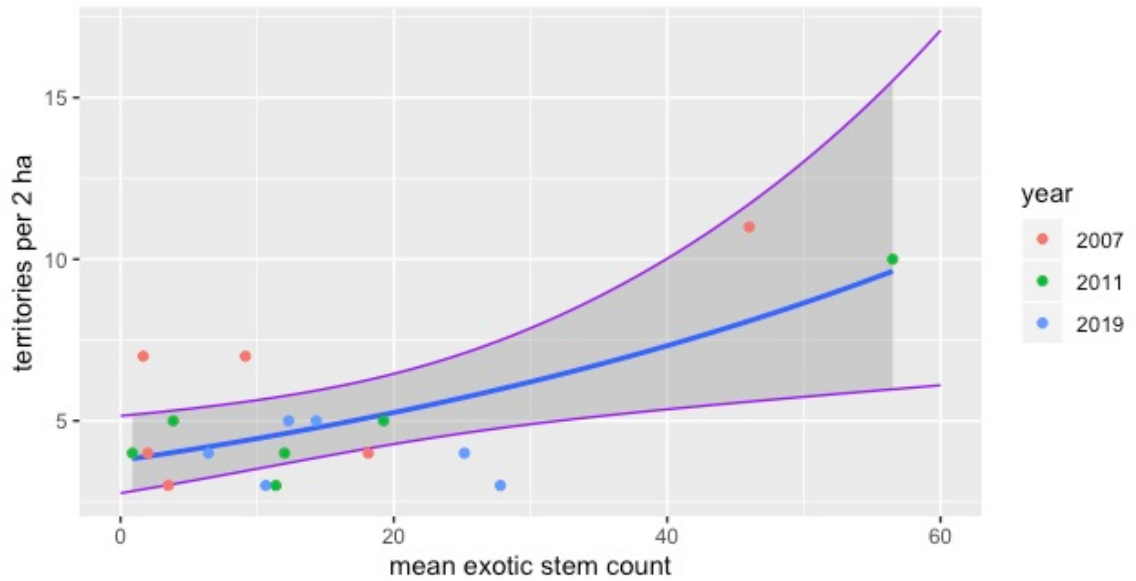


Figure 2.4. The relationship between Northern Cardinal territory density and mean exotic stem count color-coded for year in urban sites in Columbus, Ohio. Shaded area represents approximated 95% confidence interval.

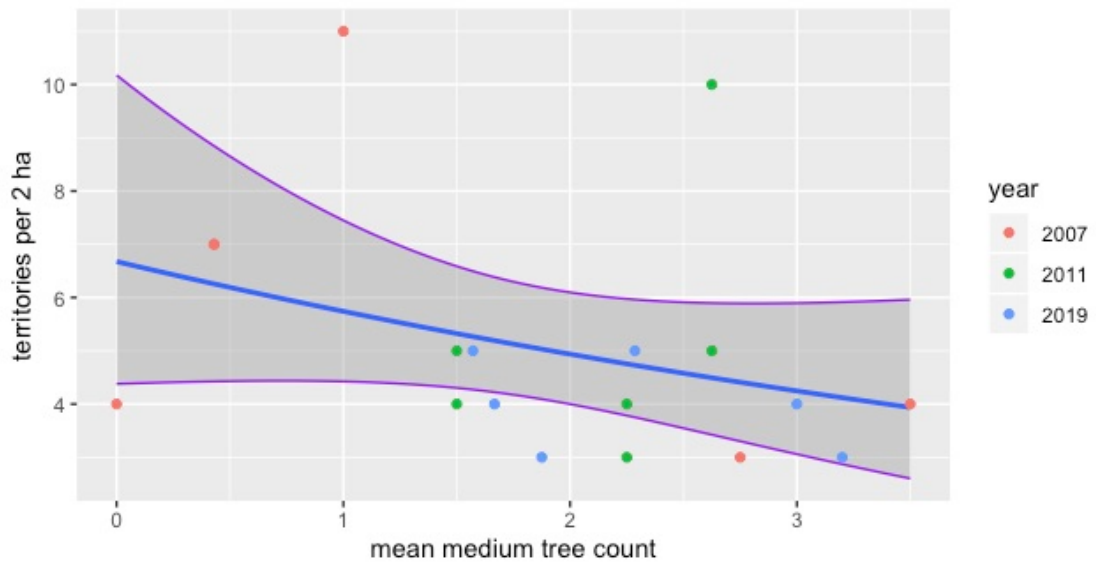


Figure 2.5. The relationship between northern cardinal territory density and mean medium tree count color-coded for year in urban sites in Columbus, Ohio. Shaded area represents 95% confidence interval.

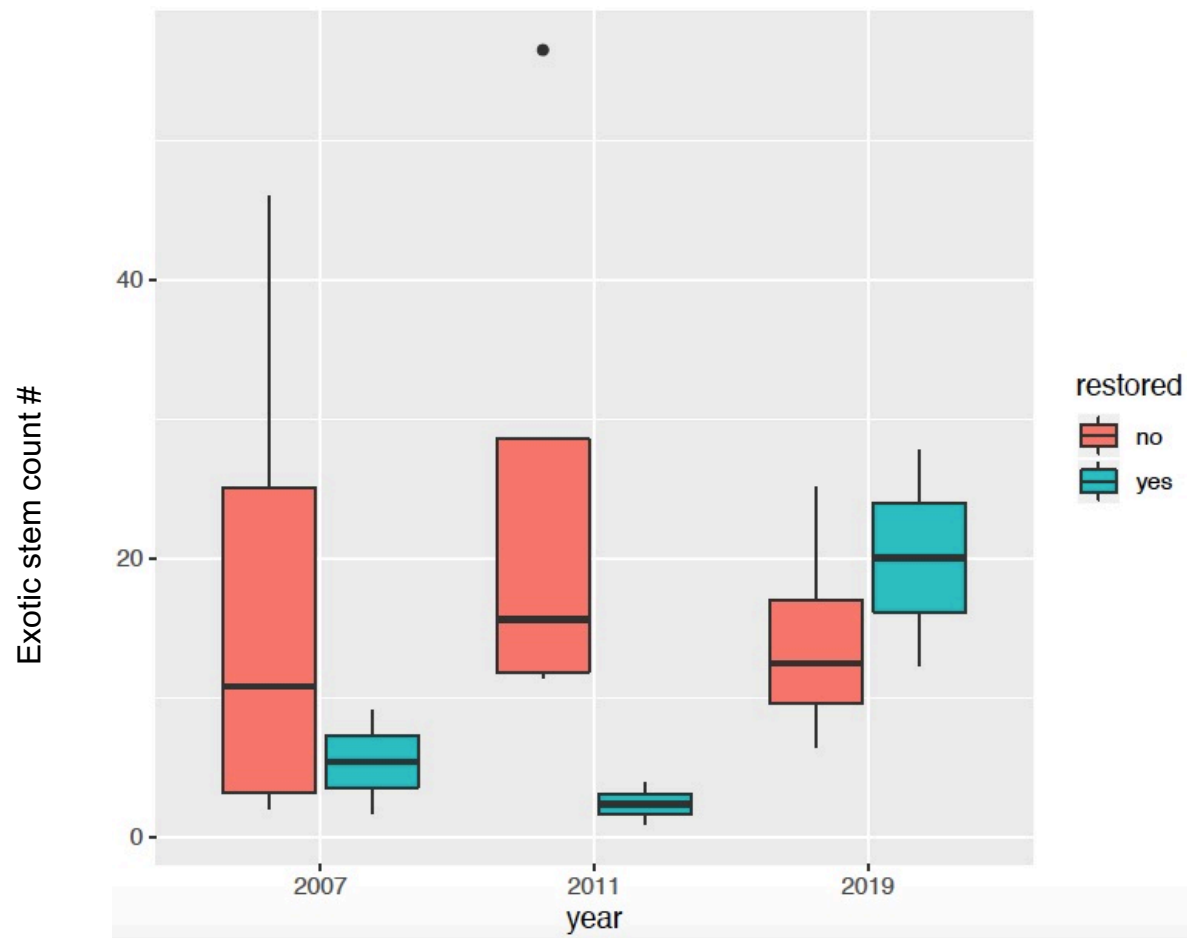


Figure 2.6. Boxplot of exotic stem count averages among restored and unrestored sites for 2007, 2011, and 2019 in urban sites in Columbus, Ohio. Restored sites had honeysuckle removed in 2007 and honeysuckle treated with herbicide until 2011. No significant differences between years among unrestored or restored sites using Welch's two sample t-tests. Restored sites included Tuttle South and Kenney South, while unrestored sites included Casto, Kenney North, Tuttle North, and Rush Run.

