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EFFECTS OF LAND MANAGEMENT ON MAMMALIAN SPECIES ABUNDANCE AND RICHNESS AMONG FOUR SITES IN WEST-CENTRAL GEORGIA

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Columbus State University

The College of Letters and Sciences

The Graduate Program in Natural Sciences

Biology Track

Effects of Land Management on Mammalian Species Abundance and Richness among Four Sites in West-Central Georgia

A Thesis in

Natural Sciences

By

Kelsey A. Champagne

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Science Natural Sciences

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I have submitted this thesis in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

In order to determine the effect of urbanization and habitat fragmentation on mammalian populations, the species abundance and richness among four 24.28 hectare sites in West-Central Georgia were estimated through the use of game camerasat baited stations between July and December 2014. Among the four sites were the following: Protected 1, which was chosen due to the work that has been done on the land over the last decade to restore it to a more native habitat; Protected 2, which has been maintained for its native vegetation for research and educational purposes; Impacted 1, which had its pine and understory clear cut during the summer of 2014; and Impacted 2, which was chosen for its rich history of varied human impacts over the past 100 years. Each site was divided into four equal plots of 6.07 hectares each. Each plot was photo-trapped for 16 days in two day increments for a total of 64 trap days per site.

A significant difference ($p=0.001$) was found between protected and impacted sites at both the species and functional group (herbivores, carnivores and omnivores) levels supporting. When examined through analysis of dissimilarity at both the species and functional group levels, the largest dissimilarities were found among the same three pairs: both impacted sites, both protected sites, and between Protected site 2 and Impacted site 2. Since two of the sites with the greatest average dissimilarity demonstrate the long term effects of rural protection and urbanization on mammalian species richness and abundance, their dissimilarity acts as a predictor to the changes that could be seen in an ecosystem as urbanization increases. With this model, it would be predicted that over

time as the landscape becomes more urbanized, herbivores and omnivores would become more abundant as the number of carnivores decreases leading to the expansion of mesopredator populations.

The hypothesis that the greatest abundance of carnivores would be seen in conjunction with the greatest abundance of herbivores was rejected. All species that were classified as carnivores were photo-trapped at Protected 2. These species rely heavily upon small mammals as prey, which can lead to possible interspecific food overlaps. In part, this sympatric behavior between coyotes and bobcats can be attributed to the partitioning of land and prey by both species due to preferences for different hunting habitats of felids and canids. Although the impacted sites had a greater abundance of mammals photo-trapped than the rural sites, the analysis of similarity between sites for the factor of impacted versus protected was not significant ($p > 0.05$).

When organisms were divided by the day versus night photo-traps a significant difference was found between species, between functional groups, between the total day versus night photo-traps for both species and functional groups, and the interaction between species and day versus night photo-traps; however, the interaction between day and night photo-traps and functional groups was not significant.

With a greater number of mesopredators photo-trapped at Impacted 2 than any other site and the contribution of the greatest average dissimilarity from the omnivores, the progression of the mesopredator release theory was demonstrated. No longer constrained by a large, apex predator, the medium sized carnivores and omnivores were able to flourish even in the highly urbanized site. As urbanization and human expansion

increase, the maintenance of native habitat becomes increasingly important to ensure the stability of mammalian species abundance and diversity. Therefore, future emphasis should be placed upon the management of original habitat patches to support native wildlife maintaining the trophic chain length to diminish the expansion of the mesopredators into urbanized environments.

Introduction

Habitat fragmentation threatens biodiversity by increasing isolation between native habitat fragments (Andrén 1997). Due to land use and development by humans, native habitats become mosaics of small patches isolated within an impacted background. Although these patches may be utilized by wildlife species to some extent, the habitats are often degraded (Yahner 1996; Andrén 1997).Each fragment, which contains its own local, isolated population, results in an exchange of individuals dependent upon individual requirements like home-range boundaries and natal dispersal. The extent and type of intervening matrix determines the distance an individual will have to move to locate resources and colonize other fragments. Due to individual deaths, changes in territory sizes and/or local turn over can occur leading to extirpation and colonization of fragments at the population level (Andrén 1997). The ability of individuals within a species to move across a landscape to recolonize fragments is dependent on their sensitivity to fragmentation (Swihart *et al.* 2003). Andren (1997), surmised that for birds and mammals there is a threshold at which the effect of habitat fragmentation is greater than that explained solely by habitat loss.

