THE IMPACTS OF URBANIZATION ON WILDLIFE IN NORTH AMERICA'S LARGEST URBAN FOREST

By

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Chapter 1: Introduction

Urbanization is one of the most important anthropogenic forces impacting earth's biodiversity (Foley et al. 2005), as it modifies landscapes more dramatically than any other form of anthropogenic land use change (Güneralp and Seto 2013). Urban growth is spreading at the fastest rates in history and is predicted to continue to accelerate (Seto et al. 2012). Because of this, urbanization is considered a major threat to the global conservation of biodiversity (Grimm et al. 2008; McDonald et al. 2008). In the United States, for example, urbanization endangers more species than any other human activity (Czech et al. 2000). Although not all species are impacted similarly by urbanization, a common consequence of this process is the loss of native species and an overall decline in biodiversity (McKinney 2002; Clergeau et al. 2006; Aronson et al. 2014). The biodiversity loss associated with urbanization is because only a subset of species can cope with such dramatic environmental changes (Kark et al. 2007; Williams et al. 2009; Sih et al. 2011). Species that cannot persist with these changes are known as urban-avoiding species, which can be identified through shared biological traits that are phylogenetically linked (Sol et al. 2017). Thus, urbanization homogenizes wildlife communities both functionally (Devictor et al. 2007), and evolutionarily (Ibañez-Alamo et al. 2017). Among multiple studies attempting to identify urban-avoiding species by common traits, increasing specialization (habitat or feeding) is consistently reported as a significant factor (Clergeau et al. 2006; Bonier et al. 2007; Devictor et al. 2007; Croci et al. 2008; Evans et al. 2011; Sol et al. 2014; Callaghan et al. 2019).

As with other forms of anthropogenic land use change, urbanization directly alters habitat and fragments it (Marzluff and Ewing 2001). In urbanized landscapes, fragments of natural habitat, often forests, are concentrated along waterways (Rodewald and Bakermans 2006). These riparian forests are more biodiverse than other forests and perform critical functions for hydrological cycles, biogeochemical cycles, and water quality (Namian and Decamps 1997). The importance of the composition of the matrix that surrounds these habitat fragments has recently been emphasized (Kupfer et al. 2006; Prugh et al. 2008). As the surrounding matrix becomes less hospitable, habitat fragments suffer a loss of biodiversity and an increased risk of local extinction (Kennedy et al. 2010; Kennedy et al. 2011). Multiple studies have found that riparian forest fragments in urban landscapes have less biodiversity than riparian forest fragments in rural landscapes (Miller et al. 2003; Rodewald and Bakermans 2006), reinforcing the idea that urbanization modifies landscapes more drastically than other forms of land use change. Species in habitat fragments that avoid the surrounding matrix tend to decline or disappear, while those that tolerate or exploit the matrix often remain stable or increase in abundance (Gascon et al. 1999). Thus, the species lost from riparian forest fragments as the matrix urbanizes are often the same urban-avoiding species that are lost when habitat is directly impacted by urbanization.

Hypotheses that explain why urban-avoiding wildlife decline within suitable habitat patches as urbanization in the matrix increases can be placed into two groups, those that are based on whether direct or indirect impacts of urbanization are most likely to explain extinction. Hypotheses related to direct impacts look to the impact of urbanization on matrix composition and fragment size. Urbanization of the matrix decreases its suitability for foraging and dispersal, leading to a decrease in the resource base and an increase in population subdivision (Kupfer et al. 2006). These hypotheses recall the principles of island biogeography (MacArthur and Wilson 1967), in which patch size and isolation determine species likelihood of occurrence, implying that urban habitat fragments are terrestrial ‘islands’ because the surrounding matrix is so inhospitable it is analogous to an ocean. Previous research has shown mixed support for the application of island biogeography to terrestrial islands of habitat surrounded by agricultural matrix (e.g., Mendenhall et al. 2014; Wolfe et al. 2015). Because urbanization modifies landscapes more dramatically than any other form of anthropogenic land use change (Güneralp and Seto 2013), it is plausible that an urbanized matrix creates habitat islands that conform to the theories of island biogeography. The second group of hypotheses regarding biodiversity loss attribute declines in urban avoiding species to the indirect impacts of nearby urbanization. Urbanization of the matrix can introduce anthropogenic impacts like noise pollution (Francis and Barber 2013), light pollution (Gaston et al. 2013), and invasive species (McKinney 2006) to wildlife living within habitat fragments. These indirect impacts can make urban forest fragments unsuitable for urban avoiders (e.g., Crooks and Soule 1999; Lewanzik and Voigt 2014; Perillo et al. 2017). The importance of direct versus indirect impacts of an urbanizing matrix on biodiversity loss in habitat fragments is unknown, as is the relative importance of different indirect anthropogenic impacts.

My study site, the Great Trinity Forest (GTF), is one of the largest urban forests in the United States, encompassing over 4,000 ha of unmanaged riparian bottomland hardwood forest within the city of Dallas, TX. Reports from local naturalists and citizen science tools indicate that the GTF, unlike other well-studied urban forests, has diverse and complete wildlife communities including urban-avoiding species. The presence of urban avoiding species in the GTF presents a unique opportunity to test hypotheses that attempt to explain the loss of urban avoiding species from urban habitat fragments. In **Chapter 2**, I examined the patterns of occurrence for the swamp rabbit (*Sylvilagus aquaticus*), a habitat specialist restricted to bottomland hardwood forests in the southeastern United States (Robinson et al. 2016). The swamp rabbit is also considered an indicator species for bottomland hardwood forests (Hillard et al. 2017), meaning that its presence indicates healthy habitat that can support a full suite of other bottomland hardwood forest specialists. Despite being an elusive and cryptic species, swamp rabbits are relatively easy to survey with non-invasive methods through their use of latrines:

swamp rabbits deposit highly visible piles of scat on top of fallen trees or stumps (Zollner et al. 1996). I compared the distribution of swamp rabbit latrines to the distribution of both the direct and indirect impacts of urbanization. Swamp rabbit latrines also provide non-invasive access to valuable genetic resources that can inform conservation. I collected DNA from fecal pellets found at swamp rabbit latrines, and in **Chapter 3**, I estimated the population size of swamp rabbits and looked for evidence that anthropogenic disturbances (e.g., highways) act as barriers for dispersal, influencing swamp rabbit population genetic structure and long-term population viability using a landscape genetics approach. In **Chapter 4**, I examined the patterns of occurrence for the songbird community. At least 13 urban-avoiding songbirds are thought to breed within the GFT, with 11 of those having no previous breeding records in urban forest fragments (Archer et al. 2019). I then compared urban-avoiding bird occurrence to the distribution of both the direct and indirect impacts of urbanization.

To my knowledge, this is the first study to examine the spatial distribution of urban-avoiding species within a single urban forest fragment. Information on the specific anthropogenic impacts governing the distributional limits of urban avoiders in the GTF will provide land managers and conservation planners with reclamation and mitigation guidelines to restore urban-avoiding species to urban parks and reserves. Enhanced knowledge of the habitat requirements of urban-avoiding species in these fragments has the potential to improve conservation and planning issues worldwide (Foley et al. 2005). The ability to conserve urban-avoiding wildlife in urban forest fragments not only helps combat the worldwide extinction crisis (Foley et al. 2005), but also provides social and educational benefits for humans in urban areas with few opportunities to experience intact wildlife communities (Miller and Hobbs 2002; Dearborn and Kark 2009).

Chapter 2: Environmental and Anthropogenic Variables Influence the Distribution of a Habitat Specialist in a Large Urban Forest

INTRODUCTION

The purpose of this study was to understand how the swamp rabbit (*Sylvilagus aquaticus*) persists in an urban forest fragment and to identify specific indirect impacts of the urban matrix that may limit their distribution. Despite being an elusive and cryptic species, swamps rabbits are easy to survey with non-invasive methods through their use of latrines, where they deposit highly visible piles of scat on top of fallen trees or stumps (Zollner et al. 1996). Latrines are used by both males and females and are thought to function as sites for the exchange of olfactory information. I used latrine surveys to assess how the indirect impacts of urbanization from the matrix and naturally occurring heterogeneity in habitat structure influenced the distribution of swamp rabbits in the GTF. This analysis will allow us to test direct versus indirect hypotheses that may explain the loss of urban avoiding wildlife from urban forest fragments. If swamp rabbits are limited to core areas of the forest where anthropogenic noise is absent or urbanization in the matrix is less intense, this would support hypotheses that the indirect impacts of the urban matrix drive extinction in urban forest fragments. If swamp rabbits use all areas of the GTF without regard for the spatial distribution of indirect impacts from the urban matrix, this would support hypotheses that the direct impacts of urbanization on the matrix may drive extinction by creating urban habitat 'islands' where dispersal and foraging opportunities in the matrix are eliminated. Enhanced knowledge of the habitat requirements of urban-avoiding species in urban forest fragments has the potential to improve conservation outcomes in urban forests and planning for future urban expansion around the world (Foley et al. 2005). The ability to conserve these species in urban forest fragments helps combat the worldwide extinction crisis (Foley et al.

2005), and provides social and educational benefits for humans in urban areas with few opportunities to experience intact wildlife communities (Miller and Hobbs 2002; Dearborn and Kark 2010).

METHODS

Study Area

The Great Trinity Forest (GTF) is a large (>4,000 ha) urban forest fragment located within the fourth largest metropolitan area in the United States, Dallas-Fort Worth (U.S. Census Bureau 2020; Figure 1a). The GTF is a bottomland hardwood forest centered on an unlevied portion of the Trinity River, giving it an intact flooding regime and making it unsuitable for further development. Bottomland hardwood forests are diverse habitats because of the natural patterns of ecological succession driven by disturbance from regular flooding events (Hodges 1997). Variation in rates of sediment deposition and wetness, which can completely change the composition of plant communities, are often driven by changes in elevation of only a few inches. Habitat diversity in the GTF is influenced by flooding regimes and amplified by anthropogenic disturbance, creating habitats varying in age from early successional grassland/savanna to mature bottomland hardwood forest. The three most common overstory tress in the GTF are cedar elm (*Ulmus crassifolia*), hackberry (*Celtis laevigata*), and green ash (*Fraxinus pennsylvanica*), with cedar elm being the dominant species in relatively drier areas and green ash dominating the wettest. In younger forest habitats, eastern cottonwood (*Populus deltoides*) and black willow (*Salix nigra*) are the most common overstory trees. In mature levee forests, where flooding is infrequent, masting trees like burr oak (*Quercus macrocarpa*), pecan (*Carya illinoinensis*), and mulberry (*Morus rubra*) are common. The most common understory plant is eastern swamp privet (*Forestiera acuminate*), especially in wetter areas, whereas dense stands of the invasive Chinese privet (*Ligustrum sinense*) dominate the understory in some of the forest's drier areas.

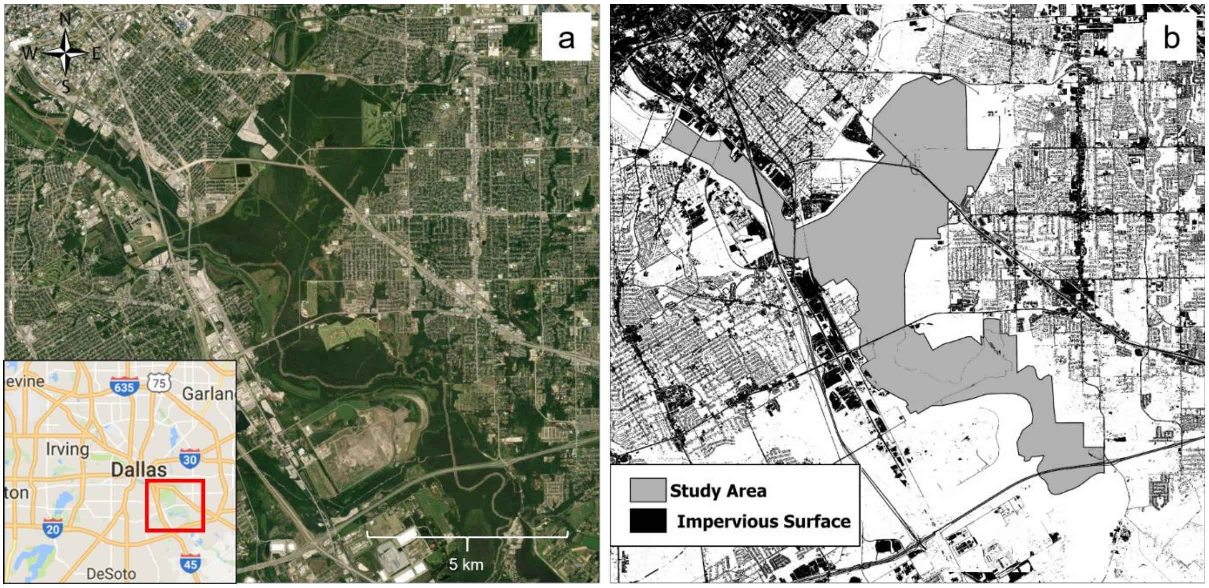

Figure 1. a) The location of the Great Trinity Forest within the city of Dallas, TX, USA (32.733043, -96.733511). b) The location of my study area within the Great Trinity Forest and its spatial relationship to impervious surface in the surrounding matrix, which was identified using supervised, object-based classification in ArcGIS Pro (version 2.2).

The GTF is surrounded by a complex urban matrix and is contained completely within the city of Dallas (Figure 1b). The highest levels of urbanization are located in the northwest portion of the forest near city center, where commercial and industrial developments are primarily found intermixed with dense residential neighborhoods. Urbanization becomes less intense moving to the southeast, where residential neighborhoods eventually intermix with agricultural land. Here the forest is also bordered by multiple golf courses and a large municipal landfill. State, U.S., and interstate highways with high traffic volume and high-speed commuter trains intersect the forest in multiple locations. Parts of the forest are also within a major flight path for commercial aircraft travelling from the Dallas Love Field Airport to Houston. The entire forest is public land managed by a variety of municipal departments and was available for my research.

Latrine Surveys

I located swamp rabbit latrines during dedicated searches and through incidental discovery during field work over a four-year period from 2018 to 2021. I performed dedicated searches for latrines during the winters of 2018/19, 2019/20, and 2020/21, when leaf-off conditions made latrines easier to locate, and swamp rabbits increase the frequency of latrine use (Zollner at al. 1996). I searched for latrines in an unstructured manner, checking all appropriately sized and aged woody debris. During each of these three winters I searched all areas of the forest. Because an important purpose of these latrine searches was also to collect swamp rabbit feces for a companion landscape genetics study, I did not use structured search methodologies (e.g., transects or plots) to look for latrines. I also spent more searching in areas where latrine density was highest to maximize the probability of collecting fresh samples from multiple locations and individuals. I also located many latrines incidentally during other field work in the GTF during the spring, summer, and autumn seasons (e.g., breeding bird surveys, drone operation). When I located a latrine, I mapped its location using ArcGIS Collector and a Bad Elf GNSS Surveyor GPS Receiver with 1-meter accuracy. When a GPS point representing a latrine was created, I took multiple photographs of the latrine and collected the following data in ArcGIS Collector: time, date, number of pellets, number of piles, and diameter of latrine (distance between piles).

Statistical Analysis

Because of the unstructured nature of my latrine searches, my large study area, and the cryptic nature of latrines, I used MaxEnt (Phillips et al. 2021), an ecological niche modelling software program that uses presence only data, to assess the influence of urbanization on swamp rabbit distribution. MaxEnt has consistently outperformed other modeling methods that rely on presence-only data (Elith et al. 2006; Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008). I developed a suite of model parameters that matched the spatial scale of my study area and study species, including environmental variables known to influence swamp rabbit distribution (vegetation structure, flooding frequency, access to refugia during flooding events, vegetation composition, and forest width) and anthropogenic variables representing the indirect impacts of the urban matrix that I hypothesized could influence swamp rabbit distribution (noise pollution, light pollution, urbanization intensity, invasive plants, and invasive animals). More detailed information on data collection and variable development for model parameters is provided in Supplementary Materials S1.

<u>Environmental variables</u>: Previous research has shown that swamp rabbits prefer habitat where canopy gaps create increased structure in the understory (Dumyahn et al. 2015). I used LIDAR point cloud data imported into ArcGIS Pro (version 2.2.0) to develop three variables that described forest structure: foliage height diversity, canopy cover, and maximum vegetation height. These three variables were the most often predictive of wildlife distributions among the many LIDAR metrics (Bakx et al. 2019).

Swamp rabbits also prefer areas of the forest that are more permanently inundated with water, but also need access to highland refugia to survive large flooding events (Zollner et al. 2000; Scharine et al. 2011). Although measurements of wetness are rarely used to explain wildlife distributions, Besnard et al. (2013) showed that topographic wetness index (TWI) successfully predicted the occurrence of bird species in a European wetland. TWI was developed to approximate flooding susceptibility and water accumulation capacity (Beven and Kirkby 1979). I used a digital elevation model of the GTF and a combination of four TWI indices used by Besnard et al. (2013) to model wetness in my study area using the SAGA GIS "Terrain Analysis Hydrology" tools (Böhner and Selige 2006). Many areas of the GTF do not have access to highland refugia as almost all areas above the flood line are developed. I mapped access to highland refugia across the forest, where access was defined as the ability to disperse to a higher elevation area that was not developed without crossing urban areas or waterways that could be a source of flooding.

Swamp rabbits have also been shown to select for habitat based on age, although different studies have found selection for both older and younger habitat (Vale and Kissell 2010; Crawford et al. 2018). I created a habitat map for the GTF, in which habitat types were based on canopy tree composition which can be linked to both successional state and flooding frequency in bottomland hardwood forests (Hodges 1997). In order to identify canopy trees, I made extensive drone flights in the fall of 2021 to obtain aerial images of the forest. I manually piloted drone flights and obtained images at the density required to effectively identify enough trees from images of their crowns to create continuous habitat maps across the entire study area. I imported images of the canopy into ArcGIS Pro for tree identification and the creation of the habitat map. I extensively verified tree identification on the ground as part of an initial training period to ensure that I could correctly identify trees from aerial images, and to determine the appropriate flight altitude at which drone images should be obtained. I continued to use on-the-ground verification where uncertainty existed about identification during the mapping process and for post-identification spot checks. I developed the following six habitat types based on canopy tree composition: cedar elm forest, climax mixed forest, early successional grassland, green ash forest, levee forest, and young mixed forest (Supplementary Materials S1).

Swamp rabbit occupancy is impacted by habitat size, where rabbits preferred larger forest patches (Scharine et al. 2009). The dominant paradigm for riparian forest conservation is that forest width is the best available indicator of ecological function (Spackman and Hughes 1995; Shirley and Smith 2005; Maure et al. 2018). Therefore, I measured forest width in ArcGIS Pro as the perpendicular distance across the forest at any point.

Anthropogenic variables: Although much of the research investigating the impacts of anthropogenic noise on terrestrial species has focused on birds (Jerem and Mathews 2020), there is evidence small mammals avoid noise from highways (Chen and Koprowski 2015). In order to assess the impact of anthropogenic noise on swamp rabbits, I used data from the 2018 National Transportation Noise Map (U.S. Department of Transportation 2020). This dataset allowed us to split noise from transportation into two different types, continuous noise from highways and intermittent noise from airplane and high-speed rail traffic, as continuous and intermittent noise may impact wildlife in different ways (Francis and Barber 2013). This data set measures a 24-hour weighted potential noise exposure across yearly average environmental conditions, making it appropriate for estimating chronic noise exposure for wildlife in the GTF. I quantified and mapped noise exposure as either "at risk for significant noise exposure" or "not at risk", with areas that met or exceeded average daily noise levels of 45 dBA were considered at risk for significant noise exposure for both continuous and intermittent noise.

Investigations of artificial light at night (ALAN) on wildlife have shown impacts on gene expression, physiology, foraging, daily movements, migratory behavior, reproductive behavior, and mortality (reviewed in Gaston et al. 2015). More specifically, small mammals can be unwilling to use brightly lit areas (Bliss-Ketchum et al. 2016). I mapped ALAN in the GTF using 2020 data from Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) in ArcGIS Pro.

The amount of impervious surface in a landscape is often used as a surrogate for the intensity of urbanization and all of its associated impacts (e.g., Donnelly and Marzluff 2004; Rodewald et al. 2013; Evans et al. 2015). As urbanization in the matrix surrounding habitat fragments intensifies, these fragments often suffer a loss of biodiversity and an increase in the risk of local extinction (Kennedy et al. 2010; Kennedy et al. 2011). I measured the amount of impervious surface in and around the GTF using ArcGIS Pro’s image classification wizard and a 2016 50-cm resolution, multi-band remote sensing image of the forest and surrounding Dallas County from the Texas Natural Resource Information System (tnris.org). I used supervised, object-based classification, to reclassify the study area into four land cover categories: impervious surface, forest, open water, and grass/cultivated land. I defined impervious surfaces as any human-made material that is impenetrable to water (e.g., roofs, concrete, building materials, etc.). Urbanization intensity in the nearby matrix was quantified as the amount of impervious surface within 1,000 m buffers from each location in the forest.

As the matrix around a habitat fragment urbanizes, invasive species become more abundant in those fragments (Johnson et al. 2020). Chinese privet (*Ligustrum sinense*) is a rapidly spreading invasive shrub in the southeastern United States and Texas (Arevilca et al. 2016), and has become dominant in the understory of some areas of the GTF. Feral hogs (*Sus scrofa*) are a destructive invasive species that have spread across the southern United States (Campbell and Long 2009). Humans have facilitated the expansion of feral hogs in the United States (Hernández et al. 2018), and feral hogs are now common in urban parks and semi-urban areas in some parts of the world because of anthropogenic food sources (Cahill et al. 2012). Rooting and wallowing behavior by feral hogs reduces plant diversity and richness as well as total vegetation cover in wetlands (Arrington et al. 1999) and forested habitat (Siemann et al. 2009); and disturbance by feral hogs can facilitate the spread of invasive plants (Cushman et al. 2004). Feral hogs are abundant in the GTF, and signs of their damaging rooting behavior are widespread. I assessed the relative abundance of both Chinese privet and feral hogs in the GTF during avian surveys in the summers of 2018, 2019, and 2020. Assessments of invasive species took place in ~140 randomly placed 5 ha plots in each summer. In each plot, I classified Chinese privet relative abundance as absent, low, moderate, or high. I classified feral hog activity as absent, low, moderate, or high based on observations of tracks, feces, and disturbance from rooting. With these data, I used empirical Bayesian kriging in ArcGIS Pro using information from all three summers (405 plots) to create a continuous map of invasive species relative abundance in the GTF.