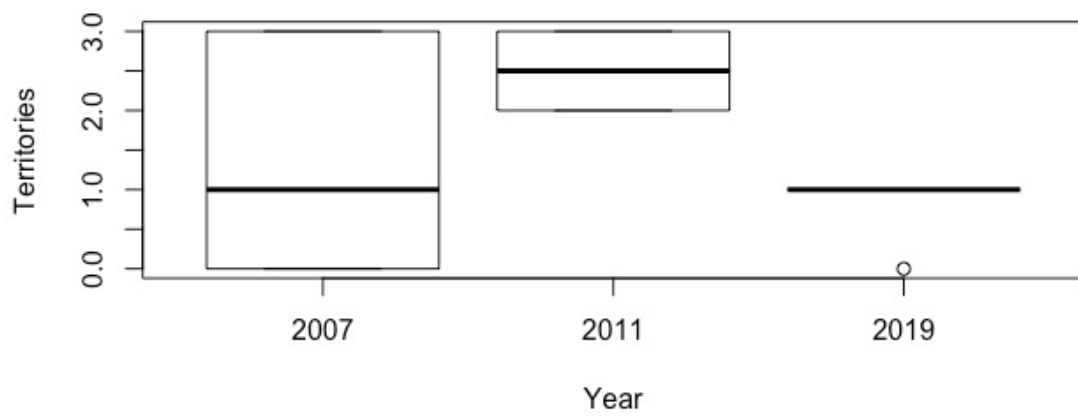


Figure 2.7. Boxplot of site territory densities for the Blue-gray Gnatcatcher in 2007, 2011, and 2019 for Casto, Kenney North, Kenney South, Rush Run, Tuttle North, and Tuttle South in urban Columbus, Ohio. No significant differences between years using Welch's two sample t-test.

Chapter 3: Foraging behaviors and tree-species preferences of songbirds in urban riparian forests

Introduction

Preferential use of different tree species may influence songbird community structure in different habitats. Holmes et al. (1979) found that guild structure was explained by differential use of tree species. Previous studies have shown that songbirds exhibit tree-species specific foraging preferences in several different study systems, which may also influence songbird diversity and abundance (Kirsch & Wellik 2017, Gabbe et al. 2002, Holmes & Robinson 1981). For instance, Holmes & Robinson (1981) found that the least abundant species were the most selective in their foraging preferences and that birds strongly preferred a few, less common tree species. Identifying which trees songbirds prefer for foraging is important in informing forest restoration efforts in regards to avian conservation.

Urban forests differ from the forests in which songbird species have evolved in that they are often fragmented and invaded by exotic plant species, which may be linked to decreased songbird diversity and survival (Mortberg 2001; Doherty & Grubb 2002, Gleditsch 2017). Examining how different songbird species use resources in altered landscapes may help to identify factors driving decreased diversity and survivorship. Specifically, shifts in arthropod abundance and composition may affect foraging opportunities for urban songbirds. Lussier et al. (2006) found that bark-gleaning species had decreased abundance with residential development while ground gleaners had

increased abundance. Thus, songbird foraging guilds that respond differently to urbanization may influence avian community composition.

Urban songbird foraging behavior may differ from that of their rural and natural forest counterparts. Due to exotic shrub invasion, arthropod diversity and abundance may be decreased in urban forests, which may limit prey availability for songbirds (Burghardt et al. 2009, Raupp et al. 2010). The enemy release hypothesis predicts that exotic plants do not support as many herbivorous arthropods due to a lack of evolutionary history (Tallamy 2004). According to this hypothesis, songbirds should use exotic plants for foraging less frequently than expected by availability. Urban environments present a novel combination of species and understanding how foraging preference may be reshaped is important to inform restoration efforts in regards to songbird conservation.

Study Objectives

Given the exotic plant abundance and decreased native plant diversity characteristic of urban riparian forests (Gleditsch 2017), my goal for this study was to understand how urban riparian songbirds use their floristic environment for insectivorous foraging and to identify foraging strategies that may explain variation in the urban songbird community. I predicted that (1) urban songbirds forage on certain woody plant species disproportionately to species availability and that (2) urban songbirds are more likely to forage on native tree and shrub species than non-native shrub species. By studying the foraging preferences of urban songbirds, I aim to elucidate foraging-related factors which may help to inform restoration in regards to maintaining biodiversity in urban forests.

Methods

Study Sites

The study sites consist of six 2 ha plots distributed across four urban riparian forest parks in the Scioto River Watershed in central Ohio (ca. 40°, -83°) and are located in and around Columbus, Ohio, a city with an estimated population of 892,533 (US Census 2018; Figure 3.1). Tuttle Park is located along the Olentangy River near the northern campus of Ohio State University. Casto Park is located along Alum Creek near Westerville, Ohio. The other two sites, Rush Run Park and Kenney Park, are located between Clintonville, Ohio and Worthington, Ohio along the Olentangy River. The major species at the sites include boxelder (*Acer negundo*), American elm (*Ulmus americana*), silver maple (*Acer saccharinum*), sugar maple (*Acer saccharum*), hackberry (*Celtis occidentalis*), eastern cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), and black walnut (*Juglans nigra*). Understory vegetation is generally dominated by Amur honeysuckle (*Lonicera maackii*), but also includes multiflora rose (*Rosa multiflora*), spicebush (*Lindera benzoin*), hawthorn (*Crataegus spp*), and overstory tree saplings. Amur honeysuckle was removed from 2 ha plots on two of the urban sites, Kenney Park and Tuttle Park, during the winter of 2007 as part of an invasive removal experiment (Rodewald et al. 2015).

Avian Surveys

I conducted spot mapping at each site every seven to ten days from the end of April through mid-July in 2018 and 2019 as described in the previous chapter. I

conducted foraging surveys at each site approximately every week during the breeding season, May to mid-July, in 2018 and 2019 between 15 minutes after sunrise and 11:00 AM following the protocol used in Gabbe et al. (2002). I systematically searched each site at a rate of approximately 1-ha per hour to locate foraging birds. I limited each foraging observation to 5 minutes, but most often I was only able to keep most birds in sight for <30 seconds. I recorded the bird species, the sex (if known), the approximate height of the bird (estimated to the nearest 1.5 m), time of day, the duration of the event, the approximate location in relation to the grid points, the behavior and number of behaviors exhibited, the tree species on which the bird was foraging and the substrate on which the bird was foraging (trunk, ground litter, leaf, etc) as described in Holmes & Robinson (1981). Only foraging behaviors directed at insect prey were included in the analysis. I described and categorized foraging behavior by the terminology defined in Holmes et al. (1979): (1) glean, a maneuver in which the bird picks at prey on the surface of the substrate while standing or hopping, (2) hover, a maneuver in which the bird picks at prey on the surface of the substrate while flying, (3) hawk, a maneuver in which the bird flies into the air in pursuit of prey, and (4) probe, a maneuver in which the bird pecks into the substrate in pursuit of subsurface prey. In order to ensure the independence of each foraging bout observation, I only recorded one songbird of the same sex and species within a 100 m radius per day and only the first tree on which the songbird foraged (Bell et al. 1990).

Vegetation Surveys

The species composition and structure of our sites were estimated from 5-8, 0.04 ha plots distributed throughout each urban site as described in Rodewald et al (2015) during the summer of 2019. The plots were originally established in 2007 to estimate overall species composition and vegetation structure (Rodewald et al. 2015). Within each plot, I identified and measured all woody plants greater than 3 cm diameter at breast height (dbh) to the closest 0.5 cm dbh.

Statistical Analyses

I investigated potential tree-species specific foraging preferences among foraging guilds using Pearson's Chi Square Test as described in Gabbe et al. (2002). Specifically, I calculated total basal area percentage for each tree species across all sites and multiplied the percentages by the total number of observations for each foraging guild to calculate expected values and compared those values to observed foraging frequencies for each tree species (Table B.1). Due to low sample size, I was not able to make species-specific conclusions, and I pooled the total number of foraging observations between 2018 and 2019 to increase sample sizes. Following the procedure from Gabbe et al. (2002), I excluded trees with basal area percentages less than 1.5% from analysis since 1 foraging observation per guild at most was recorded for such rare tree species. For bark foragers, trees and shrubs with an average dbh of less than 8 cm were excluded from analysis given bark foragers' narrow use of suitable foraging substrate. Given that all bird species had an expected value of less than 5 for several tree species, I calculated simulated *p*-values

using Monte Carlo tests with 2000 replicates and accepted $\alpha < 0.05$ as significant and $\alpha < 0.1$ as marginally significant (Sokal & Rohlf 1995).