With increased urbanization, emphasis has been placed upon the management of original habitat patches to support native wildlife (Grinder and Krausman 2001). Habitat loss tends to have larger negative consequences on biodiversity than fragmentation and can result in the reduction of trophic chain lengths. This reduction alters species interactions by reducing the number of specialist species. In addition, habitat loss

negatively affects species richness, population abundance and distribution, genetic diversity, breeding and dispersal success, predation rate, and foraging behavior (Fahrig 2003). Because large carnivores require large home ranges, tend to have low population densities, and have slow population growth rates, they are especially vulnerable to extinction by habitat loss and their population dynamics are often a good indicator of the potential fate of an ecosystem in urbanized landscapes (Ordeñana *et al.* 2010). This is especially important when subpopulations travel through divided patches of habitat in order to find a suitable environment for reproduction and resources.

When individuals must transverse into different patches of habitat that are surrounded by an unsuitable environment for breeding, they connect subpopulations into a network, a metapopulation (Elmhagen and Angerbjörn 2001). In this metapopulation model, the classical metapopulation theory, some of the habitat patches in which the metapopulation exist are occupied by subpopulations of individuals. Although any local population may go extinct, the patch can also be recolonized by individuals that disperse from other subpopulations. Therefore, each subpopulation has the same probability of extinction and recolonization. This model assumes that patches have equal population sizes and contribute equally to the addition of new colonists. Because some subpopulations suffer extinctions and recolonizations, the pattern of occupancy among the patches shifts whereas the proportion of patches that are occupied remains constant (Donovan *et al.* 1996). The ability of a metapopulation to thrive is directly linked to the balance of recolonizations, extinctions, and migrations. Examples of classical metapopulations are relatively rare, though (Elmhagen and Angerbjörn 2001). Since

subpopulations do not have uniform extinction and recolonization probabilities, most species do not meet the classical metapopulation theory assumptions. The species in which classical metapopulation theory has been documented, typically possess poor dispersal capabilities and occur in early successional habitats. Examples of such species are frogs in temporary ponds and butterflies in disturbed habitats (Donovan *et al.* 1996).

In source-sink metapopulation models, habitat quality differentiates between a source habitat and a sink habitat. Patchy populations are excluded from this model since breeding subpopulations are not distinct (Elmhagen and Angerbjörn 2001). Similar to other metapopulation models, source-sink models describe organisms as spatially distinct subpopulations. However, where the classical metapopulation model assumes that subpopulations will have equal probabilities of extinction and recolonization, the source-sink model identifies some populations as sinks, where the subpopulations are inviable without constant influx of immigrants from other subpopulations, and other subpopulations as sources, where subpopulations remain viable without the influx of immigrants. In this model, individuals who are unable to locate a breeding site in the source emigrate to the sink where breeding sites are available. When the total surplus in all of the source habitats equals the total deficit in the sink habitats, the total population reaches equilibrium (Donovan *et al.* 1996). This model has a lot in common with the mainland-island metapopulation model in which mainlands, due to their size, are less prone to extinction than islands. Because of this, island extinctions are dependent on the small sized local populations (Elmhagen and Angerbjörn 2001).

The complete or partial loss of a source subpopulation has long term effects on other subdivided populations. Therefore, it is important for conservation and management efforts to identify source habitats that produce large numbers of young per unit of area as they contribute a large number of individuals to the total population. Smaller source habitats, although of less managerial concern, may be important to the maintenance of regional populations. The importance of dispersal among local populations is demonstrated in many bird species. Because many migratory bird populations are spatially separated and linked only by dispersing individuals, the resulting discontinuity influences whether a local population and the global population can persist over time (Donovan *et al.* 1996).