<u>MaxEnt Modelling Approach</u>: I assessed possible correlations among model parameters and did not include correlated variables ($r > 0.6$) in the final MaxEnt model (Merow et al. 2013). I used MaxEnt to create a grid of cells across the GTF which did not extend beyond the searched area. Cell size selection in MaxEnt models can influence model performance (Connor et al. 2018), therefore I selected a 1 ha cell size relevant to my study species, which occupy home ranges from < 1 to 5 ha in size (Zollner et al. 2000). All parameters that were part of my final model were spatially segregated into these 1 ha cells. Bias in sampling effort across the study area can bias results from Maxent, especially when spatial sampling bias correlates with environmental covariates (Kramer-Schadt et al. 2013), as information from model parameters at presence locations (i.e., cells with at least one latrine) is compared to information from background or pseudo-absence locations (i.e., cells where no latrines were located). To account for this, I

standardized cells by search effort, which has been shown to significantly improve model accuracy (Phillips et al. 2009). For example, cells without latrines that were searched twice as often were twice as likely to be selected as background or pseudo-absence locations in order to model POP. I prescreened regularization coefficient values and feature combinations used to fit response curves of POP to model parameters (Merow et al. 2013). My goal was to create a simple model in which I could easily interpret the impact of model parameters on POP while maximizing gain. I used a regularization coefficient of 1 and only the hinge feature to fit the model. I completed 10 k-fold cross validations of the MaxEnt model for model testing, in which I withheld a random 10% of presence locations in each iteration. The mapping of POP across all cells and the response of POP to model parameters were evaluated using the average of these ten models. I used raw outputs of POP as opposed to logistic ones, as raw outputs do not rely on post processing assumptions (Merow et al. 2013). I used average area under the ROC curve (AUC) for model validation, a threshold independent statistic that represents the probability that a random presence site will be more suitable than a random background point (Fielding and Bell 1997).

RESULTS

I located 650 latrines during field work from 2018 to 2022 (Figure 2a). MaxEnt spatially segregated the study area into 3060 1 ha cells, with 248 of those cells considered presence locations (i.e., they contained ≥ 1latrine). Prescreening for correlation among model parameters revealed significant correlation between all three LIDAR derived variables describing vegetation structure. Therefore, only maximum vegetation height was included in the final model. ALAN was also closely correlated with the amount of impervious surface within 1,000 m of each cell, causing us to also exclude ALAN from the model. MaxEnt used the remaining model parameters to map POP across the study site (Figure 2b). Average AUC for the ten model replicates was 0.829, showing the model was successfully able to distinguish presence locations from background locations. Vegetation composition, vegetation structure, TWI, and feral hog activity explained the most variation in the model based on their percent contribution and permutation importance (Figure 3). POP values were higher in areas where the vegetation composition was cedar elm forest or climax mixed forest (Figure 4a), vegetation structure (maximum vegetation height) was at moderate levels (Figure 4b), and TWI was at moderate levels (Figure 4c). In contrast, POP values were lower in areas where evidence of feral hog activity was absent or high (Figure 4d).

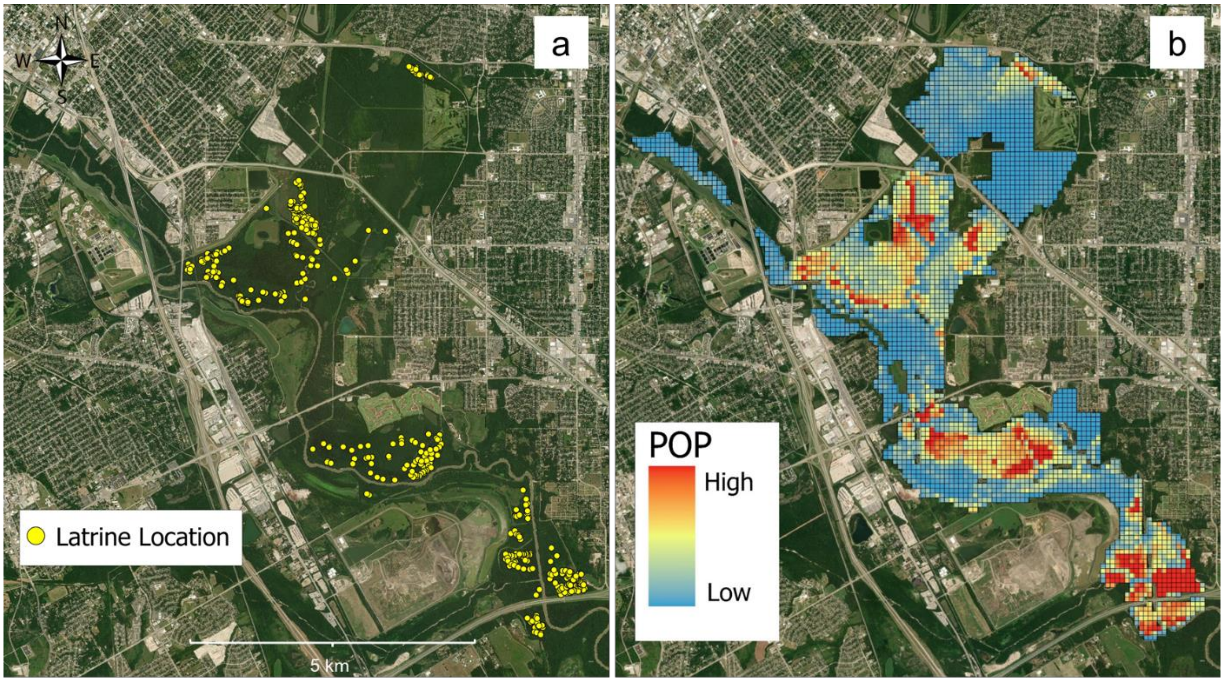

Figure 2. a) The location of all 650 identified latrines recorded over four years (2018-2021) in the Great Trinity Forest. b) Probability of swamp rabbit presence in my study as determined by MaxEnt. POP was determined for 3060 cells that were 1 ha in size each, showing that suitable habitat was heterogeneously distributed within the site.

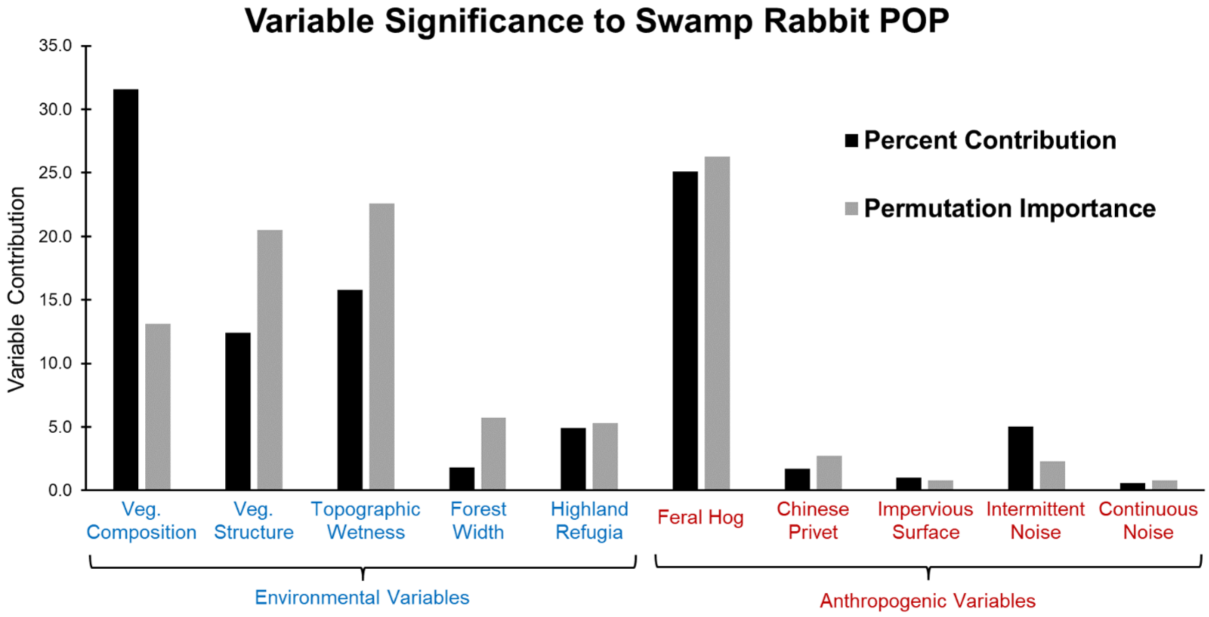

Figure 3. The percent contribution (range: 0-100) and permutation importance (range: 0-100) of all model parameters included in the final MaxEnt model. The four variables that contributed most to the variation in swamp rabbit probability of presence were vegetation structure, vegetation composition, topographic wetness index, and evidence of feral hog activity.

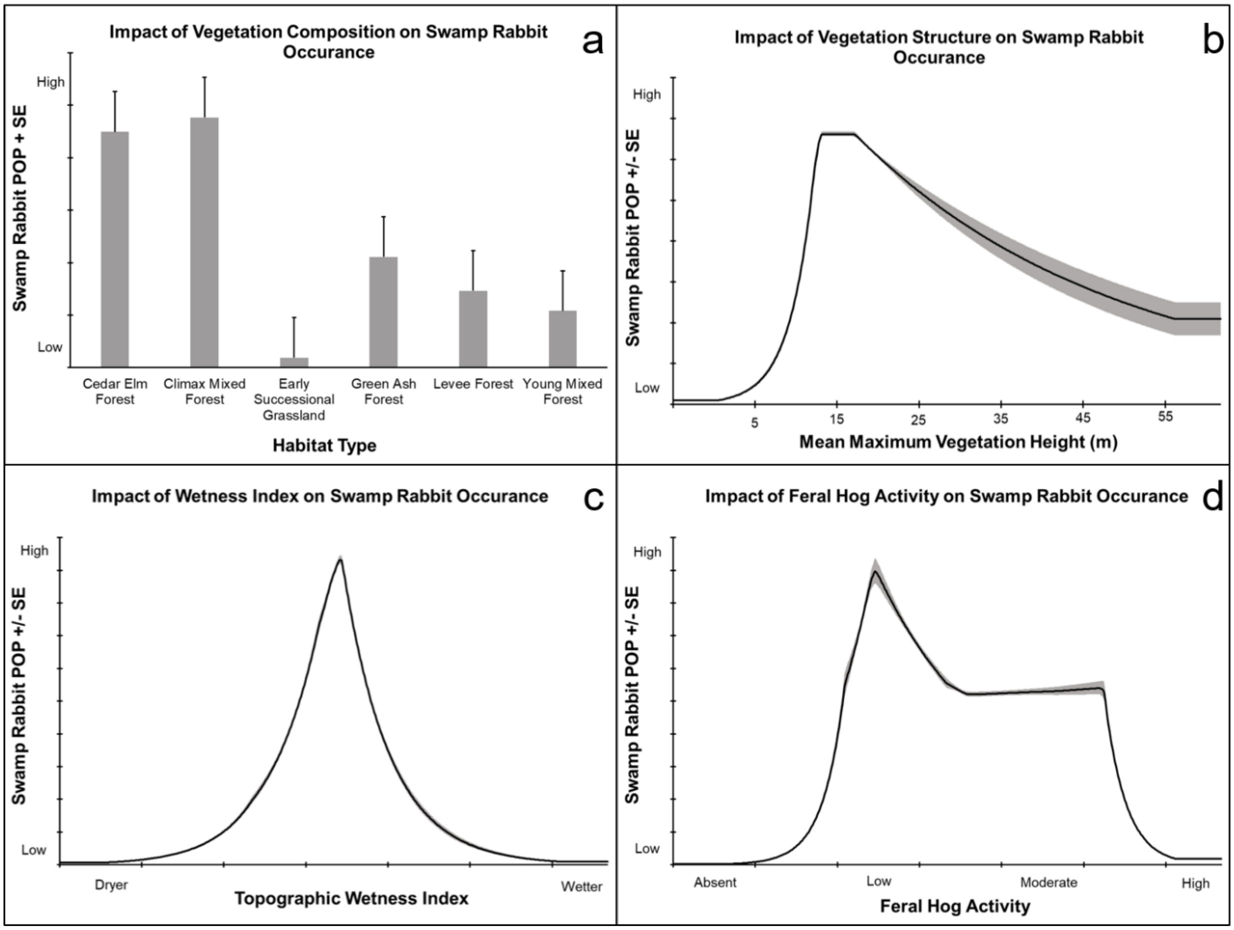

Figure 4. The response of swamp rabbit probability of presence to the four variables that explained the most variation in the model. a) Swamp rabbit POP was highest where the vegetation type was cedar elm or climax mixed forest and lowest where the vegetation type was early successional grassland. b) Swamp rabbit POP was highest where mean maximum vegetation height was between 10 m and 30 m and lowest where mean maximum vegetation height was below 5 m. c) Swamp rabbit POP was highest where levels of topographic wetness were moderate and lowest where levels of topographic wetness were the driest or wettest. d) Swamp rabbit POP was highest where evidence of feral hog activity was low to moderate, and lowest where evidence of feral hog activity was absent or high.

DISCUSSION

Four variables best explained the distribution of swamp rabbits in the GTF, and only one of which, feral hog activity, was associated with the urban matrix. Of the six model parameters associated with the urban matrix, feral hog activity has the weakest association with urbanization, as feral hogs are also spreading rapidly in rural and wild areas (Adams et al. 2005).

Highway noise, air traffic noise, invasive plants, urbanization intensity in the nearby landscape, and by proxy light pollution, were not important explanatory variables for the distribution of this urban avoiding habitat specialist. The willingness of swamp rabbits to use habitat near loud highways and intense urbanization in the matrix lends support to hypotheses that urban avoiding species are excluded from urban habitat fragments by the direct impacts of changes to the matrix that may limit dispersal and foraging opportunities (Kupfer et al. 2006). Swamp rabbits and other urban avoiding species may persist in the GTF because it is a large urban forest (>4,000 ha) and may have some connectivity to other tracts of habitat, as seen on aerial imagery of land cover, along the Trinity River as it flows southeast beyond the city limits, which is consistent with the principles of island biogeography. Urban forest fragments may not appear to be islands of habitat to species that tolerate urbanization, but for species that cannot adapt to the drastic changes associated with urbanization, urban habitat fragments become isolated islands with reduced genetic connectivity and population viability. In some cases, even urban adapting small mammals become isolated in habitat islands surrounded by dense urbanization, where dispersal abilities are reduced in ways that are consistent with the principles of island biogeography (Richardson et al. 2020).

Feral hog activity had the highest combined contribution to the model of any model parameter. The decrease in swamp rabbit POP in areas of high hog density was not surprising, but the decrease in swamp rabbit POP in areas where feral hogs were absent is less intuitive. Extensive damage from rooting by feral hogs is common in the GTF, and research has shown that this behavior reduces plant cover and diversity in forest ecosystems (Barrios-Garcia and Ballari 2012). In addition, feral hogs are significant sources of predation for small mammals (Wilcox and van Vuren 2009). Thus, not only do feral hogs alter swamp rabbit habitat and forage, but they may create a landscape of fear in areas where they are abundant (Laundre et al.

2010), making these parts of the forest even more unsuitable for swamp rabbits. The reduction in swamp rabbit POP associated with feral hog absence may be explained by both species responding to other unmeasured variables. For example, feral hogs selected for areas with high primary productivity in another urban forest (Stillfried et al. 2017). In the GTF, areas with low feral hog density, and sometimes a complete absence of hog sign, were concentrated in locations with overall lower diversity and evenness in the understory plant community and in which young monotypic stands of green ash were dominant. Feral hogs may have avoided these areas because of possible lower levels of productivity and a lack of masting trees, which are an import source of food for this species (Taylor and Hellgren 1997). Swamp rabbits, on the other hand, may have avoided these same areas because of a lack of complex understory cover or appropriate forage (Vale and Kissell 2010).

Swamp rabbits responded positively to a number of environmental variables including mature forest habitat based on canopy tree composition, and habitats at moderate levels of height and structure and levels of flooding frequency. Swamp rabbits preferred cedar elm and climax mixed forest habitat, and avoided early successional habitat. They also preferred areas with moderate levels of structure, where heterogeneity in the canopy created more structure in the understory which in turn provides more cover. In the GTF, swamp rabbit selection for older habitat with large piles of brush and debris in the understory matches the descriptions of swamp rabbit habitat selection from Scharine et al. (2011) and Dumyahn et al. (2015), but differed from the preference for dense young forest with a brushy understory observed by Scharine et al. (2009) and Vale and Kissell (2010). Swamp rabbit preference for areas of moderate topographic wetness in the GTF is somewhat surprising but may be explained by the urban matrix. Topographic wetness index reflects both wetness/water holding capacity and flooding frequency (Beven and Kirkby 1979). The literature on swamp rabbits consistently shows a preference for habitat that is highly inundated with access to nearby higher and drier areas to survive flooding events (Zollner et al. 2000; Vale and Kissell 2010; Scharine et al. 2011; Crawford et al. 2018). Lower swamp rabbit POP in areas where TWI was low is consistent with the literature, but their avoidance of areas with high topographic wetness is unexpected when examined in isolation. Despite the importance of access to highland refugia for survival during flooding events, only ~ 8% of the GTF has access to highland refugia. The border between the GTF and the urban matrix associated with the city of Dallas is in large part defined by elevation, where areas above the flood line have been developed and further development is limited by flooding in lower elevation areas that represent the GTF. It is possible that because the vast majority of swamp rabbits in the GTF do not have access to undeveloped highland refugia, that rabbits in areas that are wetter/more frequently flooded may have lower survival. Preference for wetter habitat that reduces survival in frequently flooded areas may create this strong preference for moderate levels of topographic wetness at this site.

My study indicates that urban avoiding species can be conserved in urban habitat fragments if those fragments are large and well connected, and that indirect impacts of urbanization from the matrix do not exclude urban avoiders from urban forest fragments. Direct evidence of urbanization limiting dispersal in swamp rabbits or other urban avoiding species would increase evidence justifying the application of the concepts of island biogeography to urban habitat islands and support the importance of direct impacts of urbanization on the matrix in the loss of urban avoiders from urban habitat fragments. The control of feral hogs may be critical to the conservation of sensitive species in urban habitat fragments like the swamp rabbit, but also for a broad range of small mammals in urban, rural, and wild habitats (McClure et al. 2018). My study was the first to characterize the distribution of an urban avoiding species in an urban habitat fragment, providing new and important information that may facilitate conservation in and near urban areas as urbanization spreads, a critical challenge in combatting the worldwide extinction crisis (Foley et al. 2005).

SUPPLEMENTARY MATERIALS

LIDAR

I acquired LIDAR data flow over the GTF in 2017 by the North Central Texas Council of Governments in a fixed wing aircraft. The specifications of the LIDAR data are as follows: Leica Specs-AGL LIDAR System, 0.5-meter nominal point spacing, 150 knot aircraft speed, 50-degree field of view, 230.5 kHz pulse rate, 47 Hz scan rate, and 30% average overlap. Multiple returns were recorded for each laser pulse and intensity values were recorded for all returns. Flights occurred during leaf off conditions between January 21 and February 10, 2017. Four Global Navigation Satellite System Base Stations were used in support of the LIDAR missions.

I processed LIDAR data in ArcGIS Pro using the full point cloud data. I developed a digital terrain model (DTM) to normalize all non-ground returns and LIDAR forest structure metrics against. I calculated maximum vegetation height as the average height of first returns. I calculated canopy cover as the number of returns above 4 m divided by the total number of returns. I calculated foliage height diversity using the Shannon Wiener Diversity Index comparing the number of returns in five height classes: 0 to 2 m, 2 to 4 m, 4 to 8 m, 8 to 12 m, and > 12 m.

Drone Imagery and Vegetation Types

All drone images were acquired using DJI Phanton 3 Advanced Drone (12 megapixel camera) between October 7th and October 24th 2020. Images were taken at a 90-degree angle from ~ 40m above the canopy. Image acquisition, tree identification and habitat mapping followed a workflow pictured below in Figures 5 and 6.

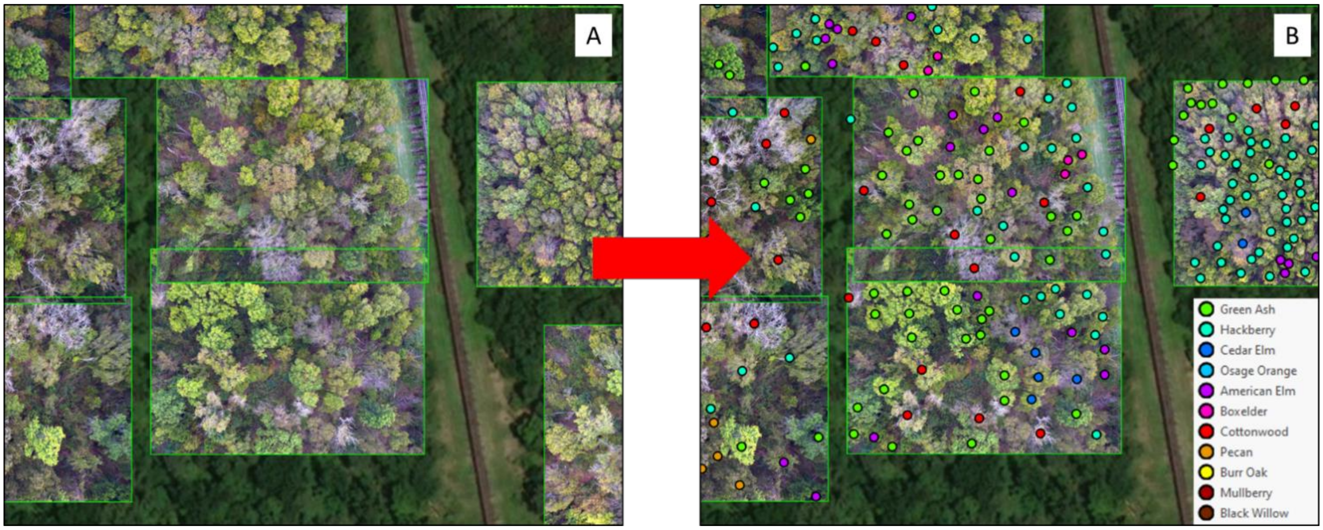

Figure 5. a) Drone images are imported into ArcGIS Pro using the software's orthomapping tools which creates photogrammetrically correct imagery. b) all individual trees are identified.