I calculated a preference index for each foraging guild using the method described in Gabbe et al. (2002). I grouped the species into guilds instead of calculating a preference index for each individual species due to low sample size of foraging observations. The preference index is defined as the sum of the absolute values of the percent deviations of the observed number of foraging bouts from the expected number of foraging bouts divided by the expected number for each tree species.

Furthermore, I conducted multivariate analyses to identify the factors most important in differentiating foraging preferences and behaviors among urban songbird species, following Holmes et al. (1979). I identified 20 common foraging factors for analysis (Table 3.1). The first 9 factors characterize foraging maneuvers directed at tree species the songbirds commonly use for foraging. The following 9 factors characterize the types of foraging maneuvers used and the substrate in which the maneuvers were directed. Only the first behavior observed per bird was used for analysis to ensure independence of observations (Bell et al. 1990). The first 18 factors were expressed in proportions of total behaviors observed for each focal species. The last 2 factors characterize the average height and the standard deviation of the heights in which each focal species was observed foraging. I chose to examine the 8 most commonly observed species that had a sufficient number of foraging observations for analysis (Table 3.1). I performed a principal components analysis and Varimax rotated factor analysis on the data matrix consisting of the 8 focal species (rows) by the 20 foraging factors (columns)

using Program R to classify similarities and differences in foraging behaviors and food resources among urban songbirds (v 3.6.1; R Core Development Team 2019).

Results

Tree-species Foraging Preferences

I included four foraging guilds in my analysis: (1) aerial insectivores consisting of Acadian flycatchers (*Empidonax virens*), eastern wood-pewees (*Contopus virens*), and great crested flycatchers (*Myiarchus crinitus*), (2) bark foragers consisting of downy woodpeckers (*Picoides pubescens*), hairy woodpeckers (*Leuconotopicus villosus*), and red-bellied woodpeckers (*Melanerpes carolinus*), (3) foliage gleaners consisting of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*), and (4) ground foragers consisting of American robins (*Turdus migratorius*), blue jays (*Cyanocitta cristata*), Carolina wrens (*Thryothorus ludovicianus*), gray catbirds (*Dumatella carolinensis*), northern cardinals (*Cardinalis cardinalis*), song sparrows (*Melospiza melodia*), and wood thrushes (*Hylocichla mustelina*). Although a diversity of foliage gleaner species were observed, I only included Carolina chickadees and tufted titmice, the two most commonly observed foliage gleaners, to lessen intra-guild variation. For the same reason, I limited bark foragers to the 3 most commonly observed woodpeckers. A total of 354 foraging events on woody plants were observed in 2018 and 2019. Ground foragers ($n = 89$) exhibited marginal significance ($\chi^2 = 86.875$, $p = 0.06947$) and showed the highest preference for black cherry, with 700% more foraging bouts than expected, and the highest aversions to osage-orange, pawpaw, sugar maple,

and honey locust, with 100% fewer foraging bouts than expected (Figure 3.3; Table 3.2). Bark foragers ($n = 95$) also exhibited marginal significance ($\chi^2 = 85.944$, $p = 0.09545$), with the greatest preference for silver maple, with 250% more foraging bouts than expected, and the greatest aversions to hackberry, osage-orange, and sycamore, with 100% fewer foraging bouts than expected for each species (Figure 3.4; Table 3.2). Foliage gleaners ($n = 74$) did not differ from expected tree species patterns ($\chi^2 = 86.111$, $p = 0.1639$; Figure 3.5; Table 3.2). Due to low sample size, I was unable to draw any meaningful conclusions regarding the foraging preferences of aerial insectivores ($n = 12$). Preference indices ranged from 10.2 for bark foragers to 16.4 for ground foragers (Table 3.2).

Foraging Guild Structure

The first principal component accounts for 40.14% of the community variance and contains high positive loadings for foraging primarily on sycamores and height and high negative loadings for maneuvers directed at litter and foraging primarily on boxelders and Amur honeysuckle (Table 3.3). Height and foraging on sycamores and black walnuts are positively correlated for this component given that they have an average dbh of 34 and 48 cm respectively at these sites and that they are generally shade intolerant, so they are rare in the understory. I plotted the 8 focal species along the first 2 principal components (Figure 3.6). This component successfully isolates the main bark foragers, the downy woodpecker and the red-bellied woodpecker from the ground foragers, the American robin, the Carolina wren, and the northern cardinal (Figure 3.6).

The second principal component accounts for an additional 22.49 % of the community variance and contains high positive loadings for hover foraging maneuvers and high negative loading for gleaning on branches (Table 3.2). This principal component separates foliage gleaners, the Carolina chickadee and the tufted titmouse from the blue-gray gnatcatcher (Figure 3.6).

The third principal component accounts for 12.6% of the variance and contains high positive loadings for foraging on black cherry and honeysuckle, which is associated with American robins, northern cardinals, and Carolina wrens (Table 3.2).

Discussion

Tree-species Foraging Preferences

Foraging behavior provides a glimpse of how individuals are using food resources in the environment. Contrary to my hypothesis, my foraging preference analysis results suggest that out of the four foraging guilds examined, ground foragers exhibit the strongest tree-species specific foraging preferences in urban forests (Table 3.2). Due to low sample size of observations, I was unable to draw any conclusions regarding the foraging selectivity of aerial insectivores. The low sample size of aerial insectivore observations may be due to their relative lack of abundance and high rates of turnover in urban riparian forests (Rodewald & Bakermans 2006; Rodewald & Shustack 2008). This may also be due to a lack of preferred prey in urban riparian forests, given that airborne insects are especially sensitive to changes in water quality (Corra 2019).

Although only marginally significant, ground foragers were observed foraging in several trees with black cherry having the highest use (Figure 3.3; Table 3.2). Tallamy & Shropshire (2009) found that *Prunus* sustained the second highest diversity of Lepidoptera out of 210 woody plant genera studied. Given that the black cherry trees in our sites tended to be smaller, with an average dbh of 16 cm, and have the potential to host a greater diversity of Lepidoptera prey, black cherries may serve as a rich, accessible food source to bird species that forage at lower heights (Table 3.1). Interestingly this guild was found to forage on Amur honeysuckle more than expected. Although *Lonicera* has been shown to host a lower diversity of Lepidoptera than many woody plant genera present in the urban sites (Tallamy & Shropshire 2009), some species of ground foragers may be attracted to areas highly invaded with honeysuckle. For example, Leston & Rodewald (2006) found that northern cardinals selected nesting sites with higher honeysuckle coverage and higher understory stem densities. Likewise, Ausprey & Rodewald (2011) reported that northern cardinal fledglings selected for habitats with higher densities of honeysuckle. Therefore, ground foragers may frequently forage in honeysuckle due to reasons other than food availability, such as low foraging height or the need to stay hidden from predators in dense understory foliage.

The foraging aversions of ground foragers may be due to a difference in arthropod prey abundance among tree species (Godfrey et al. 2017, Holmes & Robinson 1981). Black walnut, for example, contains the compound juglone, which is toxic to some insects including gypsy moths (Lindroth et al. 1990). Likewise, pawpaw contains insecticidal acetogenins (Ratnayake et al. 1992). Tree and shrub species with insecticidal

properties would likely host a lesser abundance of insect prey and thus, ground foragers may not use them for foraging as frequently.

Bark foragers also exhibited marginally significant tree-species preference which in part may have been due to tree size, since woodpeckers tended to forage higher than other species and the four largest tree species on average, cottonwood, black walnut, silver maple, and sycamore, were all used more frequently than expected for foraging (Table 3.1; Table 3.2). Bark type may also have influenced tree foraging choices. Jackson (1970) also found that downy woodpeckers foraged on honey locust less frequently than expected as honey locust may be less preferable to woodpeckers due to the thorns covering their trunks. Furthermore, woodpeckers may have a preference for tree species with higher bark insect abundances or tree species that host preferred prey. For instance, Kilham (1970) reported that downy woodpeckers foraged on paper birch trees much more frequently than expected, which they postulated may be due to the abundance of giant coccid in the bark. Similarly, Flower et al. (2014) found that bark foragers foraged preferentially on ash trees in an emerald ash borer-infested forest. Further research on urban woodpecker diet and arthropod bark sampling may help to elucidate this relationship.