Since metapopulation theory examines extinctions and recolonizations in patchy environments, it has provided management implications for populations in fragmented habitats. In fragmented habitats, there is often competition between species to utilize common resources. Two species that utilize common resources may coexist in the presence of habitat fragmentation through the division of the remaining habitat into even smaller patches. Described by Fahrig and Merriam (1994) extensive habitat, such as a forest, may contain several habitat patches that are utilized by separate, local populations. The division of patches into smaller areas has the potential to impact the recolonization ability of a population based on the number of patches available and the distribution of patches over a spatial scale. The presence of dispersal routes, components of the patch through which organisms can move, are also important to the survival of a population by permitting the movement, and therefore breeding of individuals between patches (Fahrig

and Merriam 1994). The potential of a patch is particularly important when the coexistence of two species in competition is intensified. As habitats inevitably become too small to sustain populations of two competing species, their ability to disperse is sacrificed reducing the probability of persistence of one of the species in a patch. Ultimately, the inferior competitor will colonize empty patches only to be displaced when individuals of the superior competitor arrive (Fahrig 2003). In the absence of colonization of a patch by individuals of a more competitive species; however, the population of inferior competitors can continue to grow. One such example occurs when large predators are lost from patches and mesopredator populations increase.

The process through which intermediate-sized carnivores become more prevalent in the absence of large, apex predators, has been termed the mesopredator release theory. Typically, mesopredator release is characterized by a negative effect on prey species. Prugh *et al.* (2009) defined a mesopredator as any mid-ranking predator in a food web. Therefore, a mesopredator from one ecosystem may also act as an apex predator in another ecosystem. Unlike large carnivores who typically avoid human dominated regions, mesopredators reach high densities in developed areas. Fragmented areas also provide suitable areas of population growth for mesopredators since they do not require as much area as apex predators, encounter lower levels of conflict with humans and are able to exploit the available resources (Prugh *et al.* 2009). Mesopredators are vital members of food webs because of their effect on prey behaviors, ability to cycle nutrients by scavenging carrion, and effect on plant fitness through consumption and dispersal of seeds. As populations of mesopredators increase so do their competitive interactions. As

a result, species can be displaced from their native home-ranges, which ultimately leads to changes in mesopredator behavior, prey preferences, and microhabitat selection. Because many species of mesopredators are not strict carnivores, the probability of overlapping food and habitat use effectively leads to niche compression, thereby limiting species both physiologically and morphologically (Ginger *et al.* 2003).

Interactions observed between mesopredators and apex predators are broken into categories by Prugh *et al.* (2009). A linear interaction includes a decline of the apex predator, causing a population increase in the mesopredators and decrease in prey species. However, a triangular interaction occurs when both the apex predator and mesopredator rely upon the same prey items. An example of this is the relationship between coyotes (*Canis latrans*), foxes, and lagomorphs. Both coyotes and foxes primarily prey upon lagamorphs. This intraguild predation involves the coyote preying upon the fox and the lagomorph, making it the apex predator, while the fox only preys upon lagomorphs. (Prugh *et al.* 2009). Henke and Bryant (1999) found in a controlled experiment that the removal of coyotes resulted in higher mesopredator abundances including populations of bobcats (*Lynx rufus*) and grey foxes (*Urocyon cinereoargenteus*). However, the observed increase in mesopredators did not result in a decrease in prey species.

With limited space available that is suitable for wildlife, urban environments cause an overlap in resource use for large and medium-sized carnivores and omnivores (Randa *et al.* 2009). Ordeñana *et al.* (2010) found that coyotes, large carnivores, and raccoons (*Procyon lotor*), medium-sized omnivores, increased as the proximity and

intensity of urbanization increased; however, bobcats and gray foxes, both of which are large carnivores, decreased. Since the habitat fragments that resulted from urbanization were too small or isolated to support native diets, coyotes benefitted from the availability of anthropogenic food sources. This did not alter the coyote's preference of natural habitats when they were available, though (Ordeñana *et al.* 2010; Riley *et al.* 2003). Within a home range, food availability and competitive interactions drive animals to make finer scale use of the habitat. One example of this is the competition between raccoons and Virginia opossums for resources that occurred on the microhabitat scale. Resulting from this competition, Ginger *et al.* (2003) found the density of raccoons declined as the niche of the Virginia opossum expanded due to increased resource availability.