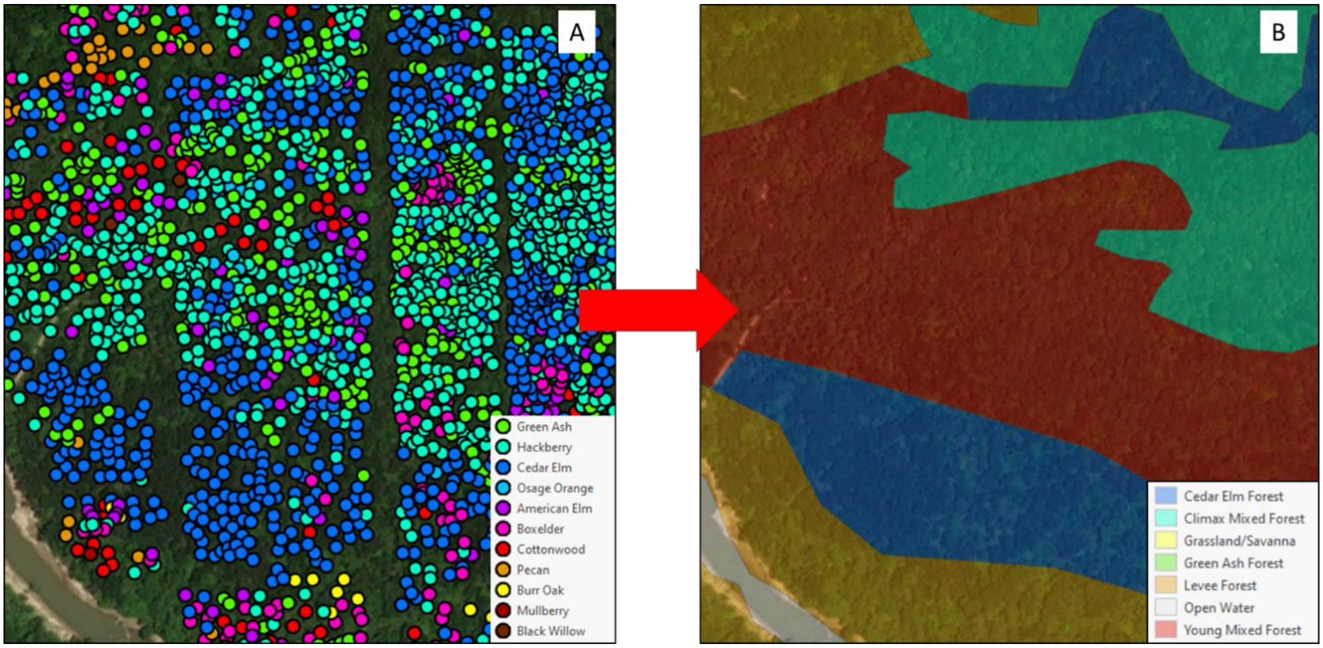

Figure 6. a) Dense imagery allows for enough tree identifications that b) habitat types can be assigned based on canopy tree composition.

I defined my six habitat types by canopy tree composition as follows: 1) climax mixed forest: >90% cedar elm, green ash, and hackberry with none of those individually accounting for >50% of trees; >5% Osage orange; 2) cedar elm forest: >75% cedar elm with Osage orange and hackberry as common minority species; <5% early successional species: American elm (*Ulmus americana*), boxelder (*Acer negundo*), eastern cottonwood, and black willow; 3) green ash forest: >75% green ash with hackberry and black willow as common minority types; <10% early successional species: American elm, Boxelder, eastern cottonwood, and black willow; 4) early successional forest: >35% early successional species: American elm, Boxelder, eastern cottonwood, and black willow; 5) levee forest: 10% to 20% masting trees: pecan (*Carya illinoinensis*), burr oak (*Quercus macrocarpa*), shumard oak (*Quercus shumardii*), and mulberry (*Morus rubra*) which account for the majority of canopy cover because of their large size; and 6) early successional grassland: <50% canopy cover of trees.

Chapter 3: Urbanization inhibits dispersal and gene flow in a habitat specialist across a large urban forest fragment

INTRODUCTION

As natural habitats become more fragmented it is critical for conservation biologists to understand how specific habitat variables facilitate or impede dispersal and gene flow (Storfer et al., 2010). Landscape genetics investigates the effects of landscape variables on population connectivity, gene flow, and dispersal (Holderegger & Wagner, 2006). Although urbanization is an important driver of habitat fragmentation (Marzluff & Ewing, 2001), landscape genetic studies in urban areas are uncommon (Manel & Holderegger, 2013; Fusco et al., 2021). In contrast, investigations of population connectivity among isolated fragments are more common, indicating that the composition of the matrix between fragments can have a significant impact on gene flow (Holderegger & Wagner, 2008). Studies of urbanization and fragmentation have indicated that an urban matrix can decrease the diversity and richness of wildlife species in habitat fragments (Rodewald & Bakermans, 2006; Kennedy et al., 2010; Kennedy et al., 2011). Using landscape genetics techniques, I understand that wildlife species can lose genetic diversity and connectivity to other fragments as the surrounding landscape urbanizes (Delaney et al., 2010; Munshi-South & Kharchenko, 2010; Unfried et al., 2013), providing a mechanism by which observed decreases in species diversity and richness might occur. Urbanization also increases the number of roads that bisect habitat fragments, which often decrease the functional connectivity of animal populations (Holderegger & Di Giulio, 2010). This is especially problematic for wildlife species in riparian habitat fragments in urban areas, as available habitat is often configured in long narrow tracts (Rodewald & Bakermans, 2006), making it more likely that the habitat will be bisected by multiple roads compared to other similarly sized fragments.

Despite being an elusive and cryptic species, swamps rabbits are readily sampled with non-invasive methods leveraging their use of latrines: locations where they deposit visible piles of scat on top of fallen trees or stumps (Zollner et al., 1996). I used fecal DNA, microsatellite markers, and landscape genetics analytical approaches to examine the impact of urbanization and highways on swamp rabbit gene flow and dispersal within a single large urban forest fragment. I predicted that urbanization would inhibit gene flow in swamp rabbits, supporting hypotheses that the direct impacts of urbanization on the matrix may drive extinction by creating urban habitat islands because dispersal and foraging opportunities are eliminated in the matrix. I also predicted that highways bisecting the forest would be barriers to gene flow in swamp rabbits, thereby creating distinct subpopulations within the forest. To my knowledge this is the first study to examine the impacts of urbanization on gene flow within a single habitat fragment, and one of the first to investigate the impacts of urbanization on gene flow in an urban avoiding species, as they are absent from most urban habitat fragments. A better understanding of factors driving the loss of urban avoiding species from urban habitat fragments will increase my ability to conserve these species in the face of rapid global urbanization (Seto et al., 2012). The ability to conserve these species in urban forest fragments will help combat the worldwide extinction crisis (Foley et al., 2005), and provide social and educational benefits for humans in urban areas with few opportunities to experience intact wildlife communities (Miller & Hobbs, 2002; Dearborn & Kark, 2010).

METHODS

Study Area

The Great Trinity Forest (GTF) is a large (>4,000 ha) urban forest fragment located within the fourth largest metropolitan area in the United States, Dallas-Fort Worth (U.S. Census

Bureau 2020; Figure 7a). It is a bottomland hardwood forest centered on an unlevied portion of the Trinity River, giving it an intact flooding regime and making it unsuitable for further development. Bottomland hardwood forests are diverse habitats because of the natural patterns of ecological succession driven by disturbance from regular flooding events (Hodges, 1997). Variation in rates of sediment deposition and wetness, which can completely change the composition of plant communities, are often driven by changes in elevation of only a few inches. Habitat diversity in the GTF is influenced by flooding regimes and is amplified by anthropogenic disturbance, creating habitats varying in age from early successional grassland/savanna to mature bottomland hardwood forest.

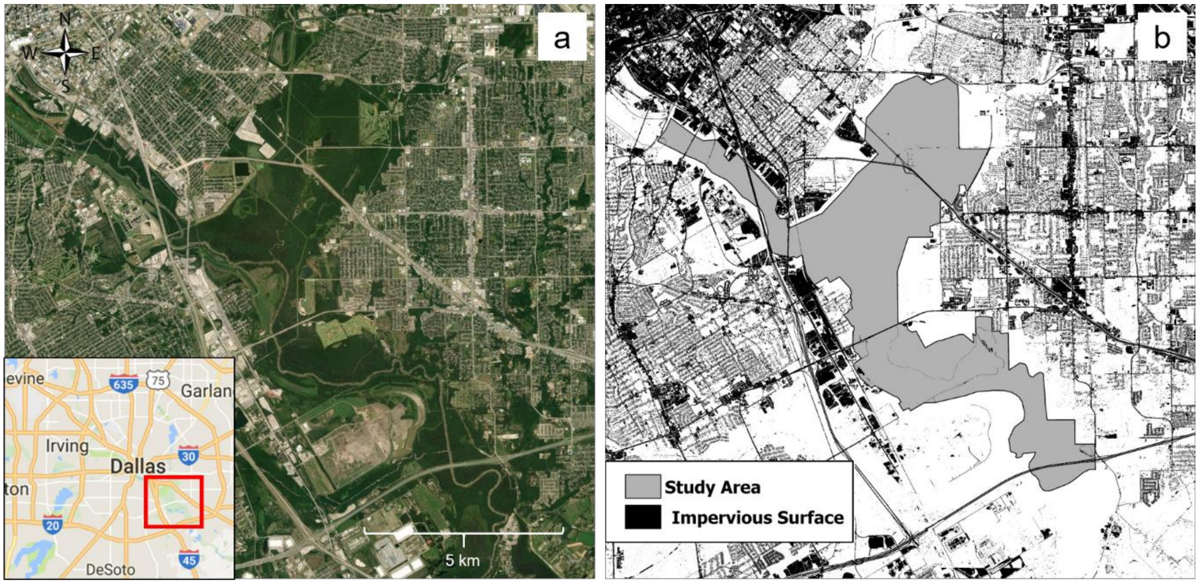

Figure 7. a) The location of the Great Trinity Forest within the city of Dallas, TX, USA (32.733043, -96.733511). b) The location of my study area within the Great Trinity Forest and its spatial relationship to impervious surface in the surrounding matrix, which was identified using supervised, object-based classification in ArcGIS Pro v. 2.2.

The GTF is surrounded by a complex urban matrix and is contained completely within Dallas city limits (Figure 7b). The highest levels of urbanization are located in the northwest portion of the forest near city center, where commercial and industrial developments are primarily found intermixed with dense residential neighborhoods. Urbanization becomes less intense to the southeast, where residential neighborhoods eventually intermix with agricultural land. Here the forest is also bordered by multiple golf courses and a large municipal landfill. The GTF is bisected by an interstate highway (I-20; 8 lanes; 2018 to 2020 mean traffic volume ~ 120,000 vehicles/day), a U.S. Highway (US 175; 6 lanes; 2018 to 2020 mean traffic volume ~ 60,000 vehicles/day), and a state highway (Loop 12; 4 lanes; 2018 to 2020 mean traffic volume ~ 28,000 vehicles/day), and high-speed commuter trains intersect the forest in multiple locations (Texas Department of Transportation AADT Annuals). Portions of the forest are also within a major flight path for commercial aircraft travelling between the Dallas Love Field Airport and Houston. The entire forest is public land managed by a variety of municipal departments and was available for my research.

Sample Collection

I located swamp rabbit latrines and collected fecal pellets during dedicated searches and through incidental discovery during field work over a four-year period from 2018 to 2021. I performed dedicated searches for latrines during the winters of 2018/19, 2019/20, and 2020/21, when leaf-off conditions made latrines easier to locate, and swamp rabbits increase the frequency of latrine use (Zollner at al., 1996). I searched for latrines in an unstructured manner, checking all appropriately sized and aged woody debris. During each of these three winters I systematically searched suitable tracts of the forest and conducted several repeat visits to areas with known latrine locations. Between February 21 and 28, 2021 I visited all known latrine locations once with a large number of searchers to make as many collections as possible during an eight-day period, which I considered a period of population closure. When I located a latrine, I mapped its location using ArcGIS Collector and a Bad Elf GNSS Surveyor GPS Receiver with

1 m accuracy. When a GPS point representing a latrine was created, I took multiple photographs of the latrine and collected the following data in ArcGIS Collector: time, date, number of pellets, number of piles, and diameter of latrine (distance between piles).

I collected fecal pellets at all latrines where pellets appeared to be <4 days old. I collected pellets of this age based on information gained in 2018 when I made daily trips to latrines that were cleared on day one to study the appearance of pellets as they aged and to test my ability to successfully extract DNA from pellets of different ages. Pellets were collected wearing latex gloves with single use autoclaved wooden toothpicks. From a single pile, I put 1 to 3 pellets into separate 5 ml tubes containing 3 ml of 8 M urea preservative buffer (Asahida et al., 1996) and then stored the samples at room temperature prior to DNA extraction. I collected multiple samples at a single latrine when there were multiple defecations of the appropriate age (i.e., <4 days old).

I obtained vouchered Sylvilagus aquaticus (n = 11) and Sylvilagus floridanus (n = 8) tissue samples from the Angelo State Natural History Collection and the Museum of Texas Tech University to test candidate microsatellite loci (Supplementary Materials).

DNA Extraction

I extracted DNA from swamp rabbit fecal pellets using the QIAamp Fast DNA Stool Mini Kit (Qia-gen Genomics, Valencia, CA). Extractions were conducted in an extraction dedicated AirClean^{TM} 600 PCR workstation according to kit manufacturer specifications. DNA extractions of Sylvilagus aquaticus and Sylvilagus floridanus tissue samples followed an ammonium acetate/isopropanol precipitation method (Korstian et al., 2013). I used a negative control in all DNA extractions.

Microsatellite Marker Development

I selected 35 microsatellite loci for testing for use in my study from multiple species including dual use markers developed for *Sylvilagus aquaticus* and *Sylvilagus floridanus* (Berkman et al., 2009), as well as markers for *Oryctolagus cuniculus* (Mougel et al., 1997; Surridge et al., 1997), *Sylvilagus transitionalis* (King et al., 2017), and *Brachylagus idahoensis* (Estes-Zumpf et al., 2008; see Supplementary Materials for loci tested). These markers were first tested on DNA extracted from tissue samples of *Sylvilagus aquaticus* and *Sylvilagus floridanus*, and then on DNA extracted from swamp rabbit fecal samples collected in the GTF. Markers that failed to amplify, were monomorphic, or gave non-specific amplification were eliminated. I chose seven final loci that were polymorphic, consistently amplified, and straightforward to genotype. These seven dye-labelled microsatellite loci were amplified and genotyped in two multiplexes of 2 or 3 loci each and as 2 single loci. (Supplementary Materials Table 2).

Genotyping

PCR reactions for fecal samples were conducted in a separate room from DNA extractions in a PCR dedicated AirClean^{TM} 600 PCR workstation, with a negative control present in each PCR amplification. PCR reactions were setup in 10 µl volumes containing 2 µl of DNA, 1 µl primer, 5 µl of AccuStart^{TM} II PCR SuperMix, 1.8 µl of distilled water, and 0.2 µl BSA. Markers StrQ32 and Sfl011 were amplified in single reactions and then coloaded with the markers in multiplexes A and B respectively (Supplementary Materials Table 2). PCR reactions were run on an ABI 2720 thermal cycler (see Supplementary Materials for PCR settings). PCR products from the same multiplex were combined and diluted with 200 µl of water. One microliter of each coload was added to 15 µl of Hi-Di formamide and 0.15 µl of GS500 ROX size standard and then electrophoresed on an ABI 3130XL Genetic Analyzer. Genotypes were visualized and scored using GENEMAPPER 5.0.

I initially ran three replicates of each fecal sample and then used the comparative method to create consensus genotypes (Frantz et al., 2003; Hansen et al., 2008; Hájková et al., 2009). A genotype at a locus was scored as a homozygote if a single allele occurred >2 times across replicates and as a heterozygote if more than one allele was scored ≥2 times across replicates. Consensus genotypes were constructed manually for each sample. If a sample had a consensus genotype with fewer than seven loci, I ran three more replicates. After this, I ran a small subset of samples three more times to reach a consensus genotype, bringing some samples to a maximum of nine replications. Genotypes were then discarded if the consensus still had ≤4 loci. Genotypes were considered identical when they matched at all loci or all but one locus. I used the multilocus analysis in GenAlEx v. 6.5 (Peakall & Smouse, 2012) to find genotyping matches.

Genetic Analysis

I calculated observed and expected heterozygosity using GenAlEx v. 6.5 and tested for deviations from Global Hardy-Weinberg equilibrium and heterozygote deficits at individual loci using GENEPOP v. 4.2 (Rousset, 2008). I also used GENEPOP to test for deviations from genotypic linkage equilibrium between loci. P-values for deviations from Hardy-Weinberg and genetic linkage equilibrium were adjusted for multiple tests using a sequential Bonferroni correction (Rice 1989). Observed heterozygosity, expected heterozygosity, tests of genotypic linkage equilibrium, and tests of Hardy-Weinberg equilibrium were performed using all unique genotypes from the closure period (i.e., Feb. 21-28, 2021).

I used GIMLET v. 1.3.2 (Valière, 2002) to determine error rates for each locus including allelic dropout and false alleles (Broquet & Petit, 2004). I used GenAlEx v. 6.5 to calculate the probability that two unrelated individuals and two siblings would have the same genotype. Error rates were calculated using all samples successfully genotyped at ≥5 loci, whereas probability of identity and probability of siblings were calculated using all unique genotypes from the closure period.

I estimated population size for swamp rabbits in the GTF using CAPWIRE (Miller et al., 2005), which utilizes multiple observations of individuals within a closed sampling session to estimate population size. I used all genotypes from the closure period for this analysis. I accounted for detection heterogeneity among individuals using CAPWIRE's two innate rates model (TIRM). I used all unique genotypes from the closure period to calculate swamp rabbit effective population size (Ne) using the linkage disequilibrium method as implemented in NeEstimator v. 2.1 (Do et al., 2014).

To look for genetic divergence among clustered sub-populations of swamp rabbits within the GTF, I calculated F_{ST} values (Weir & Cockerham, 1984) and spatial genetic autocorrelation (Smouse & Peakall, 1999; Peakall et al., 2003) in GenAlEx v. 6.5. I estimated pairwise F_{ST} values between the five largest clusters of individuals and global F_{ST} for the whole population using the infinite allele model and 999 permutations. I also calculated the standardized F'_{ST} of Meirmans & Hedrick (2011) since F_{ST} is influenced by heterozygosity. All unique genotypes from these five clusters were used in the analysis. I examined genetic spatial autocorrelation by looking for trends in multilocus correlations among individuals at five different distance categories: 1,000 m, 3,000 m, 5,000 m, 7,000 m, and 10,000 m, which spanned the largest distance between samples in my dataset. I performed this analysis with 999 permutations and 1,000 bootstraps, using only samples from the closure period.

I used Resistance to Dispersal Mapper (ResDisMapper; Tang et al., 2019) to explore the impacts of urbanization on gene flow and dispersal in swamp rabbits. ResDisMapper is an R package that maps resistance to dispersal at small spatial scales without requiring prior knowledge of the impact of environmental features on dispersal. ResDisMapper uses a four-step process to map resistance to dispersal: 1) calculates genetic and geographic distances for all possible pairs of individuals to generate isolation by distance (IBD) values, and then fits the IBD trend to generate residuals for all pairs of individuals (genetic distance can be calculated with one of six methods selected by the user); 2) visualizes the distribution of IBD residuals as line segments between individuals across the landscape; 3) creates a grid with a user defined cell size and uses IBD residual values from all line segments that intersect a grid cell to calculate that cells resistance (mean of the IBD residual values), statistical certainty of resistance, and statistical significance of resistance (positive resistance indicates a location that resists dispersal, whereas negative resistance indicates a location that facilitates dispersal); and 4) visualizes the resistance map. I used the absolute genetic distance (Prevosti et al., 1975) to calculate IBD values and generated residuals by fitting a linear trend to IBD values. I created a map with a maximum possible grid size of 20 x 20 and used all IBD residuals to calculate resistance (infinite geographic distance range). I used 95% CI to determine statistical certainty of resistance values in each grid cell, where certainty is achieved when the CIs did not overlap zero. All unique genotypes were used in this analysis.

I linked resistance to dispersal values from ResDisMapper to urbanization in the landscape using two methods. First, I built a layer of urban land use in ArcGIS Pro v. 2.2.0 that included all impervious surfaces like roads, buildings, and other concrete surfaces as well as frequently mowed areas like highway medians or yards and cleared gravel or dirt surfaces found in many industrial areas and junkyards. I then mapped grid cells from ResDisMapper where certainty for either facilitating or resisting dispersal was met in ArcGIS Pro. I then compared the amount of urbanization in cells that resisted dispersal to cells that facilitated dispersal using a two proportion Z-test, in which cells that contained >50% urban land use were given a value of 1 and cells with ≤50% urban land use were given a value of 0. I chose this analysis because ~ 70% of cells with statistical certainty for their impact on dispersal were either below 10% or above 90% in urban land use. To investigate the impact of highways on dispersal I compared IBD residual values between all six adjacent clusters using a one-way ANOVA to see if clusters separated by highways had higher resistance levels than clusters that were not separated by highways. I also applied the test of statistical certainty used by ResDisMapper to mean resistance levels between adjacent clusters to assess whether dispersal was facilitated or resisted.