Foliage gleaners did not show any significant tree-species foraging preferences or aversions (Figure 3.4; Table 3.2). Conversely, Gabbe et al. (2002) found that Carolina chickadees and tufted titmice showed preferences for American elm and silver maple and aversions to boxelder and sycamore in Illinois floodplain forests. There are several possible explanations for the lack of significant foraging preference and aversion results

among foliage gleaners in my study. First, given that many of the species in which chickadees and titmice have showed preferences in previous studies, namely oak and hickory species (Gabbe et al. 2002, Narango et al. 2017), were absent from my study sites, chickadees and titmice may have to substitute other tree species for their food resources in less diverse urban environments. Secondly, species-specific differences in tree preferences may explain the lack of conclusive results. For example, Gabbe et al. (2002) reported differing preference indices for tufted titmice and Carolina chickadees. Thus, their conflicting preferences and aversions may have negated each other when pooled together in my analysis.

Foraging Guild Structure

Foraging height plays a critical component of differentiating species space use and provide niche space for a diversity of species. Holmes et al. (1979) showed that height was a critical determinant of avian community in New Hampshire and my results provide similar insights with the first PCA axes loading heavily on this factor. My results strengthen Holmes et al. (1979)'s argument that variation in foraging height among songbird species in a community may contribute to the positive association between foliage height diversity and songbird species diversity (MacArthur & MacArthur 1961, Willson 1974). The similarity between these components suggests that foraging height may be one of the most important factors in determining foraging guild structure across different bird communities, especially considering that the songbird species, woody plant species, and other characters used in my analysis and the analysis from Holmes et al. (1979) differed. If foraging height is important in differentiating songbird species guilds,

forests with varying foliage structure would provide foraging opportunities to a greater number of species, which may result in a greater number of species occupying those forests.

The second principal component was also like that from the analysis of Holmes et al. (1979) in that it explained around a quarter of the community variance and that aerial foraging techniques, such as hovering and hawking, contained high positive loadings (Table 3.3). The similarity in the results from my study and the study from Holmes et al. (1979), despite being one being conducted in Hubbard Brook, a 10-ha hardwood forest in New Hampshire, and mine being conducted in urban riparian forests in Ohio, suggests that guild structure may be formed by the same factors in urban environments as they are in more contiguous forest areas.

Limitations

One limitation of this study is that I was not able to collect sufficient data to detect tree species foraging preferences or aversions on the species level and thus, had to group species into foraging guilds to make meaningful conclusions. Therefore, my results do not account for species variation in foraging within guilds. The small sample size may be due to decreased abundance of songbirds in urban forests in comparison to sites used in previous studies (Holmes & Robinson 1981, Gabbe et al. 2002). Another possibility is that the songbirds also use areas outside of my urban sites for foraging. Given that the urban parks used in this study are near residential areas, it is possible that some of the

songbird species' diets are supplemented by birdfeeders, which may reduce their need to forage for insects.

Another limitation of this study is that I was not able to collect sufficient arthropod sample data to explain foraging choices. Arthropod samples from the 2018 breeding season yielded fewer than 5 Lepidoptera per 25 leaf samples for black walnut, boxelder, hackberry, and American elm. Burghardt et al. (2009) reported a decreased abundance of Lepidoptera in areas dominated by non-native vegetation. Perhaps there is decreased Lepidoptera prey availability in the urban sites, which may explain my difficulty in obtaining foraging observations.

Habitat Management Implications and Future Directions

The results of this study suggest that, from a foraging perspective, maintaining foliage height diversity and native tree and shrub diversity is imperative to supporting songbird species diversity in an urban environment. One important strategy for maintaining structural diversity in urban forests is invasive shrub control and removal. Exotic shrubs, such as Amur honeysuckle, often outcompete native woody plant species, especially in fragmented, developed environments, which lowers shrub and tree species diversity and thus, decreases foliage height diversity (Hartman & McCarthy 2008, Lussier et al. 2006). Given that all four foraging guilds exhibited preferences for or did not exhibit aversions to American elm, black cherry, and silver maple, my results suggest that these species should be included in restoration plantings to support the greatest number of urban songbird species. Although Dutch elm disease poses a threat to

American elm saplings, disease-resistant elm variants could potentially make them a viable option for restoration (Knight et al. 2016). Regardless of any particular species, sustaining a diversity of native tree and shrub species and of foliage height in urban forests is important to ensure foraging opportunities for a diversity of species.

In light of recent declines in North American aerial insectivore populations (Spiller & Dettmer 2019), maintaining aerial insectivore habitat should be considered in songbird habitat management decisions. Given that one potential driver of aerial insectivore decline is decreased diversity of insect prey (Spiller & Dettmer 2019), factors affecting aerial insectivore foraging efficiency and food resources should be examined. Spiller & Dettmer (2019) suggest identifying high-quality foraging habitat to better understand aerial insectivore declines. Since urban riparian forests also function as migration stopover sites (Rodewald & Matthews 2005), measuring insect abundance and biodiversity at urban sites throughout the year is needed to further examine the role of urban forests in sustaining aerial insectivore populations.

Table 3.1. Matrix used for principle components analysis. Each column represents a bird species named by alpha code. First 18 rows represent percentage use of tree species, second 18 rows represent percentage maneuver-substrate combinations, and last 2 rows represent average foraging heights (m) and standard deviations for foraging height. All data measured in urban Columbus, Ohio in 2018 and 2019.

	AMRO	BLGN	CACH	CARW	DOWO	NOCA	RBWO	ETTI
cottonwood	40.0	12.9	14.3	22.2	16.3	0.0	22.6	7.7
boxelder	40.0	41.9	28.6	11.1	32.6	42.4	9.7	46.2
black walnut	0.0	9.7	16.3	0.0	18.6	12.1	35.5	15.4
honeysuckle	0.0	3.2	2.0	33.3	0.0	21.2	0.0	0.0
silver maple	0.0	6.5	4.1	0.0	7.0	6.1	9.7	15.4
black cherry	0.0	3.2	4.1	22.2	0	3.0	6.5	7.7
american								
elm	20.0	3.2	12.2	11.1	14.0	15.2	0.0	0.0
sycamore	0.0	6.5	10.2	0.0	11.6	0.0	16.12	0.0
hackberry	0.0	12.9	8.2	0.0	0.0	0.0	0.0	7.7
glean leaf	14.7	36.4	50.9	33.3	6.3	38.6	0.0	20.0
hover leaf	0.0	18.2	0.0	0.0	0.0	0.0	0.0	0.0
glean branch	22.0	18.2	40.0	25.0	12.5	27.3	2.4	40.0
hover branch	0.0	18.2	1.8	0.0	0.0	0.0	0.0	0.0
probe branch	0.0	0.0	0.0	0.0	14.1	2.3	11.9	0.0
glean litter	4.4	0.0	0.0	8.3	0.0	0.0	0.0	6.7
probe litter	54.4	0.0	1.8	16.7	0.0	22.7	0.0	13.3
glean trunk	4.4	9.1	5.5	8.3	15.6	9.1	19.0	13.3
probe trunk	0.0	0.0	0.0	8.3	51.6	0.0	66.7	6.7
height	3.2	11.6	10.4	4.1	10.9	4.8	12.4	6.4
sd	5.0	7.6	6.9	6.0	7.8	4.8	7.9	6.5

Table 3.2. Preference (positive) and aversion (negative) values for tree species by each foraging guild, and chi-square tests of preference indices for each foraging guild. All data collected in Columbus, Ohio in 2018 and 2019.

Tree species	Ground	Foliage	Bark
American elm	1.0	0.7	0.4
Black cherry	7.0	2.0	1.0
Black walnut	-0.4	0	0.4
Boxelder	0.3	0.4	-0.2
Cottonwood	-0.4	0.3	0.5
Hackberry	-0.7	-0.2	-1.0
Honey locust	-1.0	-1.0	-1.0
Honeysuckle	0.7	-0.9	N/A
Mulberry	0.3	2.0	-0.8
Ohio buckeye	-0.3	-0.3	-0.2
Osage-orange	-1.0	-1.0	-1.0
Pawpaw	-1.0	-1.0	N/A
Silver maple	1.0	1.0	2.5
Sugar maple	-1.0	0.3	-0.3
Sycamore	-0.3	1.5	1.0
PI ^b	16.4	12.6	10.2
Chi-square	86.9	86.1	85.9
P	0.069	0.164	0.095

Table 3.2 continued

^a Foraging guilds are listed in descending order of preference index.

^b Preference index is the sum of the absolute values of the numbers in the table. Preference index was calculated before each number was rounded, and therefore, differs somewhat from the sum of the numbers in the table.

Table 3.3. Loadings and eigen values for the most heavily weighted principle components for each of the 20 characters. All data collected in Columbus, Ohio in 2018 and 2019.