Since all mammals must rest at some point, another factor that effects their use of habitat and predation interactions are their cycles of daily activity. There are both advantages and disadvantages to being active at different times of the day. For example, activity at night decreases chances of heat stress, enhances olfactory communication, and reduces competition for food; however, visual communication is reduced at night limiting social interactions. Animals that are chiefly active at night include the herbivorous cottontail rabbit, omnivorous opossum, and omnivorous raccoon. The omnivorous armadillo and the carnivorous gray fox are also crepuscular and nocturnal. Diurnal animals are able to use vision to forage and often have complex visual communication. However, diurnal animals may suffer heat stress, may be seen by potential predators, and suffer increased competition for food. Because of this, diurnal animals tend to be larger

than nocturnal animals and live in larger, more complex social groups. Some animals, though, may be active during both the day and the night. Examples of such animals include the herbivorous white-tailed deer, the carnivorous coyote, and the carnivorous bobcat all of which are crepuscular (Feldhamer *et al.* 2015; Whitaker and Hamilton 1998).

In order to determine the effect of urbanization on mammalian populations, the species abundance and richness among four sites in West-Central Georgia were estimated through the use of cameras in both human impacted and natural habitats. It was expected that species abundances and richness would be greater in the natural sites due to their minimal habitat fragmentation and lowered disturbance levels. Additionally, in areas where the populations of herbivores were more abundant, higher populations of carnivores were expected. The objectives of this study were to (1) determine the impact of fragmentation by comparing urban, impacted sites in which fragmentation was high to rural, protected sites, with lowered fragmentation and disturbance levels; (2) assess species abundance and richness for each site; and (3) examine the dissimilarity between sites on the functional group level. Camera traps were utilized in this study because of their noninvasive nature which allowed for the examination of species richness and abundance. Mammal species reported to inhabit the region within which the study sites were found include: Virginia opossum, nine-banded armadillo (*Dasypus novemcinctus*), swamp rabbit (*Sylvilagus aquaticus*), cottontail rabbit (*Sylvilagus floridanus*), eastern chipmunk (*Tamias striatus*), eastern gray squirrel (*Sciurus carolinensis*), southern flying squirrel (*Glaucomys volans*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*),

coyote, gray fox, red fox (*Vulpes vulpes*), raccoon, long-tailed weasel (*Mustela frenata*), mink (*Neovison vison*), eastern spotted skunk (*Mephitis mephitis*), bobcat, boar (*Sus scrofa*), and white-tailed deer (*Odocoileus virginianus*) (Golly 1962).

To specifically address the effect of habitat fragmentation between urban and rural sites, the following hypotheses were tested. (1) There will be a significantly higher mammalian species richness at protected sites. (2) There will be a significantly higher mammalian species richness at protected sites on the functional group level. (3) At the site with the greatest abundance of carnivores, the greatest abundance of herbivores will be photo-trapped. (4) There will be a significantly higher total abundance during the night photo-traps for species and functional groups.

Methods

Site Description

Four locations in West-Central Georgia were used to compare mammalian species richness and abundance in protected and impacted environments in Muscogee, Harris, and Talbot counties (Fig. 1). The four sites were designated as Protected 1, Protected 2, Impacted 1, and Impacted 2 (Fig. 2 & 3). Protected 1 and Protected 2 were forested, rural sites that have been maintained to represent the native landscape of the region. The impacted sites, Impacted 1 and Impacted 2, were urbanized locations that have undergone extensive and various levels of habitat degradation. Both Protected 1 and Impacted 1 are surrounded by a rural environment in which much of the land contains low residential use or has been used for agricultural purposes, both Protected 2 and Impacted 2 are surrounded by a more densely populated landscape. Since the smallest site, Impacted 2, measured 24.28 hectares, all sites were scaled to this size. All sites except for Impacted 2 were rectangular in shape. Because of bodies of water and grass fields, the land utilized for Impacted 2 was not rectangular and included more edges in which the study site bordered pieces of unusable habitat. Each site was equally divided into four replicate plots of 6.07 hectares each.

To determine how dietary requirements for each species could affect their movements throughout the year, a review of the literature was used to determine which plants omnivores and herbivores might consume (Table 1). For analysis, mammals were divided into functional groups based on their dietary habits. That is, whether the species

is typically carnivorous, herbivorous, or omnivorous according to Fedriani *et al.* (2000) and Whitaker and Hamilton (1998). Species may occasionally span multiple classes; however, for this analysis they have been classified according to their most common food type. For example, coyotes are classified as carnivores even though they are facultative herbivorous. White-tailed deer and cottontail rabbits comprise the strict herbivores and the omnivores included raccoons, nine-banded armadillos, Virginia opossum, boar, and gray squirrel. Coyotes, bobcats, and the gray fox were considered carnivores (Fedriani *et al.* 2000; Whitaker and Hamilton 1998).