RESULTS

Of the 367 swamp rabbit fecal samples that I collected and processed, a total of 234 samples (63.8%) were successfully genotyped at five or more loci, accounting for 80 unique individuals (Figure 8). During the closure period, 121 samples were successfully genotyped at five or more loci, accounting for 42 unique individuals. There were no significant deviations from Hardy-Weinberg equilibrium, globally or at individual loci. All loci were polymorphic with an average of 6 alleles and average observed heterozygosity of 0.68. There was no evidence for heterozygote deficits at any of the loci (Supplementary Materials Table 3). There was significant genetic disequilibrium ($p < 0.002$) between 5 of the 21 possible pairwise combinations of loci: StrQ15 - StrQ32, A10 - StrQ43, StrQ32 - StrQ43, StrQ15 - StrQ46, and StrQ32 - StrQ46.

PCR success rates were high, ranging from 0.755 to 0.910. Allelic dropout rate was similar across most loci (mean = 0.23) and false allele rates were minimal (Supplementary Materials Table 3). The probability that two individuals would share the same genotype was <0.001 for consensus genotypes with 5 to 7 loci (all $p < 0.001$). Probability that two siblings would share the same genotype was also low for consensus genotypes with 5 loci ($p = 0.02$), 6 loci ($p = 0.009$), or 7 loci ($p = 0.004$).

Based on estimations from CAPRWIRE's TIRM model and the 121 successfully genotyped samples representing 42 individuals from the closure period, the estimated population size was 63 individuals (95% CI: 45-77). Effective population size was 19.7 individuals (95% CI: 14.2-27.3) when estimated by NeEstimator, with lowest allele frequency set to 0.05.

Genetic subdivision of swamp rabbits in the GTF was significant based on global F_{ST} values ($F_{ST} = 0.065$, $p = 0.001$, $F'_{ST} = 0.204$). Pairwise analysis of F_{ST} between the five largest clusters of swamp rabbits (A, B, C, D, and E) showed significant structuring between the sub-populations in all but one combination, B-C (Table 1). Results of genetic spatial autocorrelation analysis showed that swamp rabbits were more related than expected at distances <3,000 m (1000 m: $N = 147$, $p = 0.001$; 3000 m: $N = 197$, $p = 0.002$) and less related than expected at distances >5,000 m (7000 m: $N = 115$, $p = 0.009$; 10000 m: $N = 282$ $p = 0.001$; Figure 9).

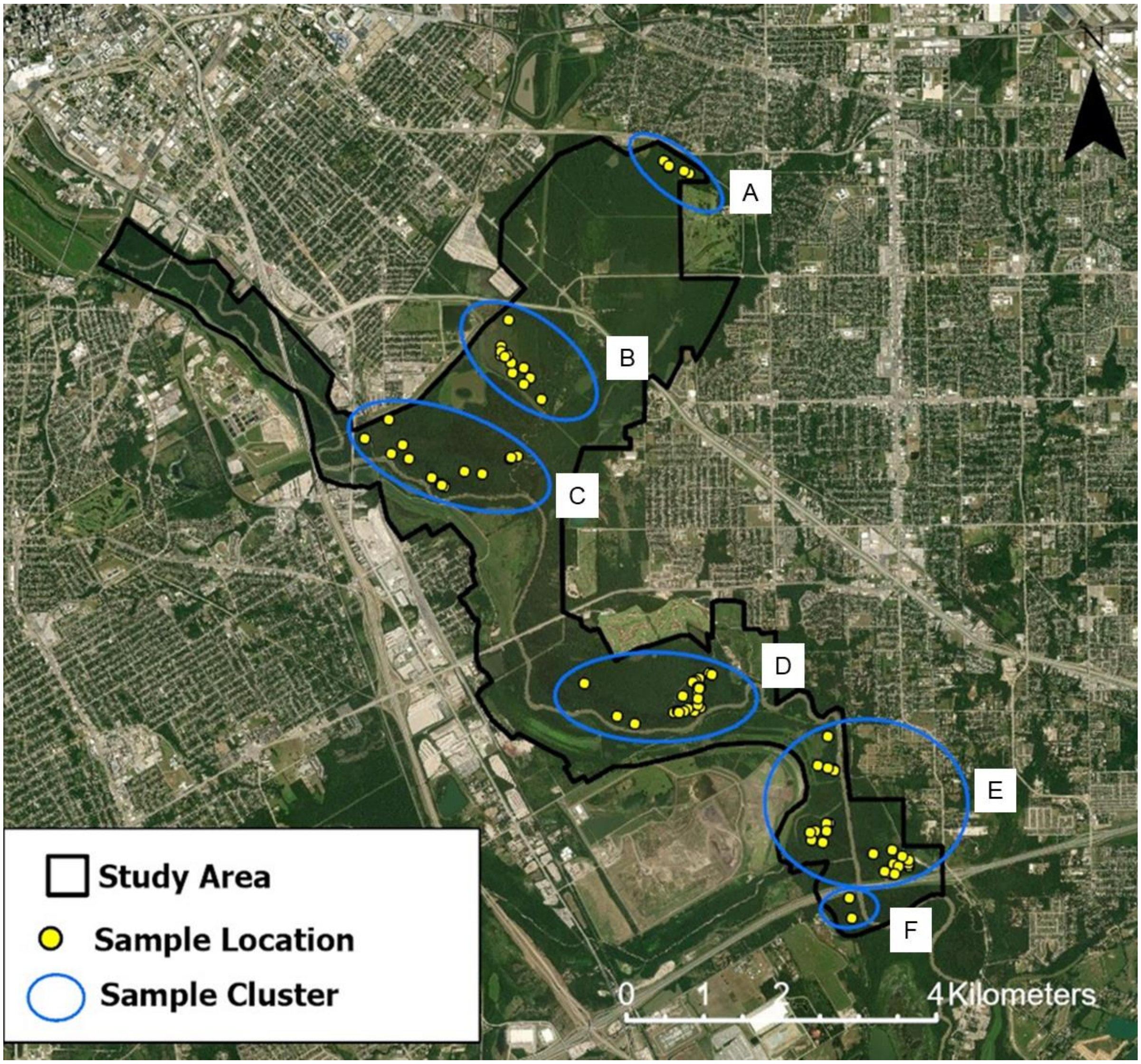

Figure 8. Sample locations representing the 80 unique swamp rabbit genotypes in the Great Trinity Forest, Dallas, TX, USA. Individuals with multiple sampling locations are represented here by a geographic centroid at each of those locations. Sample clusters are designated by letters starting with the northernmost cluster and moving south: cluster A (N = 6), cluster B (N = 12), cluster C (N = 14), cluster D (N = 23), cluster E (N = 24), cluster F (N = 2). Clusters A-B, C-D, and E-F are separated by highways.

Table 1. FST values (bold) and p-values (italicized) for all pairwise comparisons between the five largest swamp rabbit clusters in the Great Trinity Forest, Dallas, TX, USA. For FST values, moving to the right across any row or moving down any column increases geographic distance, revealing a general trend of increasing FST values with increasing geographic distance.

	A	B	C	D	E
A	0.000	**0.085**	**0.097**	**0.144**	**0.175**
B	*0.008*	0.000	**0.005**	**0.044**	**0.033**
C	*0.001*	*0.307*	0.000	**0.071**	**0.074**
D	*0.001*	*0.005*	*0.001*	0.000	**0.037**
E	*0.001*	*0.005*	*0.001*	*0.001*	0.000

ResDisMapper used IBD residuals to map resistance to dispersal across the GTF in 210 grid cells (~ 170,000 m^2 each). There was statistical certainty that 74 grid cells were associated with resistance to dispersal and 47 grid cells were associated with facilitating dispersal. Cells that resisted dispersal contained significantly more urban ground cover than cells that facilitated dispersal ($Z = 4.64$, $p < 0.0001$; Figure 10). Results from ANOVA of IBD residuals between adjacent clusters showed significant variance in IBD between different clusters ($F_{4,1122} = 10.31$; $p < 0.0001$). Tukey pairwise comparisons showed that the resistance to dispersal was lower between clusters B-C than any other adjacent cluster pair, and that resistance to dispersal between clusters E-F was higher than between clusters C-D and B-C (Figure 11; Supplementary Materials Table 4). Using ResDisMapper's method for statistical certainty of resistance (95% CI did not contain 0), I found resistance to dispersal between clusters A-F, D-E, and E-F and facilitation of dispersal between B-C (Figure 11).

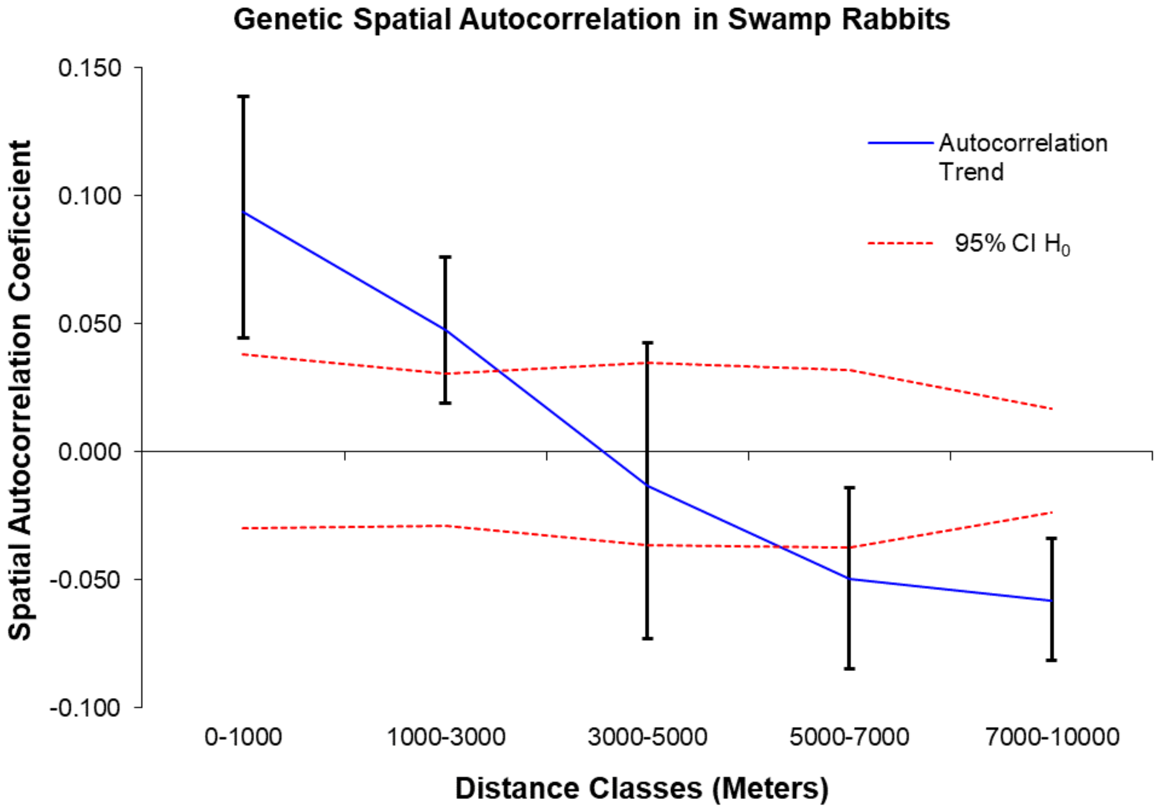

Figure 9. Results of genetic spatial autocorrelation analysis in swamp rabbits at five distance classes in the Great Trinity Forest, Dallas, TX, USA. Each distance class showed deviations from expected relatedness where positive values indicate that individuals in that distance class were more related than expected based on spatial proximity and negative values were less related. Red lines represent the 95% CI of the null hypothesis of no spatial structure. The spatial autocorrelation coefficient shows a generally linear trend in which an increase in distance between individuals creates more genetic distance than expected.

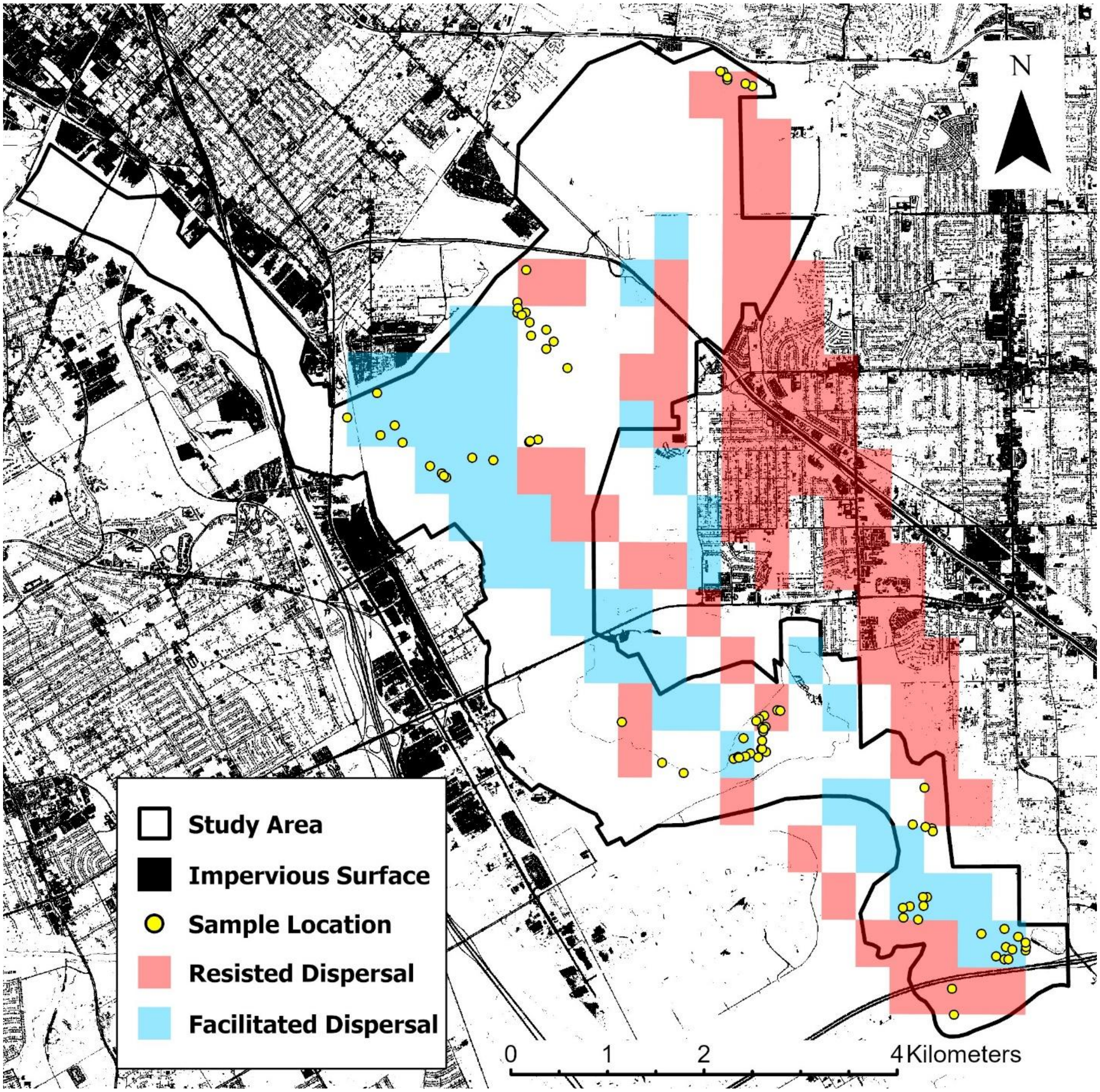

Figure 10. Locations in the landscape that resisted and facilitated swamp rabbit dispersal in the Great Trinity Forest, Dallas, TX, USA. Locations that inhibited dispersal were significantly more urban than locations that facilitated it.

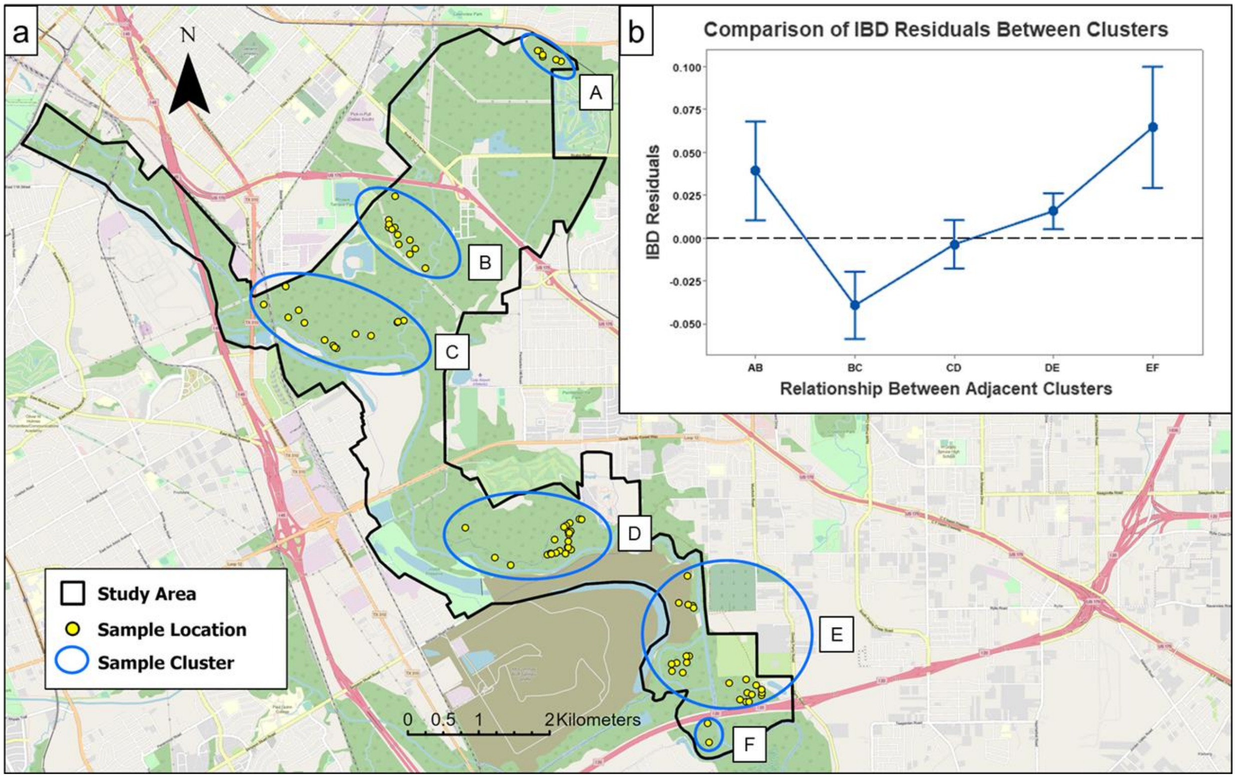

Figure 11. a) The locations of clusters of swamp rabbit sub-populations in the Great Trinity Forest, Dallas, TX in relation to major roads and highways. Clusters A-B and clusters E-F are each separated by major highways, clusters C-D are separated by a smaller highway, and clusters B-C and D-E are not separated by highways. b) Results of a one-way ANOVA (95% CI) comparing IBD residuals generated by ResDisMapper between adjacent clusters.

DISCUSSION

My study revealed significant genetic differentiation in an urban avoiding species within a single forest fragment, and that limitations to gene flow and dispersal were directly linked to urbanization, and to a lesser extent highways. Genetic spatial autocorrelation results and F_{ST} comparisons between clusters both indicated highly segmented sub-subpopulations of swamp rabbits within the Great Trinity Forest (GFT), and that increasing geographic distance between individuals or sub-populations created a disproportionate increase in genetic distance. This may be explained by the accumulation of urban barriers encountered as dispersal distances increased in the GTF. The genetic spatial autocorrelation trend crossed 0 at ~ 4,000 m, and individuals

<3,000 m apart were more related than expected and those >5,000 m apart were less related than expected. Most adjacent swamp rabbit clusters were ~ 4,000 m apart, meaning individuals <3,000 m apart were from the same cluster or from clusters B and C, the clusters closest in proximity and the only adjacent clusters to not be significantly genetically differentiated. Swamp rabbits >5,000 m apart were from more remote adjacent clusters or nonadjacent clusters. Swamp rabbits in forest fragments surrounded by a rural matrix in southern Illinois showed a greater capacity for dispersal within similarly sized habitat fragments, with genetic spatial autocorrelation showing no significant negative values across the same distance scale (0 – 10,000 m; Berkman et al., 2015). In addition, F_{ST} values from the Berkman et al. (2015) study (F_{ST} range 0.018 – 0.096) comparing genetically and geographically distinct clusters (distance range ~ 10,000 – 40,000 m; N: 22 - 51) did not approach the highest F_{ST} values for swamp rabbit clusters within the GTF.