Principle Components					
	I	II	III	IV	V
Eigen values	8.03	4.50	2.52	2.12	1.50
Contribution to community variance (%)	40.14	22.49	12.60	10.61	7.49
Cumulative (%)	40.14	62.64	75.24	85.84	93.31
American elm		-0.163	-0.184		-0.143
black cherry			0.641		
black walnut	0.199	-0.170	-0.132		
boxelder	-0.281	0.115	-0.458	0.129	0.173
cottonwood				-0.700	-0.117
hackberry	0.124	0.215			
honeysuckle	-0.206		0.311	0.400	-0.341
silver maple				0.146	0.717
sycamore	0.466				
glean branch		-0.339			
glean leaf	0.148			0.315	-0.337
glean litter	-0.342		0.346	-0.262	
glean trunk	-0.111				
hover branch		0.586			
hover leaf		0.619			
probe branch	0.107		-0.124		
probe litter	-0.373		-0.258	-0.293	-0.260
probe trunk	0.185		0.120		0.313

Table 3.3 continued

height	0.405	
sd	0.297	-0.103

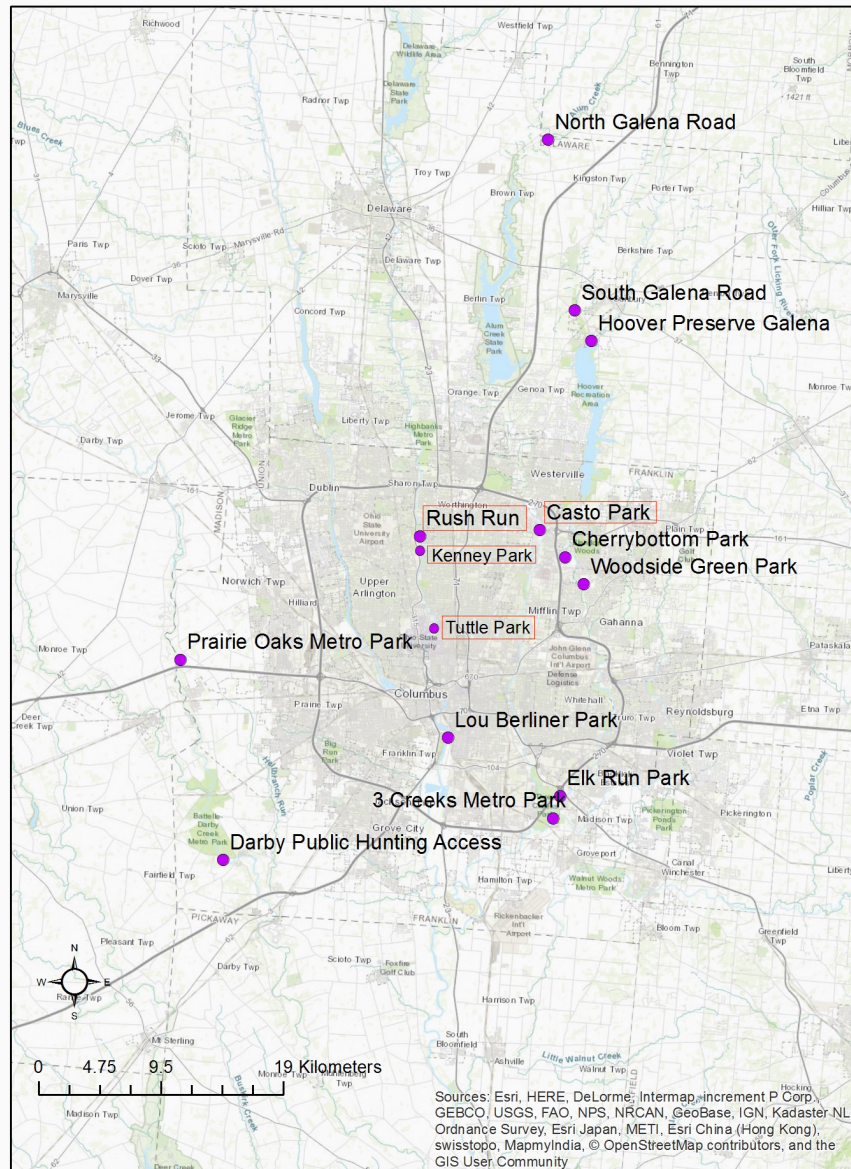


Figure 3.1. Location and names of sites used in study in Columbus, Ohio. Sites used are outlined in red.

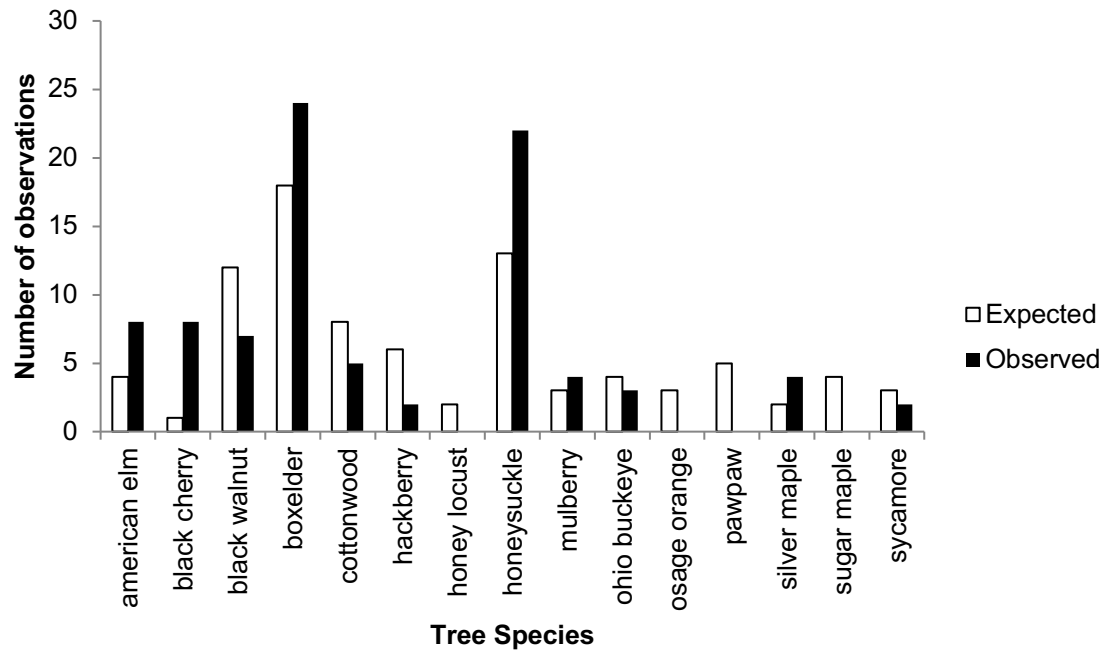


Figure 3.2. Ground forager foraging use of tree species in urban sites in Columbus, Ohio during 2018 and 2019. Expected use calculated from tree species availability.

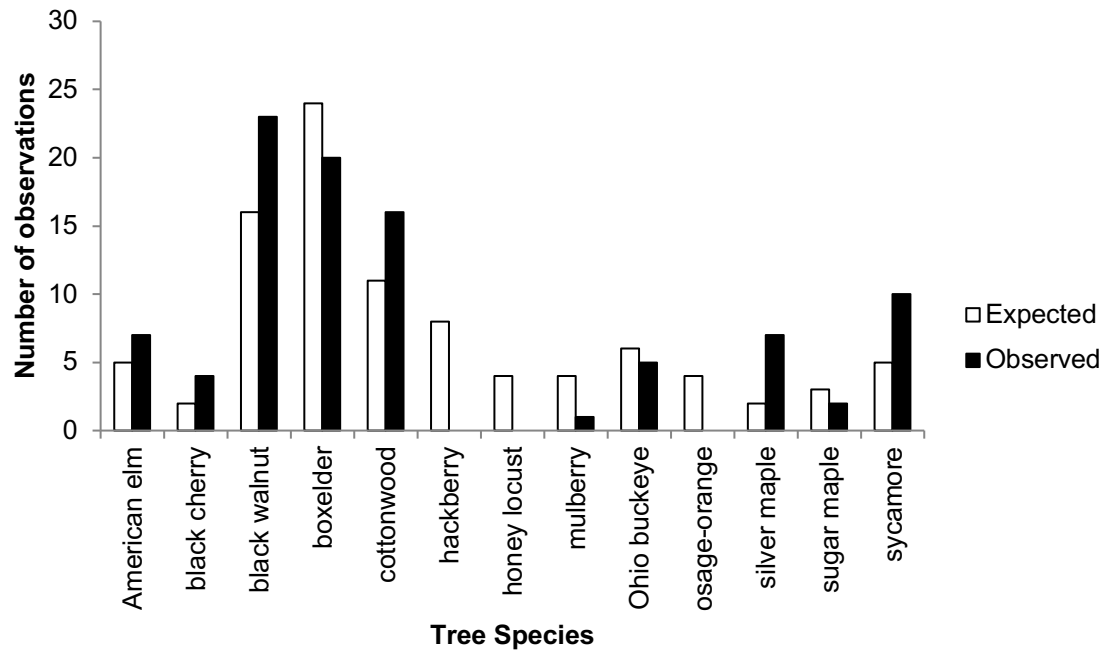


Figure 3.3. Bark forager foraging use of tree species in urban sites in Columbus, Ohio during 2018 and 2019. Expected use calculated from tree species availability.