Protected 1 was a privately owned site in Talbot County that has been restored to reflect native flora and fauna during the past decade. This site represented short-term protection from the effects of urbanization. Plant and cover analysis showed the dominant plants at Protected 1 to be Aceraceae, Aquilfoliaceae, Cornaceae, Ericaceae, Fagaceae, Hamamelidaceae, Myricaceae, Pinaceae, and Poaceae.

Protected 2, which was located in Harris County, was under the care of Columbus State University and maintained its native vegetation for research and educational purposes. Because this site has remained relatively unchanged for over five decades, it represented long-term protection from the effects of urbanization. The dominant plant species identified at Protected 2 were Aceraceae, Cornaceae, Fagaceae, Pinaceae, Poaceae, and Vitaceae.

Impacted 1 was a privately owned site located approximately 4,828m from Protected 1 in Talbot County. This site, which had its pine and understory clear cut during the summer of 2014, was an ideal site to demonstrate the impact of short-term

impact of urbanization. The property was being developed for very low density residential use. At Impacted 1, the dominant plant species were Fagaceae, Hamamelidaceae, Myricaceae, Poaceae, and Vitaceae.

Located in Muscogee County, Impacted 2 was owned and managed by Columbus Water Works and Oxbow Meadows Environmental Learning Center. This site was chosen for its rich history of varied human impact and man-made changes to its landscape. In the past 100 years, it has served as a private landfill, sand mine, and most recently, a waste treatment application field. Efforts have been made at the property to restore it to its native wetlands. This site represented the long-term effects of urbanization. Plant analysis for Impacted 2 showed that the dominant plants were Anacardiaceae, Betulaceae, Oleaceae, Poaceae, Smilacaceae, and Vitaceae.

To better define the nature of the four sites, a one-time survey of plant species during the month of October was conducted. Among all four sites, each plot was sampled for plant species presence. The location of the camera at the center of each plot was utilized the starting point for the transects. From there, a 50m tape was utilized to sample plant species in the four cardinal directions. Plants were sampled up to 1m on either side of the tape. Canopy cover was also assessed at each starting point for the plots based on visual perception of percent of sky occluded from view. Because sampling was performed in fall, the list of plant families does not include plants that are most commonly identified by their spring and summer foliage.

Procedure

Technology has increased the ability to collect data on elusive species both temporally and spatially. One method that is commonly employed to assess species richness and abundance is the use of game cameras (Hughson *et al.* 2010; Kelly and Holub 2008; Cove *et al.* 2012). During this study, four Moultrie A5 Low Glow infrared game cameras were used to photo-trap mammals between July and December 2014. Each infrared camera was set to take photographs in 5 min. increments when triggered by the movement of an animal. The Moultrie A5 Low Glow infrared game camera has a night range of up to 15.24m. Captures were stored on 8GB San Disk memory cards. Cameras were visited every 24 hours during the 48 hour period of sampling to re-bait with wet dog food and rotate full memory cards. Sampling sites near chosen coordinates were selected for low understory vegetation. Once each camera station was established, any remaining understory plants that might create false triggers were cleared. The cameras were mounted 30-40 cm above the ground to one tree at each plot with the bait approximately 3 meters from the cameras to ensure complete coverage (Fig. 4).

During the first phase of the study, phase 1, plots were chosen at each site after inaccessible areas, such as bodies of water, were excluded. Plots were chosen by overlaying a 24.28 hectare polygon over the encompassed land for each site in ArcGIS. Each sites polygon was then equally divided into four replicate plots. One camera trapping station was located close to the direct center of each 6.07 hectare plot. For the second phase of the study, phase 2, cameras were relocated to the nearest trail or forest edge inside of each plot in an effort to maximize captures since many species are known

to utilize corridors for facilitated movement. Therefore, the movement of the cameras to a corridor was expected to increase the probability of photo-trapping a carnivore. Because of their proximity, Protected 1 and Impacted 1 were sampled on the same dates as were the paired sites of Protected 2 and Impacted 2. Cameras were placed on paired, nonadjacent plots at each site for two consecutive nights in a seven day period. After a three day period of no sampling, cameras were then rotated to sample the second pair of plots. This resulted in a period of eight days between sampling at each individual site and sixteen days between sampling on the plot level. This method of moving the cameras and implementing days of no sampling was undertaken to reduce the chances that animals would become entrained to bait availability.