IBD residuals between adjacent clusters, A-B and E-F, were the highest among all adjacent clusters and both resisted dispersal with statistical certainty, although there was mixed evidence for the significance of their increase in resistance compared to other adjacent clusters. These two pairs of adjacent clusters were both separated by major highways (A-B: US 175; E-F: I-20). The mean IBD residual relationship between B-C clusters was significantly smaller than any other relationship between clusters and facilitated dispersal, which is unsurprising given their relative proximity and the lack of significant anthropogenic barriers separating the clusters. Clusters C-D were separated by a highway (Loop 12) but showed no evidence for resistance to dispersal between them. This state highway was smaller in size and traffic volume than the other highways that bisected the forest. The evidence for roads as barriers to dispersal in lagomorphs is mixed (Estes-Zumpf et al., 2010; Fenderson et al., 2014; Amaral et al., 2016; Berkman et al., 2018). In general, roads that are wider and have higher traffic are more likely to become barriers to animal dispersal (Balkenhol & Waits, 2009), and my study lends evidence to the idea that only some roads or highways may represent barriers. All the highways in my study area contain underpasses to facilitate water flow, which also allows swamp rabbits to cross under the roads without risk of collision mortality. All highways are also highly illuminated because of their proximity to the urban core area and high traffic volumes. Artificial light has been shown to deter both large and small mammals from using designed wildlife passage structures on roads and highways (Bliss-Ketchum et al., 2016), which could also increase resistance to dispersal beyond what is expected from roads alone.

Although cluster F contained only two individuals and was therefore not included in F_{ST} calculations, I did include it in IBD residual comparisons between adjacent clusters. Despite being geographically close to cluster E, the relationship between clusters E-F shows the highest mean resistance to dispersal of any adjacent clusters. This could be because the highway separating these two clusters, I-20, is the largest highway in the study area in terms of traffic volume and physical size. Previous research using species distributions models indicated that the habitat within the study area south of I-20 was highly suitable for swamp rabbits (Stevens et al., in review). Nonetheless, no swamp rabbit latrine was found on the east side of the river south of I-20, and west of the river very few samples were collected despite significant effort to make more collections, suggesting only a few individuals have occupied this habitat patch. The lack of occupancy in suitable habitat south of I-20 may indicate the strength of this large highway as a barrier to dispersal in swamp rabbits.

Urban landcover was significantly greater in locations where dispersal was inhibited than in locations where dispersal was facilitated, implicating urbanization as a main contributor to the significant genetic differentiation I observed. This supports the hypothesis that urban habitat fragments are in fact habitat islands and subject to the principles of island biogeography (MacArthur & Wilson, 1967). Urban forest fragments may not appear to be islands of habitat to species that tolerate urbanization, but for species that cannot adapt to the drastic changes associated with urbanization, urban habitat fragments may become isolated islands with reduced genetic connectivity and ultimately, population viability. Previous research has shown mixed support for the application of island biogeography to terrestrial islands of habitat (Mendenhall et al., 2014; Matthews et al., 2015; Wolfe et al., 2015). Because urbanization modifies habitat more dramatically than other forms of anthropogenic land use change (Güneralp and Seto, 2013), it is plausible that an urbanized matrix creates habitat islands that conform to the theories of island biogeography. Although my study was the first to assess the impacts of urbanization on dispersal and gene flow in an urban avoiding species, a number of studies have demonstrated that an urban matrix creates an isolating island-like effect for species in habitat fragments, even when those species are not urban avoiders (Delaney et al., 2010; Munshi-South & Kharchenko, 2010; Unfried et al., 2013; Olejniczak et al., 2018). In contrast, other studies have found that urban habitat islands impact species differently based on their dispersal ability (Richardson et al., 2020), and that species with greater dispersal ability (e.g., flight) were not genetically isolated by an urban matrix. Future research exploring why urban avoiding species with high dispersal ability are absent from urban forest fragments could reveal novel insights as to whether direct or indirect impacts of the urban matrix drive their absence.

My study indicates that urban avoiding species can persist in urban forest fragments, but the size and connectivity of those fragments is vital to their conservation value. My study was the first to characterize the impacts of urbanization on the genetic structure of an urban avoiding mammal in an urban habitat fragment, providing new and important information that may facilitate conservation in and near urban areas as urbanization spreads, a critical challenge in combatting the worldwide extinction crisis (Foley et al., 2005).

SUPPLEMENTARY MATERIALS

Catalogue numbers, Angelo State Natural History Collections: *Sylvilagus aquaticus* (ASNHC 10649; ASNHC 11042; ASNHC 11043; ASNHC 15752). Catalogue numbers, Museum of Texas Tech University: *Sylvilagus aquaticus* (TK 51624; TK 52062; TK 52063; TK 52065; TK 84514; TK 90675; TK 92526), *Sylvilagus floridanus* (TK 18127; TK 22443; TK 49666; TK 49711; TK 51658; TK 90291; TK 90292; TK 28849)

I selected 35 microsatellite loci for development in my study from multiple species including duel use markers developed for *Sylvilagus aquaticus* and *Sylvilagus floridanus* (Berkman et al., 2009; *Sfl006*, *Sfl008*, *Sfl011*, *Sfl013*, *Sfl014*, *Sfl015*), markers for *Oryctolagus cuniculus* (Sturridge et al., 1997; *sol33*, *sol44*, *sol51*, *sol62*, *sol72*), *Oryctolagus cuniculus* (Mougel et al., 1997; *Sat7*, *Sat8*, *Sat12*, *Sat16*), *Sylvilagus transitionalis* (King et al., 2017; *StrQ2*, *StrQ8*, *StrQ10*, *StrQ15*, *StrQ18*, *StrQ24*, *StrQ25*, *StrQ26*, *StrQ30*, *StrQ32*, *StrQ41*; *StrQ43*, *StrQ46*, *StrQ49*) and *Brachylagus idahoensis* (Estes-Zumpf et al., 2008; *A10*, *A121*, *A124*, *A133*, *D118*, *D121*).

I used the following PCR profile for multiplexes (fecal samples): 95 ºC for 15 min, then 40 cycles of 94 ºC for 30 s, 55 ºC or 60 ºC for 1:30 min, 72 ºC for 1 min, and then a final extension at 60 ºC for 30 min, and for single loci (fecal samples): 94 ºC for 10 min, then 40 cycles of 94 ºC for 30 s, 55 ºC or 60 ºC for 30 s, 72 ºC for 1 min, and then a final extension at 72 ºC for 5 min. Amplification of tissue samples used the same PCR profile as fecal samples but with 30 cycles.

Table 2. Characteristics microsatellite loci used for swamp rabbits.

Locus	Primer Sequences	Size Range in *S. aquaticus* (bp)	Annealing Temperature °C	Dye Label	Multiplex
StrQ15	F: GATGGTGGATAAGATAGAGGACA R: TATGGCTGGACCACACTCTG	164-188	60	TAMRA	A
StrQ32	F: TGTAACTCTGCCTTCCAAATAAATAA R: GGCTGTTTAACTTGCCATGC	160-214	60	HEX	A
StrQ43	F: GTATCTGCCGAATGAAGTGGA R: TAGGTACAGATAATTCACTTTGGACA	221-237	60	6-FAM	A
StrQ46	F: AAATGAGGAATATTTGTTGAATGC R: AGAATGAACCAGCAAATGGG	106-122	60	TAMRA	A
A10	F: TCCCACTAGAAACTTTCAAAAC R: CACGTTAGCACAGAGTTGTATC	227-246	55	HEX	B
Sfl011	F:CAGTCGGGCGTCATCAGCACAGCAGCATATTCCATGC R: GTTTCCATGAATCAATACAGGTTAATGCC	209-213	55	6-FAM	B
Sfl015	F: GTTTGCTTCTGGTTTCCATCCG R: CAGTCGGGCGTCATCATTCTACCCACTCATTGTTTGC	206-224	55	TAMRA	B

Table 3. Genetic diversity estimates for swamp rabbits at microsatellite loci using all unique genotypes from the closure period, and measures of error at microsatellite loci using genotypes that received consensus scores for at least five loci.

	Genetic Diversity					Error Rates		
Locus	N[a]	N_a[b]	H_O[c]	H_E[d]	F_{IS}[e]	SR[f]	AD[g]	FA[h]
A10	39	6	0.769	0.670	-0.162	0.825	0.248	0.003
Sfl015	39	5	0.641	0.657	0.012	0.863	0.245	0.003
Sfl011	41	3	0.610	0.496	-0.245	0.755	0.163	0.005
StrQ15	40	7	0.750	0.806	0.057	0.873	0.241	0.011
StrQ32	42	8	0.714	0.746	0.032	0.865	0.267	0.020
StrQ43	41	8	0.537	0.644	0.156	0.903	0.231	0.001
StrQ46	42	5	0.738	0.743	-0.005	0.910	0.236	0.014
Mean	40.6	6	0.680	0.680	-0.022	0.856	0.233	0.008

a Number of individuals genotyped

b Number of alleles

c Observed heterozygosity

d Unbiased expected heterozygosity

e Inbreeding coefficient

f PCR success rate

g Proportion of allelic dropout

h Proportion of false alleles

Table 4. Results of the Tukey pairwise comparison of means for IBD residuals between adjacent clusters.

Difference of Levels	**Difference of Means**	**SE of Difference**	**95% CI**	**T-Value**	**Adjusted P-Value**
BC - AB	-0.0784	0.0178	(-0.1269, -0.0298)	-4.41	0.000
CD - AB	-0.0428	0.0164	(-0.0875, 0.0020)	-2.61	0.068
DE - AB	-0.0234	0.0156	(-0.0661, 0.0193)	-1.50	0.564
EF - AB	0.0254	0.0233	(-0.0380, 0.0889)	1.09	0.810
CD - BC	0.0356	0.0123	(0.0020, 0.0693)	2.89	0.032
DE - BC	0.0550	0.0113	(0.0241, 0.0859)	4.86	0.000
EF - BC	0.1038	0.0206	(0.0476, 0.1601)	5.04	0.000
DE - CD	0.01935	0.00896	(-0.00511, 0.04382)	2.16	0.195
EF - CD	0.0682	0.0194	(0.0152, 0.1212)	3.51	0.004
EF - DE	0.0489	0.0188	(-0.0024, 0.1001)	2.60	0.070

Chapter 4: Urbanization and Invasive Species Impact Forest Bird Occupancy in a Large Urban Forest

INTRODUCTION

The impacts of urbanization are better studied in birds than other animals, with over 1,000 articles published on the subject between 2006 and 2015 (Marzluff 2016). This large body of literature has examined which factors impact the avian conservation value of urban forest fragments by looking at patterns of occurrence using either total richness or diversity of birds, presence of bird species of conservation concern, or the presence of urban-avoiding bird species. Many studies focused on the direct impacts of urbanization on the matrix of forest fragments, including the size of forest fragments, the intensity of urbanization in the matrix, and structural characteristics of forest fragments. The majority of studies found that as the size of forest fragments increased, the value for avian conservation increased (Rottenborn 1999; Mortberg and Wallentinus 2000; Mortberg 2001; Donnelly and Marzluff 2004; Morimoto et al. 2006; Rodewald and Bakermans 2006; Mason et al. 2007; Callaghan et al. 2018; Shoffner et al. 2018), although not all of these studies found size to be the most important or only factor driving patterns of occurrence. Studies also found that increasing the intensity or amount of urbanization in the surrounding matrix decreased the avian conservation value of forest fragments (Rottenborn 1999; Miller et al. 2003; Donnelly and Marzluff 2004; Dunford and Freemark 2004; Morimoto et al. 2006; De Wan et al. 2009; Kennedy et al. 2010; Kennedy et al. 2011; Pennington and Blair 2011; Shoffner et al. 2018), with Rodewald and Bakermans (2006) finding that the composition of the matrix was more important than fragment size.

In addition to the direct impacts of urbanization on forest fragments, indirect impacts like light pollution, noise pollution, and invasive species have also been investigated. Light pollution can impact the physiology (Ouyang et al. 2017) and reproductive timing and behavior (Kempenaers et al. 2010) of birds in urban areas. Anthropogenic noise produced by urban environments (Francis et al. 2009; Perillo et al. 2017) and roads (Goodwin and Shriver 2011; McClure et al. 2013) have been shown to decrease the avian conservation value of forests. Multiple studies have also found that levels of anthropogenic noise surpass fragment size in their ability to explain patterns of avian occurrence (Gonzalez-Oreja 2017; Kleist et al. 2017). For instance, anthropogenic noise filters bird communities based on vocal frequency, where birds with lower vocal frequencies are less likely to tolerate environments with large amounts of anthropogenic noise (Hu and Cardoso 2009; Francis et al. 2011; Halfwerk et al. 2011; Proppe et al. 2013; Cardoso et al. 2018). Invasive species associated with the urban matrix can cause local extinction of bird communities in urban habitat fragments (Crooks and Soule 1999) and create ecological traps for breeding birds (Nordby et al. 2009; Rodewald et al. 2010).

I now know that urbanization drives worldwide loss of evolutionary history in bird communities (Sol et al. 2014; Sol et al. 2017), not only when habitat is converted to urban lands, but also when the surrounding matrix is urbanized (Rodewald and Bakermans 2006; Kennedy et al. 2010; Kennedy et al. 2011). Urban growth is spreading at the fastest rate in history and is predicted to accelerate (Set et al. 2012). It is critical to understand how I can conserve urban-avoiding birds in habitat patches near and within urban areas as urbanization expands, especially because predicted areas of future urban expansion are concentrated in areas of high endemism (McDonald et al. 2018). The key to combating this extinction crisis is understanding the habitat requirements of species in urban areas and incorporating them into conservation efforts (Foley et al. 2005). The ability to conserve urban-avoiding wildlife in urban forest fragments as urbanization expands not only helps combat the worldwide extinction crisis, but also provides social and educational benefits to human populations in urban areas with few opportunities to experience intact wildlife communities (Miller and Hobbs 2002; Dearborn and Kark 2010).

I used single visit occupancy models to examine the impacts of urbanization in the matrix on a diverse breeding bird community in a large urban forest fragment. Although previous research has examined impacts of an urban matrix on wildlife in isolation, e.g., urbanization intensity (Rodewald and Bakermans 2006; De Wan et al. 2009; Shoffner et al. 2018), anthropogenic noise (Gonzalez-Oreja 2017; Kleist et al. 2017), or invasive species (Schneider and Miller 2014), few studies have attempted to assess multiple impacts from the urban matrix simultaneously in order to determine which factors require the most urgent conservation measures. Additionally, previous research examining the impacts of an urban matrix on wildlife in habitat fragments was often limited by which species still persisted in these habitats, with many urban avoiding species being absent. This study is one of the few that will be able to examine the impacts of an urbanizing matrix on a large diverse bird community containing a full complement of urban avoiding species, likely in large part due to the large size of the urban forest fragment serving as the study location. I predicted that multiple anthropogenic impacts from urbanization in the matrix would negatively impact avian occupancy in the GTF, and that these negative impacts would be more common in urban avoiding species than species that can adapt to urban habitats.

METHODS

Site Description

The Great Trinity Forest (GTF) is a large (>4,000 ha) urban forest fragment located within the fourth largest metropolitan area in the United States, Dallas-Fort Worth (U.S. Census

Bureau 2020; Figure 12). It is a bottomland hardwood forest centered on an unlevied portion of the Trinity River, giving it an intact flooding regime, and making it unsuitable for further development. Bottomland hardwood forests are diverse habitats because of the natural patterns of ecological succession driven by disturbance from regular flooding events (Hodges 1997). Habitat diversity in the GTF is amplified by anthropogenic disturbance, creating habitats varying in age from early successional grassland/savanna to mature hardwood forest. In the GTF, patterns of natural and anthropogenic disturbance create two broad categories of habitat types that I summarize as levee/upland forest and floodplain forest (Figure 13). Levee forests occur near the river where frequent disturbance from sediment deposited in flooding events creates a slightly higher elevation embankment where inundation does not occur. Two early successional trees, eastern cottonwood (*Populus deltoides*) and black willow (*Salix nigra*), thrive in these high disturbance areas along with trees adapted to more upland habitats, specifically masting species like burr oak (*Quercus macrocarpa*), pecan (*Carya illinoinensis*), and mulberry (*Morus rubra*). Upland habitats are other areas of the GTF that are above the line of regular inundation. These areas contain the most significant and recent anthropogenic disturbance - two large reclaimed illegal dumping sites, and have tree communities like the levee forest where early successional species dominate the areas of more recent anthropogenic disturbance and masting trees remain scattered throughout. Levee/upland forest types are the most diverse forests in the GTF in which a variety of early/mid successional and masting species occur in addition to the five tree species already mentioned. Dense stands of the invasive Chinese privet (*Ligustrum sinense*) dominate the understory in some levee/upland forest. Floodplain forests occur behind the levee forest and are frequently inundated. Here anthropogenic disturbance is less common and vegetation communities approach their succession climax. In floodplain forests, changes in elevation of only a few inches can change the frequency of inundation and vegetation communities. Three tree species dominate the overstory in the GTF floodplain: cedar elm (*Ulmus crassifolia*), hackberry (*Celtis laevigata*), and green ash (*Fraxinus pennsylvanica*), with cedar elm being the dominant species in relatively drier areas and green ash dominating the wettest. The most common understory plant in floodplain forest is eastern swamp privet (*Forestiera acuminate*), especially in wetter areas where it associates with a green ash overstory. Osage orange (*Maclura pomifera*) is a common midstory tree associated with old growth floodplain forest.

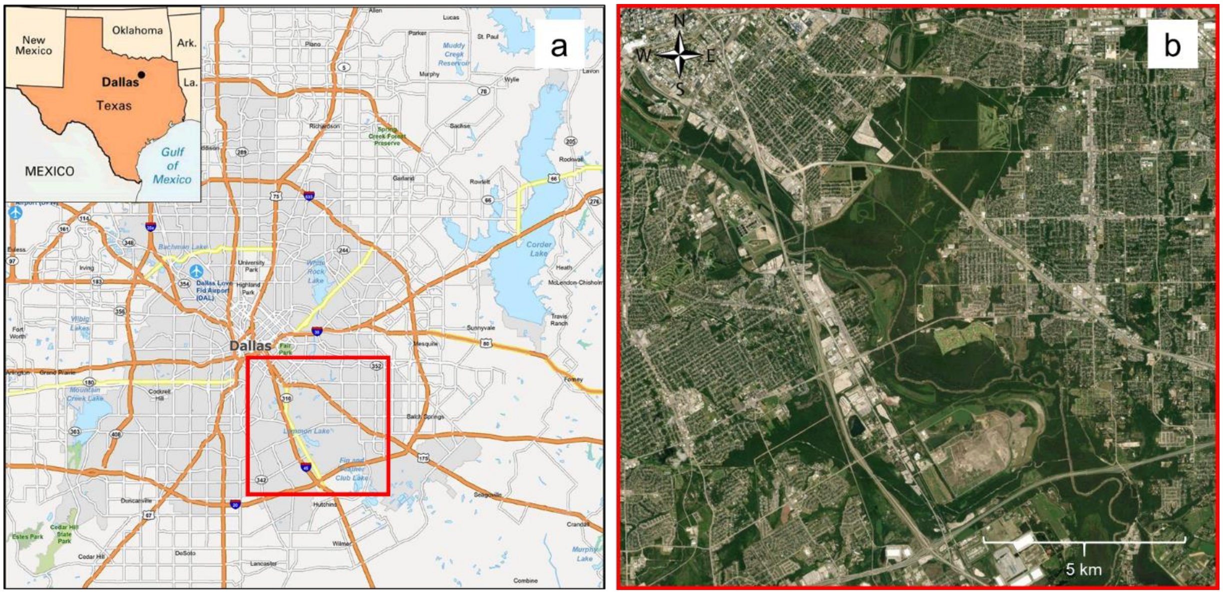

Figure 12. a) The location of the Great Trinity Forest within the city of Dallas, TX, USA (32.733043, -96.733511). b) Aerial image of the cutout from a) showing the Great Trinity Forest.

The GTF is surrounded by a complex urban matrix and is contained completely within the city of Dallas (Figure 14). The most intense urbanization of the matrix occurs in the northwest portion of the forest near city center, where commercial and industrial developments are intermixed with dense residential neighborhoods. Urbanization becomes less intense to the southeast, where residential neighborhoods eventually intermix with agricultural land. Here the forest is also bordered by multiple golf courses and a large municipal landfill. The GTF contains multiple roads and highways, including being completely bisected by an interstate highway (I-20; 8 lanes; 2018 to 2020 mean traffic volume ~ 120,000 vehicles/day), a U.S. Highway (US

175; 6 lanes; 2018 to 2020 mean traffic volume ~ 60,000 vehicles/day), and a state highway (Loop 12; 4 lanes; 2018 to 2020 mean traffic volume ~ 28,000 vehicles/day; Texas Department of Transportation AADT Annuals). In addition, high-speed commuter trains intersect the forest in multiple locations. Parts of the forest are also within a major flight path for commercial aircraft travelling between the Dallas Love Field Airport and Houston. The entire forest is public land managed by a variety of municipal departments and was available for my research.

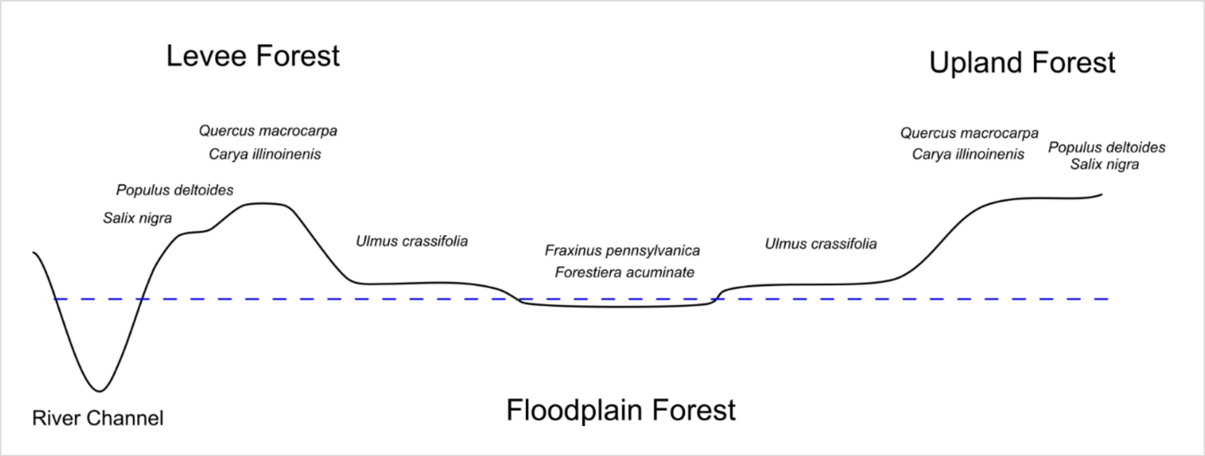

Figure 13. Cross section of habitat types and dominant tree species in the Great Trinity Forest, Dallas, TX. Areas of upland forest are the most likely to contain significant anthropogenic disturbance and early succession grassland or savanna habitat and are often the interface between the GTF and the urban matrix.