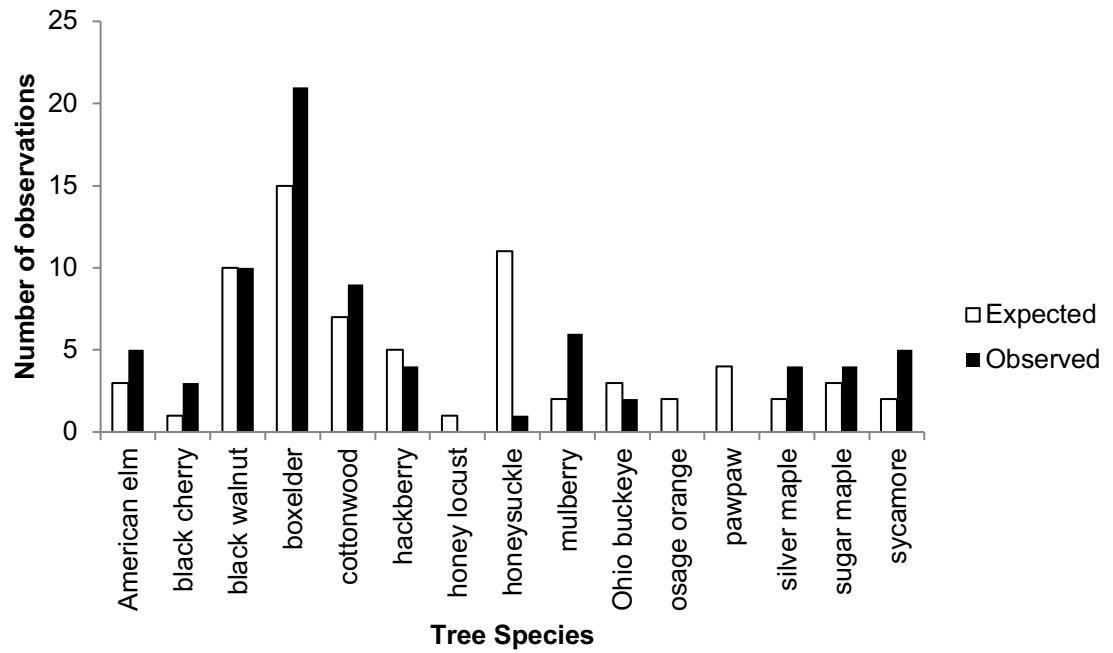


Figure 3.4. Foliage gleaner foraging use of tree species in urban sites during 2018 and 2019 in Columbus, Ohio. Expected use calculated from tree species availability.

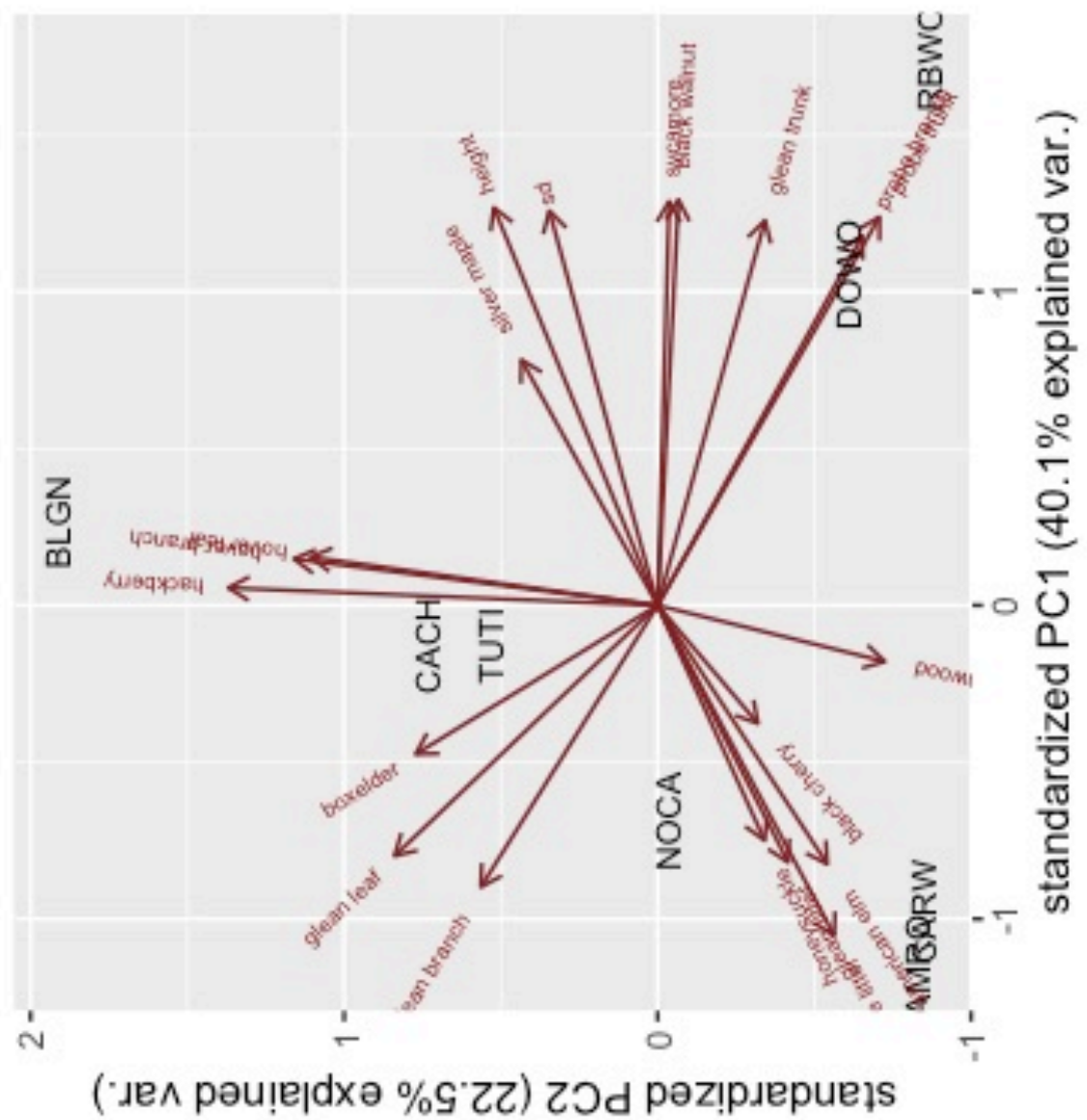


Figure 3.5. Bird species (represented by alpha codes) plotted along first two principle components. All data collected in Columbus, Ohio in 2018 and 2019.

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Appendix A: Chapter 2 Supplemental Materials

Table A.1. Covariance table for vegetation variables used to develop territory density models. Vegetation variables taken from surveys conducted in Columbus, Ohio in 2007, 2011, and 2019.

	Year2011	Year2019	Canopy	Saplings	Small trees	Medium trees	Large trees	Exotic stems	Native stems	Tree stems
Year2011	28.16	25.48	-10.43	-0.08	0.27	5.27	1.62	0.08	0.05	-0.37
Year 2019	25.48	24.74	-9.83	-0.08	0.22	4.59	1.45	0.11	-0.27	-0.32
Canopy	-10.43	-9.83	4.22	0.03	-0.09	-1.97	-0.60	-0.04	0.06	0.14
Saplings	-0.08	-0.08	0.03	0	0	-0.05	0	0	0	0
Small trees	0.27	0.22	-0.09	0	0	-0.03	0.02	0	0	0
Medium trees	5.27	4.59	-1.97	-0.05	0.03	2.05	0.35	0.04	0.18	-0.04
Large trees	1.62	1.45	-0.60	0	0.02	0.35	0.10	0	0.02	-0.02
Exotic stems	0.08	0.11	-0.04	0	0	0.04	0	0	0	0
Native stems	0.05	-0.27	0.06	0	0	0.18	0.02	0	0.14	0
Tree stems	-0.93	-0.32	0.14	0	0	-0.03	-0.02	0	0.01	0.01

Figure A.1. Vegetation variable means taken from vegetation surveys at Casto in Columbus, Ohio.