The duration of the camera-trapping survey was 64 sampling nights for all sites combined beginning on the night of July 23rd. Each sampling period in which all four plots were sampled at each site took approximately two weeks to complete; this period of time represents one replicate of the study. Phase 1 of the study, in which cameras were placed at the center of the plot, included ten weeks of sampling. The last ten weeks of sampling, phase 2, began with the movement of the cameras to a forest edge or trail.

Photo-traps were analyzed for animal presence or absence. Pictures were evaluated for species identification, and number of trap visits. Any photograph that contained unidentifiable mammals were discounted. Additionally, if the same species visited a bait station more than once in an hour, it was counted as a single visit. To discern between day and night captures of organisms, sunrise and sunset data was obtained from the Astronomical Applications Department of the U.S. Naval Observatory

for each day and site of the study. If the photo-trap was taken on or before sunrise and after sunset it was considered a night photo-trap. Day photo-traps included those taken after sunrise and before sunset.

Data Analysis

To analyze which site had the greatest relative abundance of each species photo-trapped, the number of mammals photo-trapped per site was divided by total number of trap days to calculate trap effort. Univariate analysis of variance was used to determine if there were significant differences in the abundances between mammals photo-trapped during the day and night, between the individual species abundances between day and night photo-traps, and the interaction between day and night photo-traps among functional groups using Microsoft Excel.

In order to analyze community abundance and richness differences, the statistical software package Primer 6 (Premier Biosoft) was used to analyze data for dissimilarity between sites for species and functional groups. Bray Curtis dissimilarity matrices were calculated from the relative abundance matrix. The data were analyzed for dissimilarities using a two-way nested analysis of similarities that tested for effects of protected versus impacted using replicates and testing among sites using replicates. An α level of 0.05 was used to determine significance of all statistical tests. Non-metric multi-dimensional scaling plots were used to illustrate differences in community structure among sites for species and functional groups. The stress, found from Kruskal's stress formula 1

multiplied by 100, was interpreted using the Kruskal's rules of thumb (McCune and Grace 2000). A two-way nested analysis of similarity with replicate nested within site was used to assess the species abundance and functional group data. Similarity percentages of species contributions and functional group contributions were then analyzed. The percent each species contributed and functional group contributed to the dissimilarity was found for each site. The resulting one-way, pair wise test was cut off at 90%. A second two-way nested analysis of similarity with replicate nested within impacted versus protected was conducted for the species and functional group data.

Results

A total of 393 mammals were photo-trapped and identified to species during the sixty four trap nights (Table 2 and Table 3). Most abundant among the species observed were white-tailed deer, Virginia opossum, raccoon, and nine-banded armadillo accounting for 88.5% of all species observed. The remaining 11.5% of species observed were divided among gray squirrel, cottontail rabbit, coyote, bobcat, boar, and gray fox (Table 4).

During phase 1 when traps were located centrally within the plot without regard to location of forest edge, 207 mammals were trapped. Of the total number of mammals photo-trapped during phase 1, 24.3% were photo-trapped at Protected 1, the rural property in Talbot County. The dominant species at that site were Virginia opossum (42.0%), white-tailed deer (28.0%), and raccoon (14.0%) respectively. The remaining 16.0% of photo-traps were of nine-banded armadillo, cottontail rabbit, and a single boar (Table 2). Photo-trapping at Protected 2, which has remained un-impacted for over five decades, yielded 14.5% of the mammals for this phase. Of this, the dominant species photo-trapped were, Virginia opossum (53.3%), white-tailed deer (23.3%), and raccoons (10.0%). The remaining 10% of photo-traps were made up of nine-banded armadillo, and single coyote (Table 2).

Photo-trapping at Impacted 1, the site of low density residential use, yielded 15.0% of the mammals for this phase. The dominant species were white-tailed deer (35.5%), Virginia opossum (32.3%), and nine-banded armadillo (22.6%). The remaining

9.7% of photo-traps were of raccoon (Table 2). Photo-trapping at Impacted 2, which over the last 100 years has been impacted by various human activities, yielded 46.4% of mammals for this phase. The dominant species were Virginia opossum (41.7%), raccoon (34.4%), and nine-banded armadillo (16.7%). The remaining 7.3% of photo-traps were of white-tailed deer, boar, coyote, and gray squirrel respectively (Table 2).