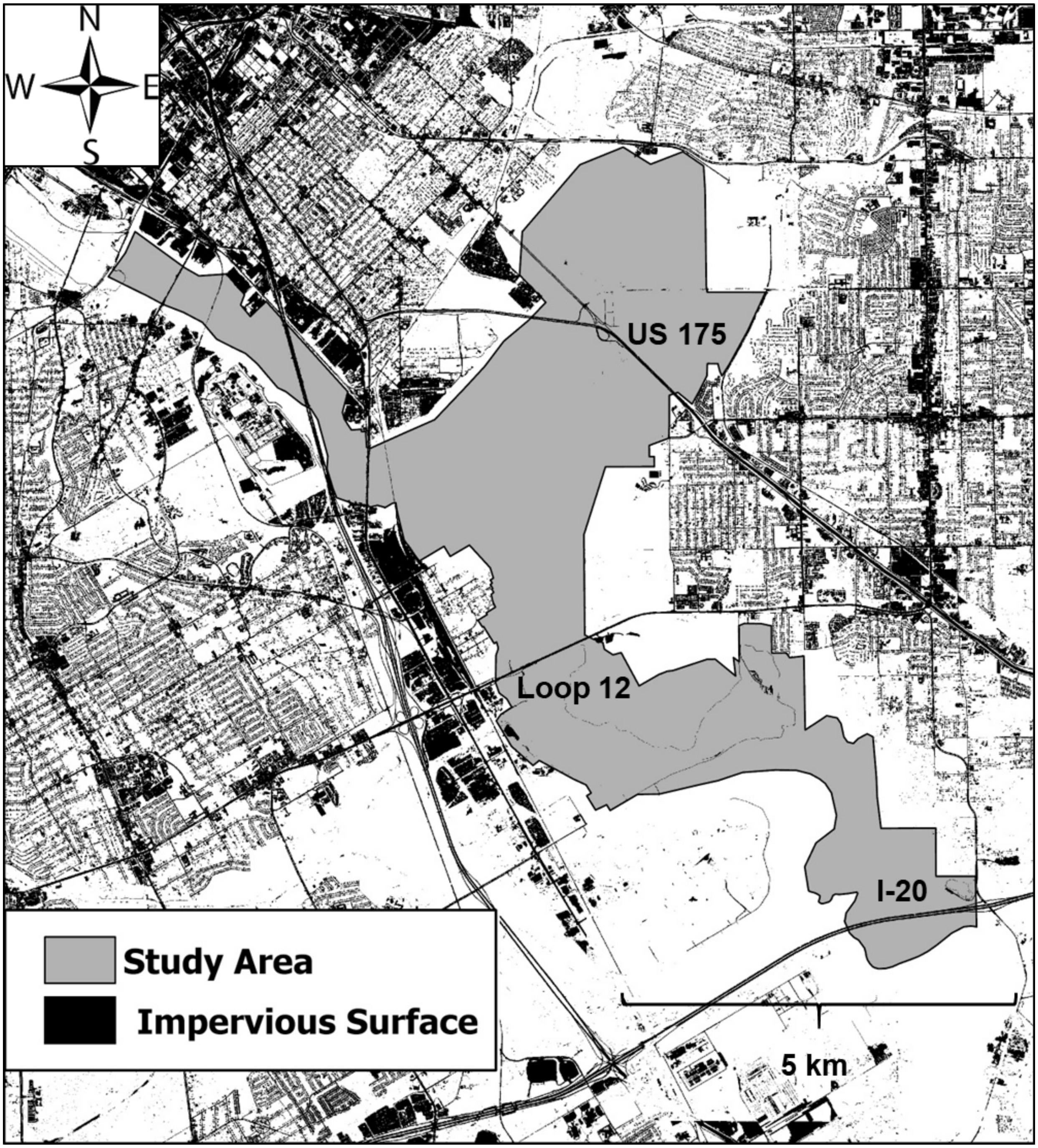

Figure 14. Impervious surface representing urbanization intensity in the matrix surrounding the Great Trinity Forest, Dallas, TX. Three major highways that bisect the forest are labelled.

Occupancy Modelling Approach

Occupancy models are designed to estimate species occurrence while accounting for false absences, the most widespread type of error that leads to imperfect detection (Guillera-Arroita 2017). Traditional occupancy models account for false absences by surveying a single location multiple times, creating a record of species presence and absence. The ratio of presence to absence is then used to model the species detectability when there is at least one survey resulting in presence (MacKinzie et al. 2002; Tyre et al. 2003). Occupancy models are hierarchical models that contain an occupancy sub-model and a detection sub-model linked together with the logit-link function that can linearly model the impacts of predictors on both occupancy and detectability. Occupancy models have been widely used in ornithology (Hayes and Monfils 2015), as field studies of birds experience imperfect detection, especially when aural detections are used in forested habitats (Alldredge et al. 2007). Despite the popularity of occupancy modelling, many ornithological studies are violating key assumptions of traditional occupancy methods (Simons et al. 2007; Rota et al. 2009). The violation of the closure assumption, the assumption that a site is closed to movements of individuals in and out of the site between repeated surveys, is the most commonly cited and debated (e.g., Hutto 2016). For example, when survey plots do not represent discrete habitat patches (i.e., ponds for aquatic wildlife), but instead are arbitrarily placed in continuous habitat, violations of the closure assumption are possible, especially for mobile animals like birds (Efford and Dawson 2012). During a typical sampling season for breeding birds (May-July), violations of the closure assumption are common as birds often move territories or adjust habitat use in response to changes in resource availability within a single season (Rota et al. 2009; McClure and Hill 2012), and even small amounts of movement can lead to bias in occupancy estimations (Efford and Dawson 2012).

Although traditional occupancy requires multiple surveys to model detectability, there are extensions of the occupancy concept that require only a single visit to a site, addressing the violation of the closure assumption (Marques et al. 2017). Garrard et al. (2008) developed a time-to-detection occupancy model in which each plot is visited once and the time at which a species is first detected is used to model its detectability. This model was adapted from exponential time-to-failure models while allowing for ‘failure’ or true absence. Time-to-detection models are as accurate as traditional occupancy models for estimating occurrence while correcting for false absences (Bornand et al. 2014). In addition to addressing the violation of the closure assumption, single visit methods also reduce costs and allow more unique plots to be surveyed in a limited amount of time. Subsequently, the use of time-to-detection occupancy models has garnered significant interest in recent years (Medina-Romero et al. 2019; Whittington et al. 2019; Henry et al. 2020; Halstead et al. 2021; Strebel et al. 2021). I used single season, single species time-to-detection occupancy models to assess the impact of anthropogenic variables on breeding bird occupancy in the GTF while accounting for environmental covariates and variation in detectability.

Bird Surveys

I adapted survey methods designed for time-to-detection occupancy studies in plants by Garrard et al. (2008) to survey the GTF’s breeding bird community. I searched 5-ha plots for 30 minutes, during which I moved freely throughout the plot recording the first time of detection for each species encountered, using both aural and visual detection. I selected a plot size of 5-ha based on territory sizes for species in the GTF breeding bird community (most species <5-ha; Billerman et al. 2020), as biased estimates of occupancy occur when the size of the survey plot is significantly smaller than the territory size of the target species (Efford and Dawson 2012; Hayes and Monfils 2015). I selected a survey length of 30 minutes after preliminary surveys were used to investigate the time needed to move through a 5-ha plot in the GTF and the average times of first detection for different species in the breeding bird community. I used ArcGIS Pro (version 2.2.0) and ArcGIS Explorer to map the plots on aerial images for navigation during searches. I searched plots between May 15 and July 15 in 2018, 2019, and 2020. These dates encompassed the majority of the breeding season while avoiding detecting migrants earlier in the spring and avoiding territory abandonment later in the summer (Benson and Arnold 2001). I searched plots between 30 minutes after dawn and 11:00 am, allowing us to search ~ 6 plots per day. In each of my three field seasons I randomly populated my study area with a unique group of 5-ha plots, where plots were at least 100 m apart in each field season.

Before further analysis, I assigned all species observed during searches a category of urban tolerance using traditional terminology: avoider, adapter, and exploiter (Blair 1996; McKinney 2002) and a review of relevant literature (Sol et al. 2014; Archer et al. 2019; Billerman et al. 2020). Urban exploiters were species that reach their highest levels of density in urban habitats. Urban avoiders were species that are common in natural habitats and can adapt to urban habitats. Urban avoiders were species that do not tolerate urban habitats or occur in urban habitats at far lower densities than natural habitats, and usually in fragments of natural habitats within urban areas.

Anthropogenic Variables

I assessed the impact of six anthropogenic variables associated with the urban matrix on the GTF breeding bird community: urbanization intensity in the surrounding matrix (direct impact), light pollution (indirect impact), continuous anthropogenic noise (indirect impact), intermittent anthropogenic noise (indirect impact), feral hog activity (indirect impact), and

Chinese privet abundance (indirect impact). These variables were previously linked with, or hypothesized, to alter avian distributions. Before models were built, all anthropogenic variables were tested for correlation (r > 0.6).

The amount of impervious surface in a landscape is often used as a surrogate for intensity of urbanization (e.g., Donnelly and Marzluff 2004; Rodewald et al. 2013; Evans et al. 2015). Previous studies have found that Neotropical migrants (Rodewald and Bakermans 2006), forest interior species (De Wan et al. 2009), and specialized species (Kennedy et al. 2011) all declined as urbanization increased in the surrounding matrix. I quantified the amount of impervious surface in and around the GTF using ArcGIS Pro's image classification wizard and a 2016 50-cm resolution, multi-band remote sensing image of the forest and surrounding Dallas County from the Texas Natural Resource Information System (tnris.org). I used supervised, object-based classification, to reclassify the study area into four land cover categories: impervious surface, forest, open water, and grass/cultivated land. I defined impervious surfaces as any human-made material that is impenetrable to water (e.g., roofs, concrete, building materials, etc.). Urbanization intensity in the nearby matrix was quantified as the amount of impervious surface within 1,000 m buffers from each searched plot.

Investigations of light pollution on wildlife have shown impacts on gene expression, physiology, foraging, daily movements, migratory behavior, reproductive behavior, and mortality (reviewed in Gaston et al. 2015). I mapped light pollution in the GTF using 2020 data from Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) in ArcGIS Pro.

Continuous anthropogenic noise is produced by multiple highways and roads that surround and intersect GTF. Some of the largest highways bisect the GTF, introducing noise into core areas of the forest far away from other components of the urban matrix. Anthropogenic noise produced by roads has been shown to decrease the avian conservation value of forests (Goodwin and Shriver 2011; McClure et al. 2013), especially for species with lower vocal frequencies that may be unable to communicate because their calls are masked by anthropogenic noise (Hu and Cardoso 2009; Francis et al. 2011; Halfwerk et al. 2011; Proppe et al. 2013; Cardoso et al. 2018). Intermittent noise may impact birds in different ways than continuous noise (i.e., not masking communication but creating disturbance through fear or flight response), but studies of the impacts of intermittent noise on wildlife are rare (Francis and Barber 2013). The GTF experiences significant intermittent anthropogenic noise from both commercial airplanes and commuter trains. In order to assess the impact of anthropogenic noise on breeding birds, I used data from the 2018 National Transportation Noise Map (U.S. Department of Transportation 2020). This dataset quantified both continuous noise from highways and intermittent noise from airplane and high-speed rail traffic. This data set measures a 24-hour weighted potential noise exposure across yearly average environmental conditions, making it appropriate for estimating chronic noise exposure for birds in the GTF. I quantified noise exposure in search plots as either "at risk for significant noise exposure" or "not at risk", with plots that met or exceeded average daily noise levels of 45 dBA considered at risk for significant noise exposure for either continuous or intermittent noise (Ortega and Francis 2012).

As the matrix around a habitat fragment urbanizes, invasive species become more abundant in those fragments (Johnson et al. 2020). Feral hogs (*Sus scrofa*) are a destructive invasive species that have spread across the southern United States (Campbell and Long 2009). Humans have facilitated the expansion of feral hogs in the United States (Hernández et al. 2018), and feral hogs are now common in urban parks and semi-urban areas in some parts of the world because of anthropogenic food sources (Cahill et al. 2012). Rooting and behavior by feral hogs reduces plant diversity and richness as well as total vegetation cover in wetlands (Arrington et al. 1999) and forested habitat (Siemann et al. 2009), and disturbance by feral hogs can facilitate the spread of invasive plants (Cushman et al. 2004). Feral hogs are abundant in the GTF, and signs of their damaging rooting behavior are widespread. I assessed the relative activity of feral hogs in each searched plot as absent, low, moderate, or high based on observations of tracks, feces, and disturbance from rooting.

Chinese privet (*Ligustrum sinense*) is a rapidly spreading invasive shrub in the southeastern United States and Texas (Arevilca et al. 2016) and has become dominant in the understory of some areas of the GTF. There is evidence for avian decline associated with invasive plants, but many studies report no impact from invasion (Nelson et al. 2017). I assessed the relative abundance of Chinese privet in each plot as absent, low, moderate, or high.

Environmental Covariates

To account for naturally occurring environmental variables that could influence avian occupancy, I created four spatially explicit environmental covariates with strong associations to changes in bird distributions: vegetation structure, vegetation composition, wetness, and forest width. Before models were built, all anthropogenic variables were tested for correlation ($r > 0.6$).

Heterogeneity in vegetation structure is an important factor influencing the distribution of songbirds found in bottomland hardwood forests (Bowen et al. 2007). Light detection and ranging (LIDAR) is a source of remote sensing that produces high resolution geospatial and three-dimensional information well-suited for examining forest structure (Vierling et al. 2008). Measures of forest heterogeneity derived from LIDAR are highly predictive of avian distributions (Goetze et al. 2007; Seavy et al. 2009; Goetze et al. 2010; Muller et al. 2010; Huber et al. 2016). I used LIDAR point cloud data imported into ArcGIS Pro (version 2.2.0) to develop three variables that described forest structure in search plots: foliage height diversity, canopy cover, and maximum vegetation height. These three variables were the most often predictive of avian distributions among the many LIDAR metrics (Bakx et al. 2019). I acquired LIDAR data flow over the GTF in 2017 during leaf off conditions by the North Central Texas Council of Governments in a fixed wing aircraft. The specifications of the LIDAR data are as follows: Leica Specs-AGL LIDAR System, 0.5-meter nominal point spacing, 150 knot aircraft speed, 50-degree field of view, 230.5 kHz pulse rate, 47 Hz scan rate, and 30% average overlap. I processed LIDAR data in ArcGIS Pro using the full point cloud data. I developed a digital terrain model (DTM) to normalize all non-ground returns and LIDAR forest structure metrics. I calculated maximum vegetation height as the average height of first returns in each plot. I calculated canopy cover as the number of returns above 4 m divided by the total number of returns in each plot. I calculated foliage height diversity using the Shannon Wiener Diversity Index comparing the number of returns in five height classes in each plot: 0 to 2 m, 2 to 4 m, 4 to 8 m, 8 to 12 m, and >12 m.

Vegetation species composition can be more important than vegetation structure when explaining avian distributions (Adams and Matthews 2019). I created a habitat map for the GTF, in which habitat types were based on canopy tree species composition. In order to identify canopy trees, I made extensive drone flights in the fall of 2021 to obtain aerial images of the forest. I manually piloted drone flights and obtained images at the density required to effectively identify enough trees from images of their crowns to create continuous habitat maps across the entire study area. I imported images of the canopy into ArcGIS Pro for tree identification and the creation of the habitat map (Figure 15). I extensively verified tree identification on the ground as part of an initial training period to ensure that I could correctly identify trees from aerial images, and to determine the appropriate flight altitude at which drone images should be obtained. I continued to use on-the-ground verification where uncertainty existed about identification during the mapping process and for post-identification spot checks.

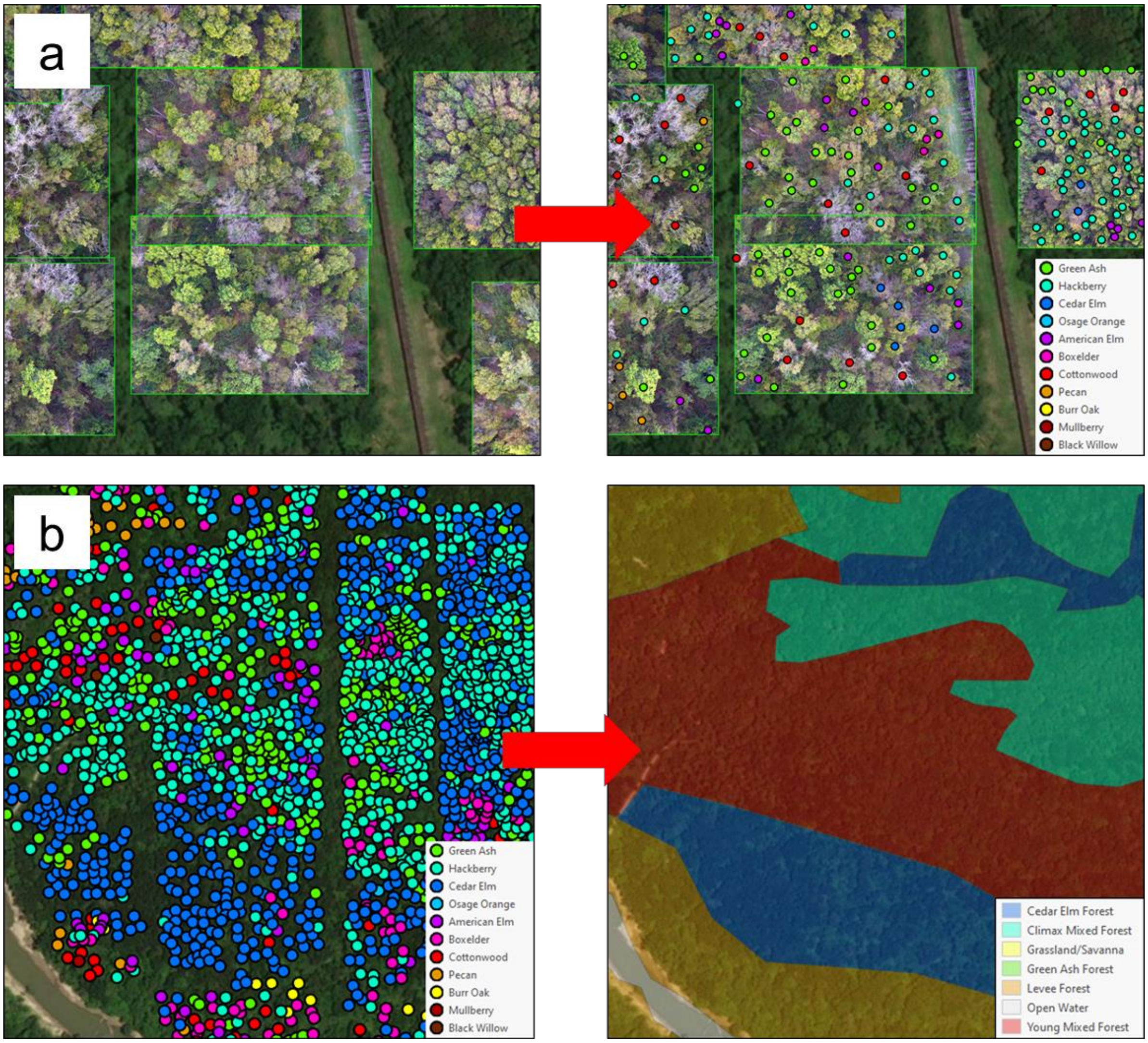

Figure 15. a) Tree identification based on drone imagery of tree crowns in ArcGIS Pro in the Great Trinity Forest, Dallas, TX. b) Identifying habitat types based on canopy tree composition.

I developed the following six habitat types based on canopy tree composition: climax mixed forest, cedar elm forest, green ash forest, early successional forest, levee forest, and early successional grassland. I defined my six habitat types by canopy tree composition as follows: 1) climax mixed forest: >90% cedar elm, green ash, and hackberry with none of those individually accounting for >50% of trees; >5% Osage orange; 2) cedar elm forest: >75% cedar elm with Osage orange and hackberry as common minority species; <5% early successional species: American elm (*Ulmus americana*), boxelder (*Acer negundo*), eastern cottonwood, and black willow; 3) green ash forest: >75% green ash with hackberry and black willow as common minority types; <10% early successional species: American elm, Boxelder, eastern cottonwood, and black willow; 4) early successional forest: >35% early successional species: American elm, Boxelder, eastern cottonwood, and black willow; 5) levee forest: 10% to 20% masting trees: pecan (*Carya illinoinensis*), burr oak (*Quercus macrocarpa*), shumard oak (*Quercus shumardii*), and mulberry (*Morus rubra*) which account for the majority of canopy cover because of their large size; and 6) early successional grassland: <50% canopy cover of trees. In order to simplify model selection and improve model performance, these six habitat types were consolidated into two habitat types: 1) diverse disturbed habitat generally associated with levee/upland forest type detailed in the site description (early successional grassland, levee forest, and young mixed forest), and 2) less diverse climax forest habitat associated with the floodplain forest type detailed in the site description (cedar elm forest, climax mixed forest, and green ash forest). These two habitat types were combined into a single variable accounting for the proportion of disturbed to climax habitat type present in each plot.