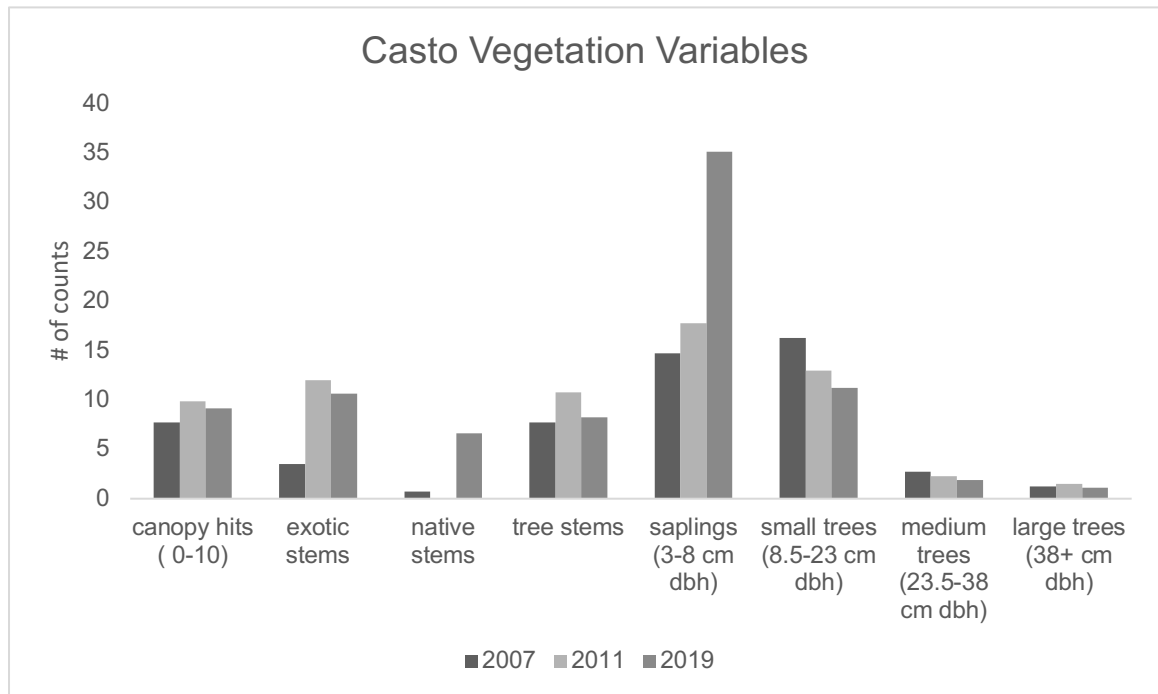


Figure A.2. Vegetation variable means taken from vegetation surveys at Kenney North in Columbus, Ohio.

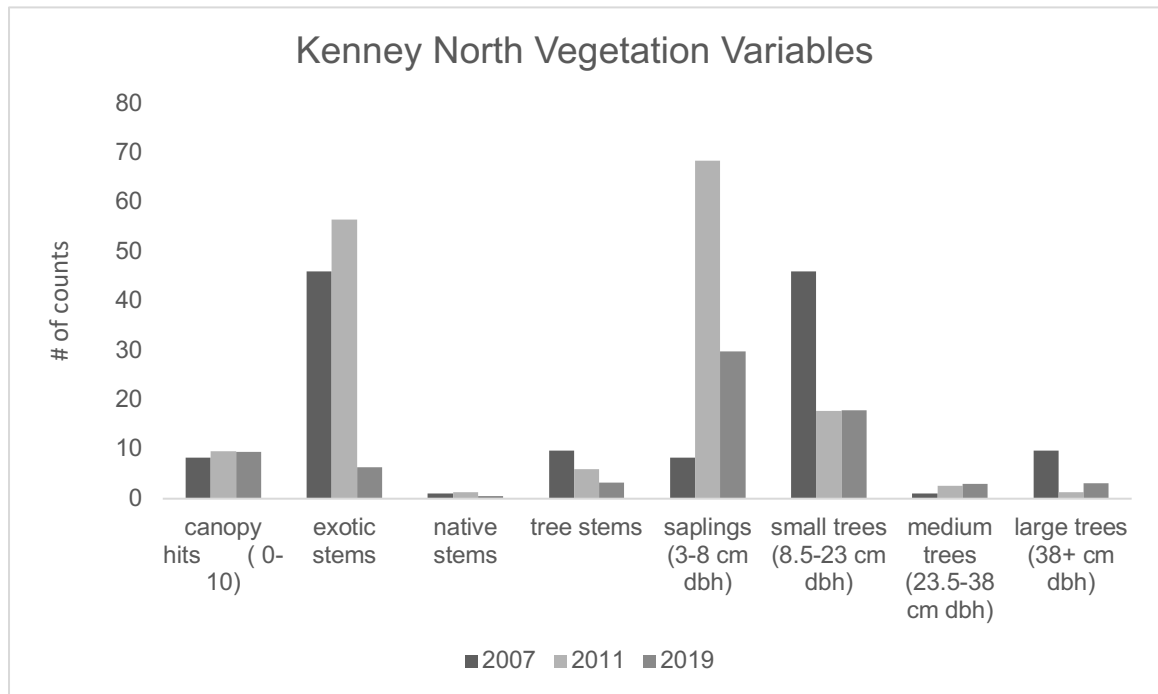


Figure A.3. Vegetation variable means taken from vegetation surveys at Kenney South in Columbus, Ohio.

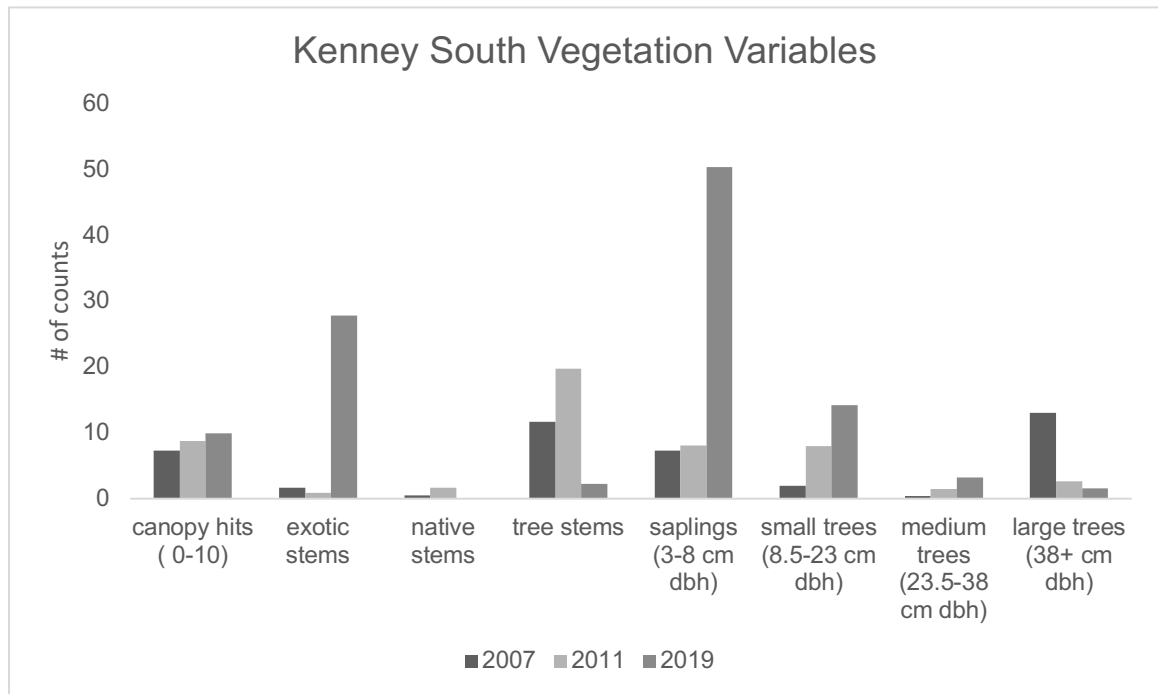


Figure A.4. Vegetation variable means taken from vegetation surveys at Rush Run in Columbus, Ohio.