During phase 2, when cameras were moved to sites adjacent to open canopy areas such as game trails, driving paths, and hiking trails, 186 mammals were photo-trapped. Of the total number of mammals photo-trapped during this phase, 26.3% were photo-trapped at Protected 1. The dominant species were white-tailed deer (61.2%) and gray squirrels (16.32%). The remaining 22.45% of photo-traps were of raccoons, Virginia opossums, cottontail rabbits, nine-banded armadillos, bobcats, and coyotes respectively (Table 3). Photo-trapping at Protected 2 yielded 17.74% of the mammals for this phase. The dominant species were gray squirrels (30.3%), white-tailed deer (21.2%), raccoon (18.2%), and Virginia opossum (18.2%). The remaining 12.1% of photo-traps were bobcats, a coyote, and a gray fox (Table 3). Photo-trapping at Impacted 1 yielded 12.9% of the mammals for this phase. The dominant species were white-tailed deer (54.2%) and raccoon (33.3%). The remaining 12.5% of photo-traps were of a rabbit, a coyote, and a bobcat (Table 3). Photo-trapping at Impacted 2 yielded 43.0% of the mammals for this phase. The dominant species were white-tailed deer (35.0%) and raccoons (40.0%). The remaining 25.0% of photo-traps were of Virginia opossums, cottontail, coyote, nine-banded armadillos, and gray squirrels (Table 3; Fig. 5).

During sampling in phase 1, when cameras were placed at center points of the plots, 39 herbivores, 166 omnivores, and 1 carnivore were photographed (Fig. 6). When comparing the distribution of individuals photo-trapped per trap night by functional group between each of the four sites, Protected 1 had a significantly greater number of herbivores, Impacted 2 had a significantly greater number of omnivores, and Protected 2 had a significantly greater number of carnivores. Based off of photo-trap number per trap effort, the greatest number of white-tailed deer and cotton-tail rabbit were photo-trapped at Protected 1. The greatest number of gray squirrels, bobcats, and the only gray fox were photo-trapped at Protected 2. Nine-banded armadillos, Virginia opossum, raccoon, and coyotes were photo-trapped the most at Impacted 2. The same number of boars were photo-trapped at both Protected 1 and Impacted 2. (Fig. 5).

The division of day and night photo-traps by functional groups was found to be statistically significant ($p=0.05$; $df=1$; $F= 4.22$). The difference in day and night total abundances for functional groups were found to be statistically significant ($p=0.04$; $df=2$; $F=3.94$). The interaction between the day and night photo-traps among the functional groups was found to not be statistically significant ($p=0.09$; $df=2$; $F=2.71$) (Fig. 8). The division of day and night photo-traps by species abundance was found to be statistically significant ($p=0.0008$; $df=1$; $F=12.43$). The difference in day and night total abundances were found to also be statistically significant ($p=1E-05$; $df=9=$; $F=5.75$). The interaction between day and night photo-traps among the species was found to be statistically significant as well ($p=0.002$; $df=9=$ $F=3.51$) (Fig. 7).

A two-way nested analysis of similarity with replicate nested within impacted versus protected did not show a statistically significant difference in community abundance or species richness at each site ($p= 0.15$). The two-way nested analysis of similarity with replicate nested within site was significant ($p = 0.001$). The largest average dissimilarity was found between Protected 2 and Impacted 2 (68.43%). Of this, raccoons made up 37.07%, Virginia opossums made up 24.60%, white-tailed deer made up 16.42%, nine-banded armadillos made up 10.04%, and gray squirrels made up 6.39%. The second largest average dissimilarity was found between the two urban sites, Impacted 1 and Impacted 2 (67.81%). Between these sites, raccoons made up 35.25%, Virginia opossums made up 27.50%, white-tailed deer made up 16.20%, and nine-banded armadillos made up 12.27%. The third largest average dissimilarity was found between the two rural sites, Protected 1 and Protected 2 (61.09%). Of this, white-tailed deer made up 32.99%, Virginia opossums made up 26.04%, and gray squirrels made up 12.24%. The remaining contributors to this dissimilarity were raccoons, cottontail rabbits, and nine-banded armadillos respectively.