In wetlands, flood regime is a driving factor of the distribution of species (Leyer 2005). Although measurements of wetness are rarely used to explain wildlife distributions, Besnard et al. (2013) showed that topographic wetness index (TWI) successfully predicted the occurrence of bird species in a European wetland. TWI was developed to approximate flooding susceptibility and water accumulation capacity (Beven and Kirkby 1979). I use a digital elevation model of the GTF and a combination of four TWI indices used by Besnard et al. (2013) to model wetness in my study area using the SAGA GIS "Terrain Analysis Hydrology" tools (Böhner and Selige 2006). I calculated the mean TWI in each plot.

The dominant paradigm for riparian forest conservation is that forest width is the best available indicator of ecological function (Spackman and Hughes 1995; Shirley and Smith 2005; Maure et al. 2018). Therefore, species that are area-sensitive may not occupy areas of riparian forest where width is below a specific threshold. The GTF varies in width greatly within the study area, ranging from 4,000 m at its widest point to 450 m at its narrowest. I measured forest width in ArcGIS Pro as the perpendicular distance across the forest at each searched plot.

I also included year as a possible variable in the occupancy sub-model, as rainfall and flooding intensity varied among my three field seasons.

Detection Covariates

To control for the impact of imperfect detection on bird observations and isolate the impacts of anthropogenic variables on my metric of interest, occupancy, I created four variables that I believed could influence detectability of GTF breeding birds: ambient noise, vegetation structure, time of day, and day of the season. Before models were built, all anthropogenic variables were tested for correlation, and correlated variables were not included in the model selection process ($r > 0.6$). Background noise reduces detectability of birds when using aural detection methods (Simons et al. 2007). I used a sound level meter (Extech 407730) to measure levels of ambient noise during searches. Variation in ambient noise between plots was driven by both anthropogenic sources such as highways, and natural sources such as Cicadas (*Tibicen* spp.) I took three measurements of the minimum and maximum sound levels for 30 sec at 3 different times/locations during each search. I then averaged the 3 minimum sound measurements to acquire a single estimate of sound exposure for each search plot. I chose to use minimum noise exposure as maximum levels were more reflective of loud sounds that were short in duration and may not have impacted my ability to hear birds. I used the LIDAR derived canopy cover, which is also an environmental covariate, to model changes in detectability associated with variation in vegetation structure. Plots with denser and taller vegetation impede observer sight and reduce sound transmission (Pacifici et al. 2008). Finally, I used time of day and day of the season to model detectability. Multiple studies have shown that birds vocalize less frequently later in the day and later in the breeding season (Thompson et al. 2017; Morelli et al. 2022).

Model Selection and Data Analysis

I used single season, single species time-to-detection occupancy models to assess the impact of anthropogenic variables on breeding bird occupancy in the GTF while accounting for environmental covariates and variation in detectability. All analyses were performed in R (R Core Team 2020) using the package unmarked (Fiske and Chandler 2011). For all species with at least 40 detections across all three field seasons, I created a single season time-to-detection occupancy model using a combination of secondary candidate and build-up model selection strategies (Morin et al. 2020). The goal of this method was to maximize model fit using Akaike information criterion (AIC) in both the detection sub-model and among environmental covariates in the occupancy sub-model to improve inferences about the impact of anthropogenic variables on occupancy. Correlated covariates were not included in the model selection process. First, I determined the model of best fit using all combinations of detection variables while holding occupancy constant. The model with the lowest AIC, and any models <5 AIC from the best model, continued to the second stage. Next, I determined the model of best fit using only environmental covariates in the occupancy sub-model while holding detection constant. The model with the lowest AIC, and any models <5 AIC from the best model, continued to the third stage. In the third stage, all possible combinations of models maximizing fit in the detection sub-model, and models maximizing fit in the occupancy sub-model using only environmental covariates were tested for fit, with the lowest AIC and any models <5 AIC from the best model continuing to the final stage. In the final stage, all possible candidate models from the second stage were combined with all anthropogenic variables (excluding anthropogenic variables that were correlated) and the model with the lowest AIC was used to predict the impact of urbanization on species occupancy. All numeric variables were standardized using the 'scale' function in R before modelling.

I used the 'predict' function and the model of best fit for each species to assess the impact of anthropogenic variables on species occupancy. First, all variables except the anthropogenic variable of interest were held constant at their mean values. Then, I modelled the impact of the variable of interest on occupancy by supplying all observed values of the variable of interest to the model. I then calculated the slope of occupancies response to the anthropogenic variable to determine its significance and positive or negative association. I then repeated this process for all anthropogenic variables in each species. To determine the significance of an anthropogenic variable's relationship to occupancy, I calculated confidence intervals for the slope (± 1.96 mean SE) from all occupancy calculations produced by supplying all observed values of the variable of interest to the model. If the confidence interval included zero, I concluded that the anthropogenic variable had no effect on occupancy for that species. In contrast, if the confidence interval did not include zero, I concluded that the anthropogenic variable had a positive or negative impact on occupancy for that species.

RESULTS

I searched 140 plots in 2018, 132 plots in 2019, and 131 plots in 2020 for a total of 404 plots used to build occupancy models for each species. I observed 49 species during these searches, including 26 species that were considered urban avoiders (Table 5). All three LIDAR-derived variables describing vegetation structure were closely correlated, so only canopy cover was included as an environmental covariate for model building. Because urbanization intensity and light pollution were also closely correlated, I omitted light pollution from the occupancy models. For urbanization intensity,200 plots (49.5%) had 100,000 m^2 of impervious surface within a 1,000 m buffer. For noise pollution, 45 plots (11.1%) were at risk for significant continuous noise expose from highways and175 plots (43.3%) were at risk for significant intermittent noise expose from air traffic and high-speed rail. And finally for invasive species, 171 plots (42.3%) had moderate or high levels of feral hog activity, and 25 plots (6.2%) had moderate or high levels of Chinese privet abundance.

Table 5. All bird species (listed by Family) observed in the Great Trinity Forest, Dallas, TX in the breeding season (2018-2020). For each species I include the urban association (adapter, avoider, exploiter), total number of plots where a species was recorded, and mean time-to-detection (TTD).

Scientific Name	Common Name	Urban Association	Observations	Mean TTD
Columbidae				
Zenaida macroura	Mourning Dove	Adapter	7	9.14
Cuculidae				
Coccyzus americanus	Yellow-billed Cuckoo	Avoider	201	10.69
Trochilidae				
Archilochus sp.	Ruby-throated/Black-chinned Hummingbird	Adapter	31	17.06
Picidae				
Melanerpes carolinus	Red-bellied Woodpecker	Adapter	203	10.25
Dryobates pubescens	Downy Woodpecker	Adapter	241	10.32
Dryobates villosus	Hairy Woodpecker	Adapter	3	18.67
Dryocopus pileatus	Pileated Woodpecker	Avoider	32	11.63
Tyrannidae				
Myiarchus crinitus	Great Crested Flycatcher	Adapter	41	12.46
Tyrannus verticalis	Western Kingbird	Adapter	23	9.09

Tyrannus tyrannus	Eastern Kingbird	Adapter	1	17.00
Tyrannus forficatus	Scissor-tailed Flycatcher	Avoider	3	13.00
Contopus virens	Eastern Wood-pewee	Avoider	2	20.50
Empidonax alnorum	Alder Flycatcher	Avoider	1	12.33
Sayornis phoebe	Eastern Phoebe	Adapter	41	11.05
Vireonidae				
Vireo griseus	White-eyed Vireo	Avoider	347	4.51
Vireo bellii	Bell's Vireo	Avoider	1	11.00
Vireo flavifrons	Yellow-throated Vireo	Avoider	1	1.00
Vireo olivaceus	Red-eyed Vireo	Avoider	214	7.98
Corvidae				
Cyanocitta cristata	Blue Jay	Adapter	92	11.48
Corvus brachyrhynchos	American Crow	Exploiter	114	7.88
Paridae				
Poecile carolinensis	Carolina Chickadee	Adapter	382	4.31
Baeolophus bicolor	Tufted Titmouse	Adapter	339	6.14
Troglodytidae				
Thryothorus ludovicianus	Carolina Wren	Adapter	363	4.83
Polioptilidae				
Polioptila caerulea	Blue-gray Gnatcatcher	Avoider	323	5.99
Turdidae				
Sialia sialis	Eastern Bluebird	Avoider	2	6.50
Catharus ustulatus	Swainson's Thrush	Avoider	6	7.33
Turdus migratorius	American Robin	Adapter	2	14.50
Mimidae				
Mimus polyglottos	Northern Mockingbird	Adapter	11	6.55
Bombycillidae				
Bombycilla cedrorum	Cedar Waxwing	Adapter	4	8.25
Fringillidae				
Haemorhous mexicanus	House Finch	Adapter	3	3.67
Passerellidae				
Melospiza lincolnii	Lincoln's Sparrow	Avoider	2	5.00
Melospiza georgiana	Swamp Sparrow	Avoider	1	16.00
Icteridae				
Icterus spurius	Orchard Oriole	Avoider	1	20.00
Agelaius phoeniceus	Red-winged Blackbird	Adapter	13	7.46
Molothrus ater	Brown-headed Cowbird	Adapter	100	10.17
Quiscalus quiscula	Common Grackle	Exploiter	32	9.91
Parulidae				
Mniotilta varia	Black-and-white Warbler	Avoider	2	11.50
Protonotaria citrea	Prothonotary Warbler	Avoider	49	10.00
Geothlypis trichas	Common Yellowthroat	Avoider	10	11.20
Setophaga ruticilla	American Redstart	Avoider	3	7.00
Setophaga americana	Northern Parula	Avoider	15	14.47

Setophaga petechia	Yellow Warbler	Avoider	1	18.00
Cardellina pusilla	Wilson's Warbler	Avoider	1	20.00
Cardinalidae				
Piranga rubra	Summer Tanager	Avoider	71	11.07
Cardinalis cardinalis	Northern Cardinal	Adapter	394	2.56
Passerina caerulea	Blue Grosbeak	Avoider	19	9.00
Passerina cyanea	Indigo Bunting	Avoider	329	5.03
Passerina ciris	Painted Bunting	Avoider	169	7.58
Spiza americana	Dickcissel	Avoider	29	2.34

I created occupancy models for 17 of the 19 species with over 40 observations each (Table 6). I did not create an occupancy model for American Crows as their territory size is far larger than my plot size, which can bias estimates of occupancy (Efford and Dawson 2012; Hayes and Monfils 2015). I attempted to create an occupancy model for the Eastern Phoebe, but the model failed to converge and could not give reliable estimates of occupancy. Vegetation structure, vegetation composition, and flooding frequency were the environmental covariates most frequently included in final models, each appearing in final models for more than half the species. Forest width was only included in models for 4 species, the least of any covariate. Vegetation structure was the detection covariate that appeared in the most models, and all four detection covariates appeared in models for at least 8 species. Urbanization intensity negatively impacted occupancy in 8 species, more than any other anthropogenic variable, and positively impacted occupancy in 3 species (Figure 16). Continuous noise negatively impacted occupancy in 2 species and positively impacted occupancy in 2 species (Figure 17). Intermittent noise negatively impacted occupancy in 7 species and was the only anthropogenic variable to not positively impact occupancy in any species (Figure 18). Feral hog activity negatively impacted occupancy in 4 species and positively impacted occupancy in 5 species, the largest positive response to any anthropogenic variable in this study (Figure 19). Chinese privet negatively impacted occupancy in 2 species and positively impacted occupancy in 1 species, significantly impacting fewer species than any other variable (Figure 20). In total, urbanization intensity had the largest impact on avian occupancy, while Chinese privet had the smallest (mean squared error of the slope of occupancy response to each variable: urbanization intensity = 0.0971; continuous noise = 0.0162; intermittent noise = 0.0126; feral hog activity = 0.0404; Chinese privet abundance = 0.0056).

Table 6. Results of the model selection process for all species with occupancy models indicating which covariates were included in the final model for each species. UI: urbanization intensity; FH: feral hog activity; CP: Chinese privet abundance; CN: continuous noise; IN: intermittent noise; VS: vegetation structure; VC: vegetation composition; WT: wetness; FW: forest width; AN: ambient noise; TD: time of day; DS: day of the season.

	Occupancy Sub-model										Detection Sub-model			
	Anthropogenic Variables					Environmental Covariates					Detection Covariates			
	UI	FH	CP	CN	IN	Year	VS	VC	WT	FW	AN	VS	TD	DS
Yellow-billed Cuckoo	X	X	X	X	X	X		X			X		X	X
Red-bellied Woodpecker	X	X	X	X	X		X	X	X		X		X	X
Downy Woodpecker	X	X	X	X	X		X		X		X	X		
Great Crested Flycatcher	X	X	X	X	X	X			X	X				X
White-eyed Vireo	X	X	X	X	X			X		X	X	X		
Red-eyed Vireo	X	X	X	X	X	X	X	X	X					
Blue Jay	X	X	X	X	X	X	X	X				X		X
Carolina Chickadee	X	X	X	X	X	X	X		X		X	X	X	X
Tufted Titmouse	X	X	X	X	X		X	X				X	X	X
Carolina Wren	X	X	X	X	X		X		X	X		X	X	
Blue-gray Gnatcatcher	X	X	X	X	X			X	X		X	X		X
Brown-headed Cowbird	X	X	X	X	X		X		X					
Prothonotary Warbler	X	X	X	X	X	X				X		X	X	
Summer Tanager	X	X	X	X	X			X	X					
Northern Cardinal	X	X	X	X	X						X		X	
Indigo Bunting	X	X	X	X	X		X	X				X	X	
Painted Bunting	X	X	X	X	X	X	X	X			X	X		X
Total Inclusions	17	17	17	17	17	7	10	10	9	4	8	10	8	8

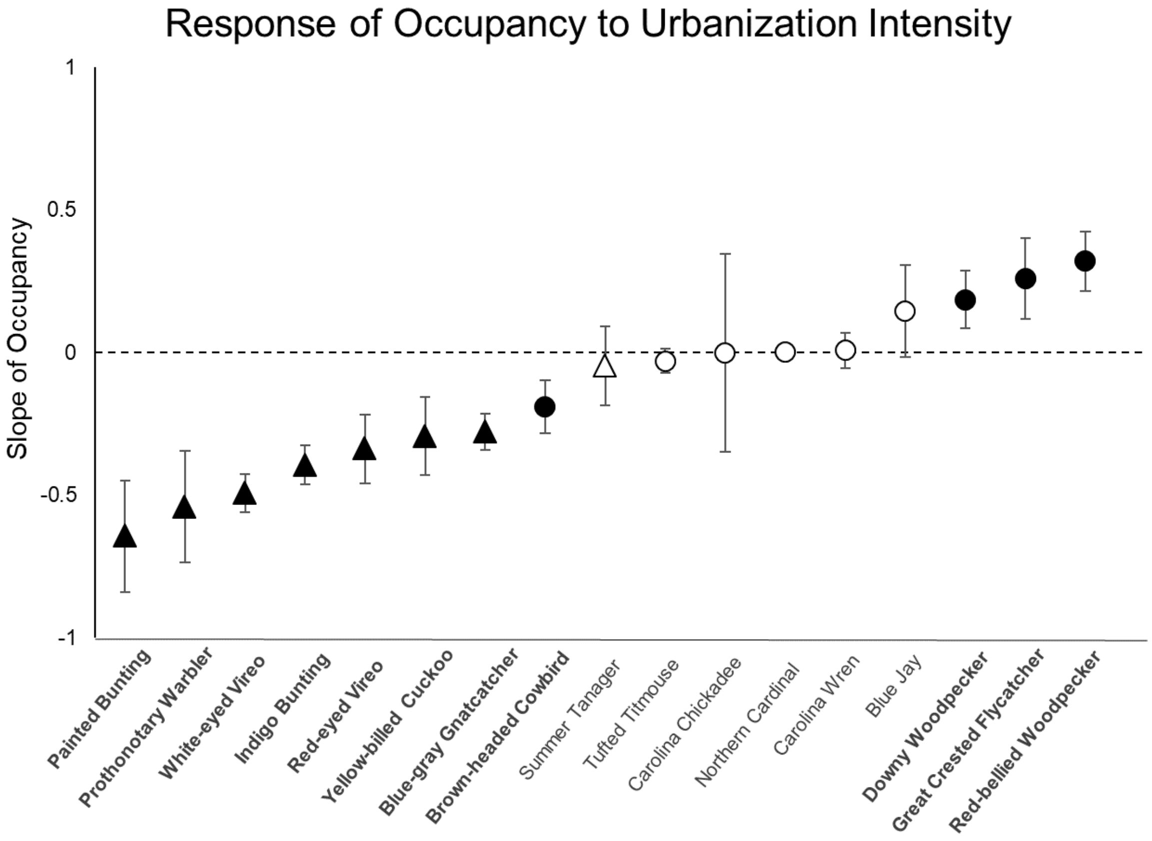

Figure 16. Response of occupancy to the amount of impervious surface within 1,000 m plot buffers by species (CI: mean ± 1.96 (SE)). Filled symbols and bold names indicate significant response. Triangles represent urban avoiding species, circles representing urban adapting species.

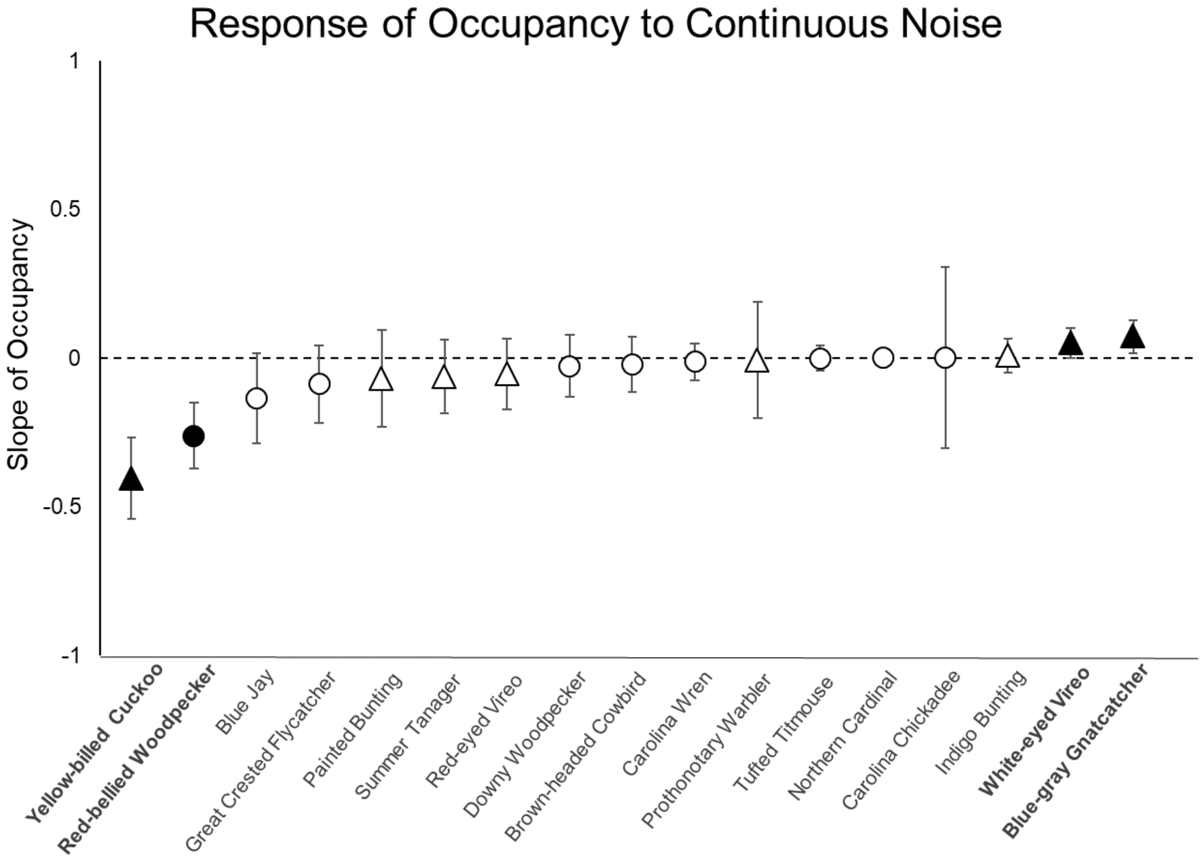

Figure 17. Response of occupancy to continuous noise exposure by species (CI: mean ± 1.96(SE)). Filled symbols and bold names indicate significant response. Triangles represent urban avoiding species, circles representing urban adapting species.