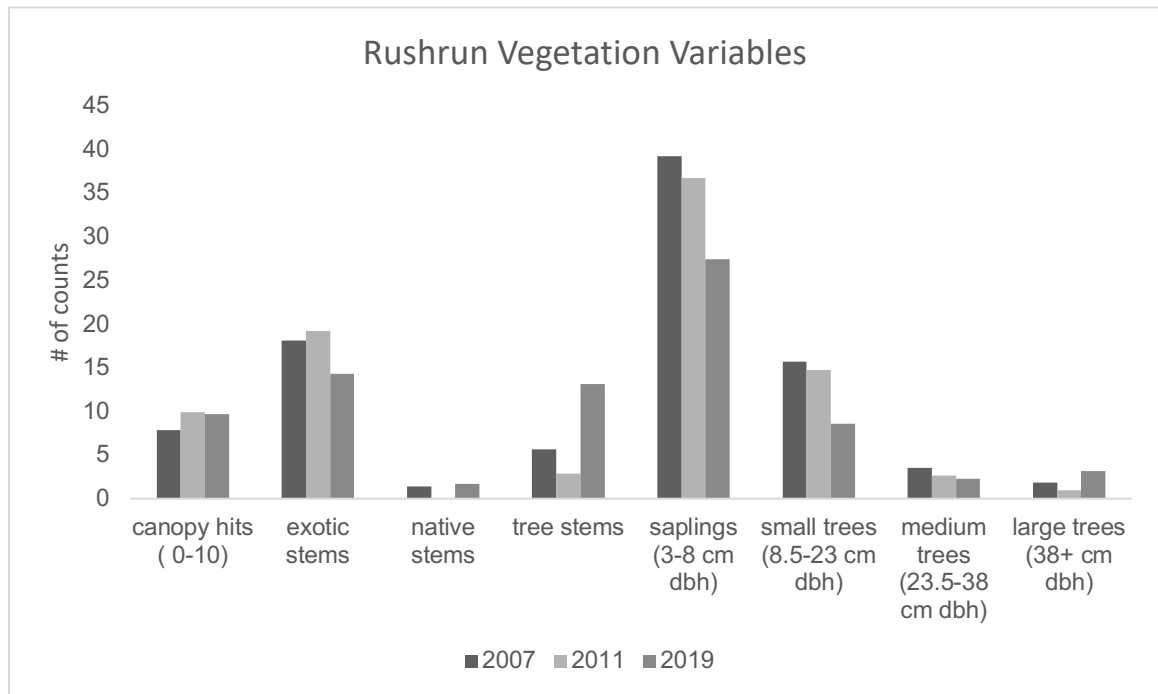


Figure A.5. Vegetation variable means taken from vegetation surveys at Tuttle North in Columbus, Ohio.

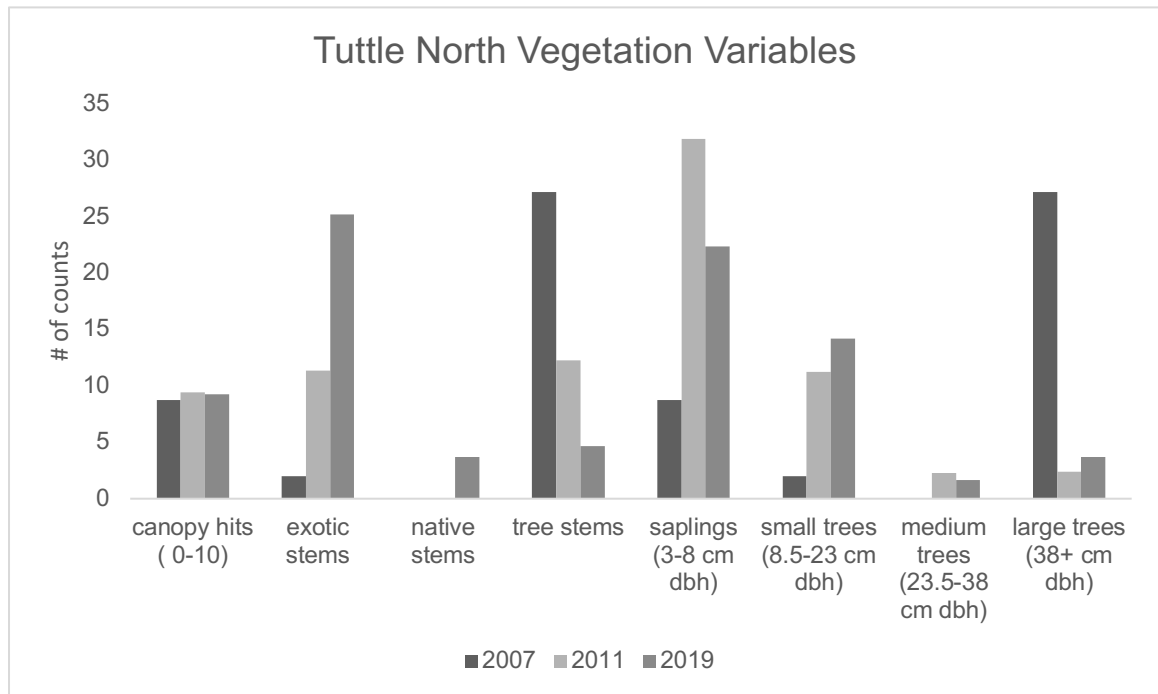
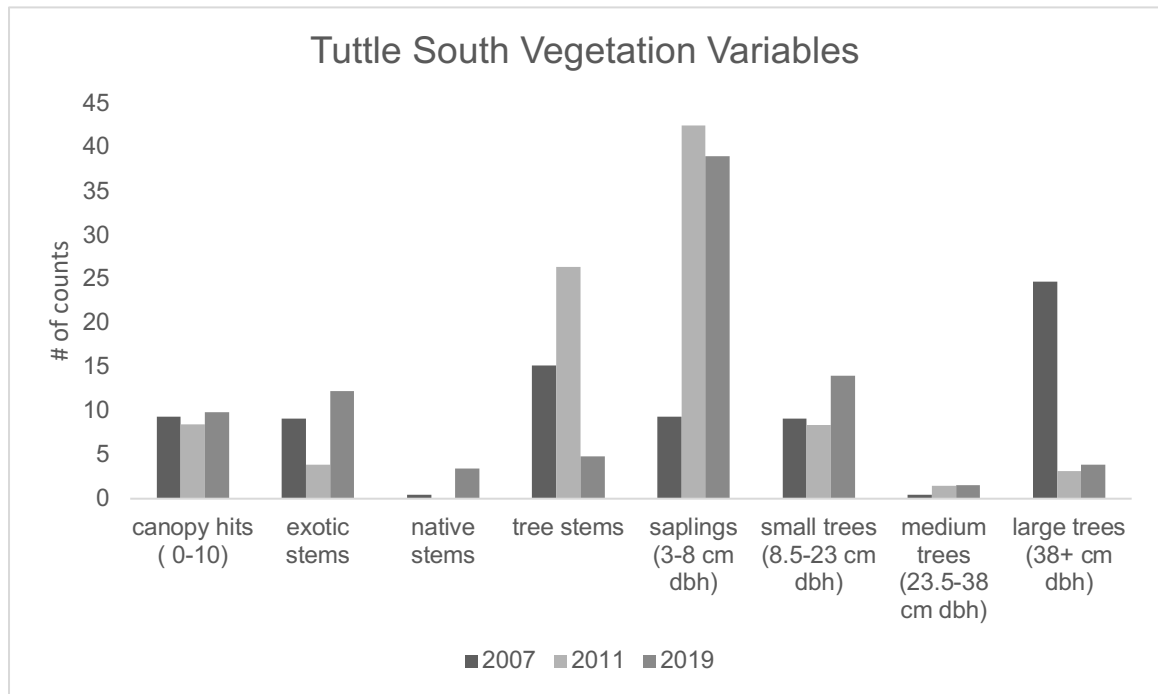


Figure A.6. Vegetation variable means taken from vegetation surveys at Tuttle South in Columbus, Ohio.



Appendix B. Chapter 3 Supplemental Materials

Table B.1. The total basal area percentage of each tree species among Casto, Kenney North, Kenney South, Rush Run, Tuttle North, and Tuttle South in Columbus, Ohio taken from 2019 vegetation surveys.

Species	Percentage
boxelder	19.9
honeysuckle	14.4
black walnut	13.2
cottonwood	8.9
hackberry	7.2
pawpaw	5.2
Ohio buckeye	4.7
sugar maple	4.1
American elm	4.0
mulberry	3.3
osage orange	3.2
sycamore	3.0
silver maple	2.4
honey locust	2.0
black cherry	1.6
red maple	1.5
ash	0.7
hickory	0.6

Table A.1 continued

hawthorn	0.2
ailanthus	0.1