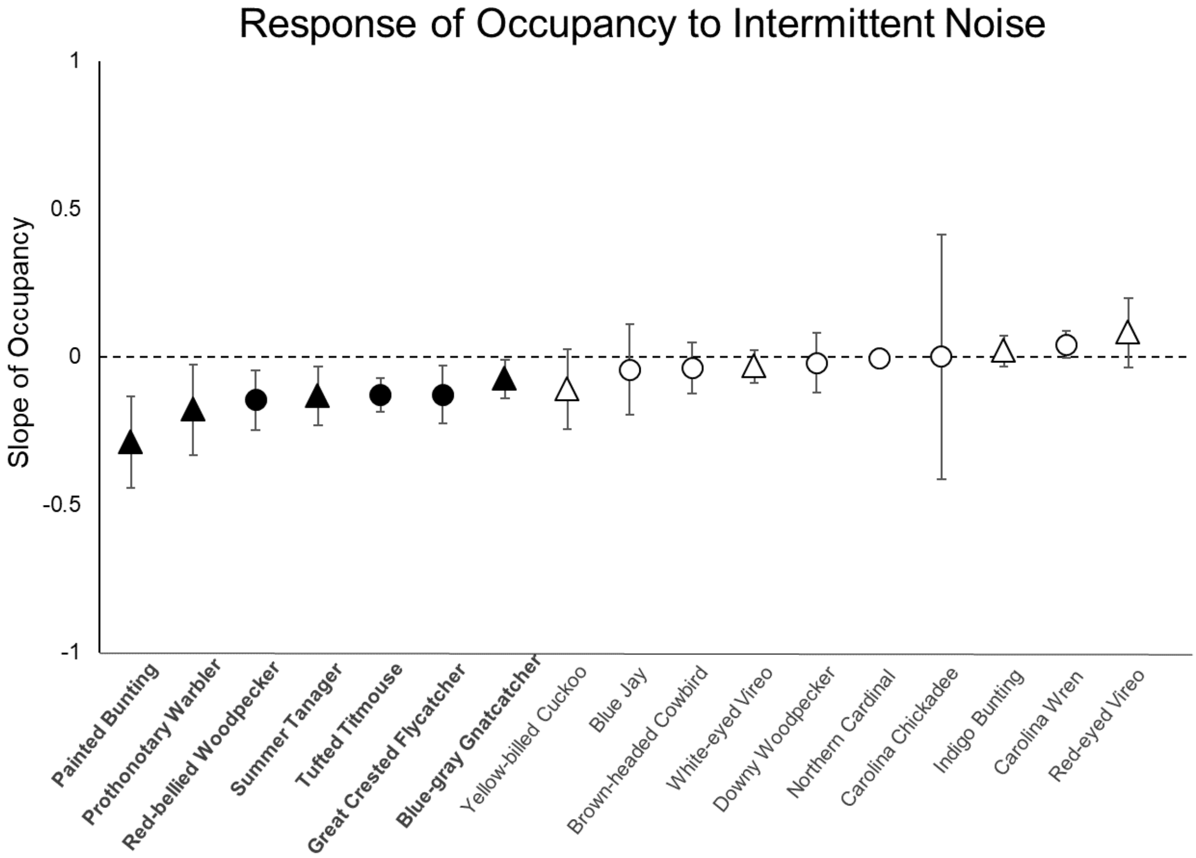

Figure 18. Response of occupancy to intermittent noise exposure by species (CI: mean ± 1.96(SE)). Filled symbols and bold names indicate significant response. Triangles represent urban avoiding species, circles representing urban adapting species.

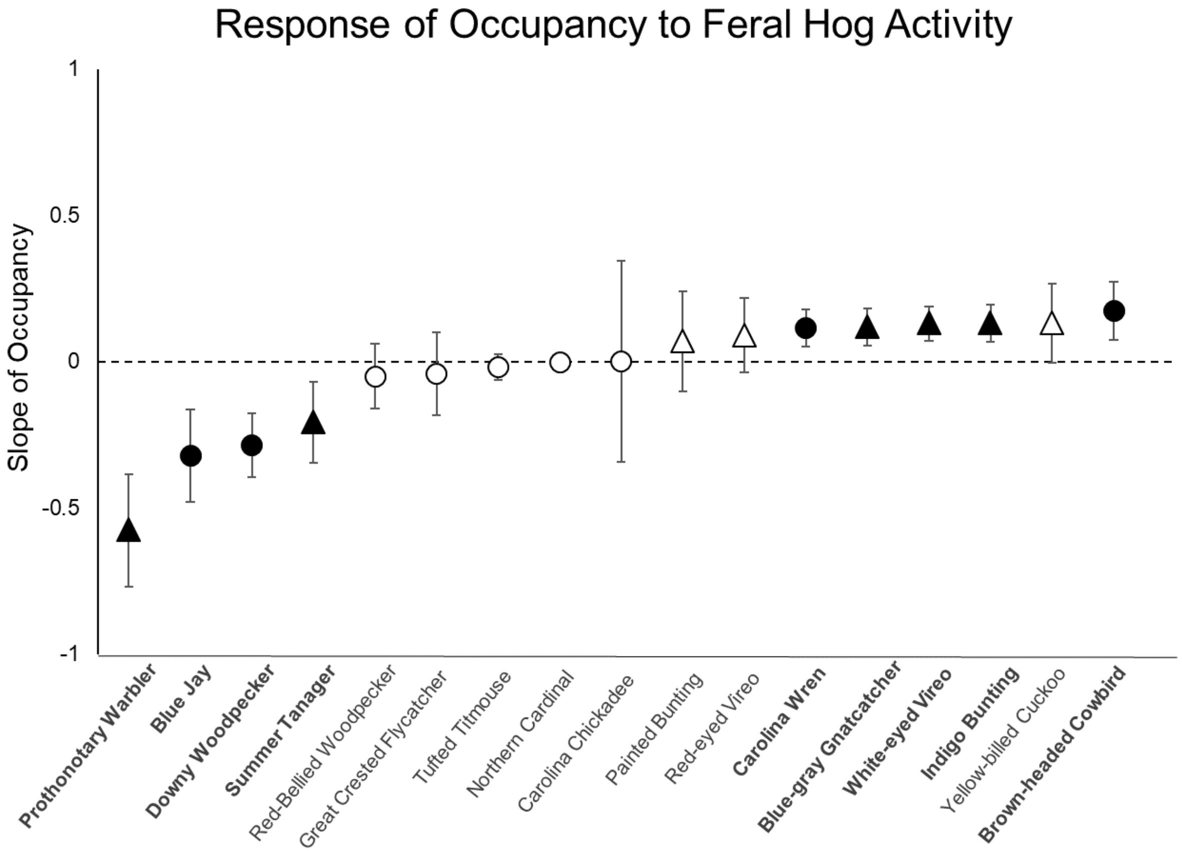

Figure 19. Response of occupancy to feral hog activity by species (CI: mean ± 1.96(SE). Filled symbols and bold names indicate significant response. Triangles represent urban avoiding species, circles representing urban adapting species.

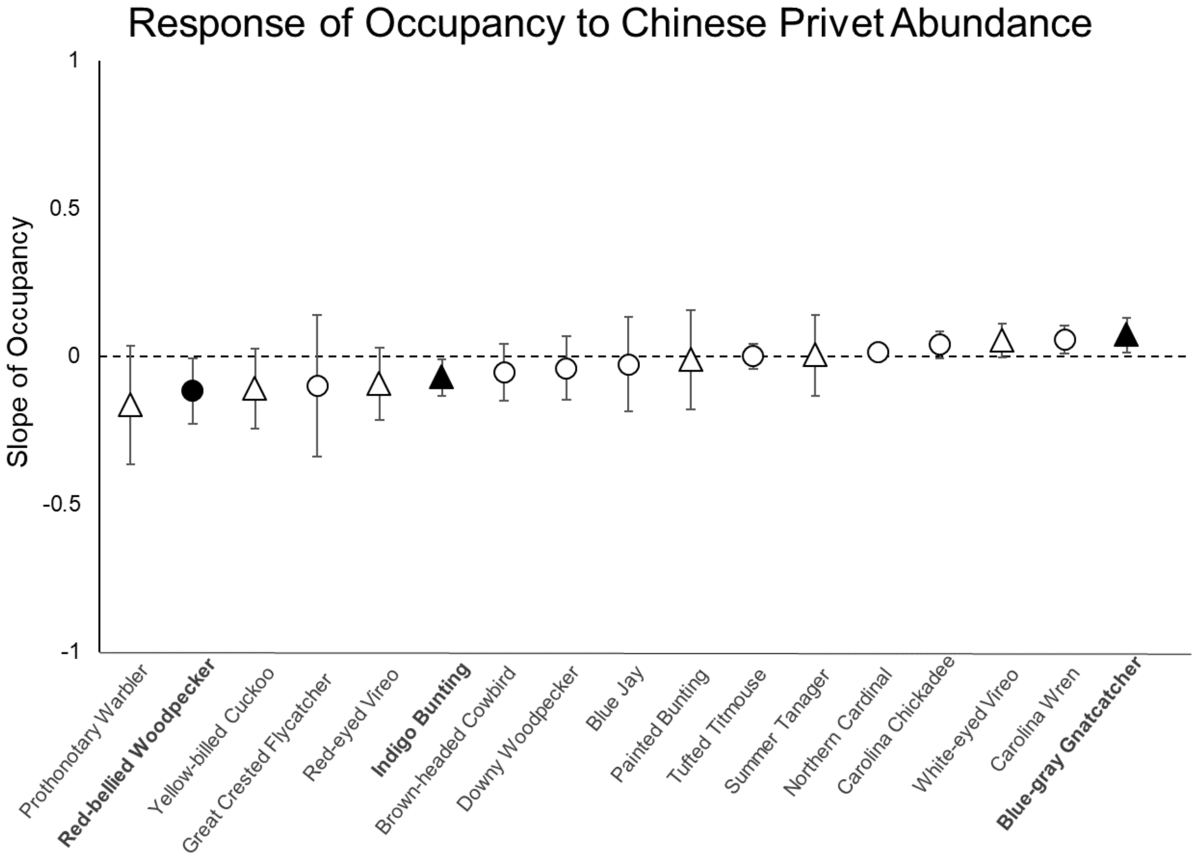

Figure 20. Response of occupancy Chinese privet abundance by species (CI: mean ± 1.96(SE)). Filled symbols and bold names indicate significant response. Triangles represent urban avoiding species, circles representing urban adapting species.

DISCUSSION

Urbanization in the surrounding matrix and its associated impacts significantly influenced the distribution of breeding birds in the GTF. All five anthropogenic variables measured in this study had significant negative associations with occupancy in multiple species. More than half of the 17 species for which I modelled occupancy were urban adapters, so unsurprisingly there were positive associations between occupancy and anthropogenic variables in some species. Even though 9 of the 17 modelled species were urban adaptors, there were twice as many negative associations between the urban matrix and occupancy as positive associations across all species and variables. Previous studies assessing the impacts of an urban matrix on wildlife have not accounted for the different ways in which urbanization can impact wildlife, making it difficult to understand the mechanism behind the negative associations between the urban matrix and species distributions, especially when variables like urbanization intensity and anthropogenic noise may be spatially correlated, or are not accounted for individually. My study design, and characteristics of my study location, allowed us to test for multiple impacts of the urban matrix simultaneously and independently on species with a broad range of urban tolerance, increasing my understanding of the mechanisms driving biodiversity loss from urban habitat fragments.

Urbanization Intensity

Urbanization intensity had the largest impact on avian occupancy of any anthropogenic variable in this study, reinforcing the importance of the direct impacts of urbanization on the matrix, even for species with high dispersal abilities. Because I were able to untangle urbanization intensity from stressors like anthropogenic noise or invasive species, I were able to treat urbanization intensity as a direct impact of an urbanizing matrix. In other words, I can attribute negative associations between urbanization intensity in the nearby matrix and occupancy to the inability of those species to use an urbanized matrix, and the loss of resources associated with this consequence (Kupfer et al. 2006; Kennedy et al, 2010). Gascon et al. (1999) found that species that avoided a specific matrix type were not found in habitat fragments embedded in that matrix. My results support these conclusions, as 7 of the 8 urban-avoiding species investigated in this study showed a significant negative response to urbanization intensity in the nearby matrix.

Previous research documenting the effects of an urban matrix on birds in habitat fragments found a negative association between an urban matrix and occupancy in forest interior specialists and species that were susceptible to edge effects (De Wan et al. 2009). My study found that a negative association with an urban matrix was not limited to forest interior species, as 5 of the 7 species negatively associated with urbanization intensity are closely associated with edge habitats or early successional habitat (Yellow-billed Cuckoo; White-eyed Vireo; Blue-gray Gnatcatcher; Indigo Bunting; Painted Bunting). A negative association between edge-adapted species and urbanization in the matrix has not previously been identified in the literature, and is an important consideration for future conservation planning, as a focus on forest interior species is common when considering the impacts of habitat fragmentation on avian conservation. Urban-avoiding edge-specialists may be even more vulnerable to urbanization in the matrix than forest interior species, as edges will be spatially proximate to the matrix in many cases, while forest interior species may be able to isolate themselves from the urban matrix in the center of larger fragments. My study supports results from Rodewald and Bakermans (2006) linking a negative association with an urban matrix to Neotropical migrant status. All species in my study that were significantly negatively associated with urbanization intensity were Neotropical migrants, while seven of the nine species that showed no effect or a positive response to urbanization were residents. The three species that showed a positive relationship between occupancy and urbanization intensity were urban-adapted species that are able to use an urban matrix.

Anthropogenic Noise

Continuous anthropogenic noise from roads significantly impacted the distribution of two species with low vocal frequencies in the GTF, the Yellow-billed Cuckoo and Red-bellied Woodpecker, with large effect sizes. Continuous sources of noise can inhibit communication in species with low vocal frequencies (Hu and Cardoso 2009; Halfwerk et al. 2011) and can lead to displacement from locations with chronic continuous noise (Rheindt 2003; Proppe et al. 2013;

Cardoso et al. 2018). Yellow-billed Cuckoos and Red-bellied Woodpeckers were the two species with the lowest minimum vocal frequency of any modelled species based on recordings from my field location (~ 1,000 Hz for each species) and were the only two species with significant evidence for displacement by highway noise. This agrees with the hypothesis that continuous noise filters bird communities by vocal frequency and previous results showing significant displacement by traffic noise in the Yellow-billed Cuckoo (Goodwin and Shriver 2011).

Intermittent noise from airplane traffic and high-speed rail negatively affected occupancy in seven different species, while continuous noise only negatively affected two species. Intermittent noise displaces wildlife through a fear or stress response to the perception of a threat as opposed to masking vocalizations (Francis and Barber 2013). Intermittent noise and fear response are poorly studied in relation to continuous noise and vocal masking (Francis and Barber 2013), but experimental evidence showed a greater displacement effect from intermittent noise than continuous noise in Sage Grouse (*Centrocercus urophasianus*) in one of the only studies to compare the effects of intermittent and continuous noise (Blickley et al. 2012). My results support the importance of addressing intermittent noise as an avian conservation issue. Many studies are unable to separate intermittent noise from continuous noise in loud urban environments. I suspect that in cases where urban noise displaces birds at a variety of different vocal frequencies (e.g., Gonzalez-Oreja 2017), that the bird communities are being impacted by both continuous noise (noise masking communication) and intermittent noise (unpredictable louder noises that produce a fear response) simultaneously. I treated traffic noise in my study as continuous noise because traffic volumes were so high that they produced constant noise. In cases where traffic volume is lower, roads will often represent intermittent noise. The impact of air traffic, the more pervasive of the two sources of intermittent noise in this study, on wildlife is poorly understood (Alquezar and Macedo 2019). Although studies have found changes in behavior (Klett-Mingo et al. 2016; Sierro et al. 2017) and a fear-based response to air traffic, the impact of air traffic on avian distributions is unstudied.

Invasive Species

Feral hog activity was the second most important anthropogenic variable contributing to changes in avian occupancy, with species responding both positively and negatively to this invasive species. Feral hogs are an abundant, destructive invasive species in the southern United States (Campbell and Long 2009; Siemann et al. 2009; Bevins et al. 2014), but their impact on wildlife communities is poorly studied (Risch et al. 2021). Previous research in the GTF found that avoidance of areas with high feral hog activity was the most important variable explaining the distribution of a bottomland hardwood forest specialist small mammal (Stevens et al. in review). Feral hogs are significant sources of predation for small mammals (Wilcox and van Vuren 2009), and their destructive rooting behavior can significantly alter habitat for terrestrial species (Hone 2002; Barrios-Garcia and Ballari 2012), but the mechanism by which they could negatively affect avian distributions is unclear. Another bottomland hardwood forest specialist, the Prothonotary Warbler, suffered the largest negative impacts on occupancy of any species in my study. One possible explanation for this is that high levels of feral hog activity can reduce invertebrate diversity and abundance (Carpio et al. 2014), which could reduce food resources for birds. In a tropical forest ecosystem, an overabundance of another Suiforme, (*Pecari tajacu*), was linked to changes in forest structure and declines in understory avian insectivores (Michel et al. 2015). Positive associations between feral hog activity and some avian species observed in the GTF may also be explained by changes in forest structure creating new feeding opportunities. Areas where invasive feral hogs were rooting and feeding were associated with a temporary decline in avian abundance, but after feral hogs left the area, avian abundance increased as birds exploited new feeding opportunities (Natusch et al. 2016). Thus, the divergent response of the GTF bird community to feral hog activity may be driven by which species can tolerate the disturbance associated with an abundant and destructive large mammal, and which species can effectively exploit new feeding opportunities.

Chinese privet was the least impactful anthropogenic variable on avian occupancy in the GTF. Previous research found no impact of Chinese privet abundance on breeding songbirds in the southeastern United States (Wilcox and Beck 2007). Alternatively, Chinese privet created an important dense understory structure associated with Swainson's Warbler (*Limnothlypis swainsonii*) breeding territories (McNair 2019).

Conclusions

Previous research on swamp rabbits in the GTF demonstrated that the direct impacts of urbanization on the matrix impeded dispersal and gene flow, while the indirect impacts of the matrix had little impact on this species distribution (Stevens et al. in review). Dispersal and gene flow are not inhibited by an urban matrix in species with increased dispersal ability (e.g., flight; Richardson et al. 2020), but my study has found that the direct impact of urbanization on the composition of the matrix can still negatively impact species with high dispersal ability by restricting individuals' resource base. Because the GTF is so large there are locations in the forest where individuals can be spatially distant from the urban matrix, but in smaller fragments this may not be possible. This may explain the loss of many urban avoiding species from many other urban forest fragments and their persistence in the GTF. The indirect impacts of an urban matrix also significantly impacted avian occupancy. Continuous noise from roads displaced species with low vocal frequencies, whereas intermittent noise from air traffic and high-speed rail negatively impacted a broader group of species. Feral hog activity was associated with significant negative impacts on occupancy for some species, but positive impacts for others.

Future research on the negative impacts of intermittent noise is needed, specifically understanding which species are vulnerable and will exhibit fear/stress-based displacement. In the past, research on the impacts of anthropogenic noise have focused on birds because of their reliance on vocalizations to communicate, but because intermittent noise is unrelated to interruptions in communication, a far broader group of wildlife may be impacted. More research is needed to understand the impact of feral hogs on wildlife, especially in the southern United States where they are an abundant invasive species. My research shows that two bottomland hardwood forest specialists endemic to the southeastern United States, the Prothonotary Warbler and the swamp rabbit, are unable to persist in areas of high feral hog activity (this study and Steven et al. in review). It is possible that some species may benefit from large ecosystem changes associated with feral hog activity, but I have little understanding of which species those are or how these new opportunities may be exploited.

Mitigation of anthropogenic noise and invasive species will be necessary to conserve complete wildlife communities in urban forest fragments, but even if these mitigation measures are taken, urban avoiding species will likely require large habitat fragments to persist. These important discoveries provide new and important information that may facilitate conservation in and near urban areas as urbanization spreads, a critical challenge in combatting the worldwide extinction crisis (Foley et al. 2005).

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VITA

Professional Preparation

Ph.D., Biology, Texas Christian University, May 2022

M.S., Environmental Science, Texas Christian University, December 2011

B.S., Environmental Science, Texas Christian University, May 2008

Selected Publications

Stevens, T. K., D. Biffi, A. S. Chipps, A. M. Hale, and D. A. Williams (2022) Urbanization inhibits dispersal and gene flow in a habitat specialist across a large urban forest fragment. Ecological Application (In Review).

Stevens, T. K., A. M. Hale, and D. A. Williams (2022) Environmental and anthropogenic variables influence the distribution of a habitat specialist in a large urban forest. Animal Conservation (In Review).

Schenk, A. R., T. K. Stevens and A. M. Hale (2022) Predator-prey dynamics are decoupled in the raptor community in a large urban forest. Diversity. 14:177 https://doi.org/10.3390/d14030177

Stevens, T. K., A. M. Hale, K. B. Karsten and V. J. Bennett (2013) An analysis of displacement from wind turbines in a wintering grassland bird community. Biodiversity and Conservation 8:1755-1767.

Stevens, T. K. (2012) A new location for the Tody Motmot (*Hylomanes momotula*) in Costa Rica. Wilson Journal of Ornithology 124:815-817.

Awards

2022: Texas Conservation Symposium 2022 Graduate Student Oral Presentation: 1st Place ($200)

2019: Science and Engineering Research Center Graduate Grant, Texas Christian University ($1,935)

2018: College of Science and Engineering Dean's Graduate Student Research Fund, Texas Christian University ($3,000)

2018: Research and Creative Activities Fund, Texas Christian University ($4,500)

2011: Travel Award: American Ornithologists Union ($347)

2011: Institute for Environmental Studies Professional Growth Award, Texas Christian University ($500)

2011: Graduate Student Travel Grant, Texas Christian University ($400)

2010: Adkins Fellowship, Biology Department, Texas Christian University ($3,000)

Teaching Experience

Instructor, Contemporary Issues in Biology, (2019-2022), Biology Department, Texas Christian University

Graduate Teaching Assistant, Avian Biology (2018), Biology Department, Texas Christian University

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Graduate Teaching Assistant, Contemporary Issues in Biology Laboratory (2010-2011), Biology Department, Texas Christian University

ABSTRACT

THE IMPACTS OF URBANIZATION ON WILDLIFE IN NORTH AMERICA'S LARGEST URBAN FOREST

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Urbanization endangers more species in the United States than any other human activity as it dramatically modifies natural landscapes, fragments previously intact habitats, and is spreading rapidly. Species with specialized habitat requirements are more severely impacted by urbanization than other species and are usually absent from habitat fragments surrounded by an urban matrix. I studied the impacts of urbanization on a diverse wildlife community in the Great Trinity Forest Dallas, Texas, the largest urban forest in the United States. I used species distribution models to study the impacts of urbanization on swamp rabbit (*Sylvilagus aquaticus*) distribution. I used a landscape genetics approach to study the impact of urbanization on dispersal and gene flow in the swamp rabbit. I also studied the impact of urbanization on occupancy of breeding birds. The distribution of swamp rabbits was negatively associated with invasive species, but did not respond to other impacts of urbanization. I found that urbanization and highways significantly limited swamp rabbit gene flow and dispersal. And finally, I found that the avian community responded to anthropogenic impacts of urbanization in the matrix in diverse ways. To conserve urban avoiding species in urban habitat fragments it may be necessary to maintain large habitat tracts with uniform shapes that are not bisected by highways, and mitigate for the indirect effects of the matrix like noise and invasive species.