When the mammals photo-trapped were assigned to functional groups to assess the community structure of each site, the two-way analysis of similarity with replicate nested within urban versus rural was not statistically significant ($p > 0.05$). The two-way nested analysis of similarity with replicate nested within site was significant ($p = 0.001$). The final stress of the best solution was 0.10 making these results a fair ordination (Fig. 9). Based off of goal of Kruskal's rules of thumb, the final stress of 10 can provide a useable picture in which different objects are placed far apart in the ordination of space

and similar objects are placed close together (McCune and Grace 2000; Gotelli and Ellison 2013). The largest average dissimilarity was found between Impacted 1 and Impacted 2 (61.84%). Of that, omnivores made up 76.03% and herbivores made up 20.82%. The second largest dissimilarity was found between Protected 2 and Impacted 2. Of the 57.50% dissimilarity between Protected 2 and Impacted 2, omnivores made up 72.87% and herbivores made up 22.39%. The average dissimilarity between both rural sites, Protected 1 and Protected 2, was 50.71%. Of this, omnivores made up 47.73% and herbivores made up 45.74%.

Discussion

Using dissimilarity analyses, mammalian species richness and functional group diversity was found to be higher at the protected sites than at the impacted sites, which supports the original prediction that there would be a significantly higher mammalian species richness and at the protected sites. From the analysis of these data, a significant difference was found between sites on both the species and functional group levels supporting both of the hypotheses. The largest average dissimilarity in sites for species was found between Protected 2 and Impacted 2. For functional groups, Protected 2 and Impacted 2 had the second largest average dissimilarity. Since these sites represent the long term effects of rural protection and urbanization on mammalian species richness and abundance, their dissimilarity acts as a predictor to the changes that could be seen in an ecosystem as urbanization progresses through time. With this model, it would be predicted that over time as the landscape becomes more urbanized, herbivores and omnivores would become more abundant as the number of carnivores would decrease, leading to the expansion of mesopredator populations. This trend would occur in response to the loss of land needed for species with large home ranges, increase in habitat fragmentation, and increase in anthropogenic food sources in the human impacted landscape.

On the species level, the second and third largest average dissimilarities were found between both impacted sites and both protected sites. This dissimilarity may be attributed to length of time the effect, urbanization or rural protection, has been

occurring. For example, although both impacted sites are urbanized, Impacted 1 has only undergone changes to its environment since 2014. On the other hand, Impacted 2 has undergone various levels of human disturbance for over the last 100 years. Additionally, when comparing both of the protected sites, which were considered to be located in rural habitats, the length of time of protection also differs. Although at Protected 1 efforts have been made over the last decade to restore the native habitat, Protected 2 has remained unaltered for over the last five decades. Between the two urbanized sites, herbivores and carnivores would be predicted to decrease over time, while omnivores would increase as the effect of urbanization grew. Among the rural sites, the proportions of herbivores, omnivores, and carnivores would be predicted to remain stable as the habitat would remain unaffected by fragmentation and disturbance. When examined on the level of the functional group, the largest dissimilarities were found among the same three pairs: both impacted sites, both protected sites, and between Protected 2 and Impacted 2.

Protected 2 had the lowest abundance of herbivores with the highest number of carnivores photo-trapped relative to the total number of mammals photo-trapped at the site. Therefore, the hypothesis that the greatest abundance of carnivores would be seen in conjunction with the greatest abundance of herbivores was rejected. According to Riley (2006), bobcats may represent a carnivore with intermediate sensitivity to urbanization and fragmentation since they may be able to coexist with development as long as some functional, natural habitat remains. Unlike coyotes and gray foxes who have complex social systems, bobcats are generally solitary and territorial. All three species of carnivores, though, rely heavily upon small mammals as prey, which can lead to possible

interspecific food overlaps. Additionally, unlike nocturnal coyotes and gray foxes, bobcats are active throughout the circadian cycle making them a greater predator on diurnal gray squirrels (Fedriani *et al.* 2000). In part, this sympatric behavior between coyotes and bobcats can be attributed to the partitioning of land and prey by both species due to preferences for different hunting habitats of felids and canids (Chamberlain and Leopold 2005). The lack of gray foxes photo-trapped at Impacted 2 may be explained by the relative abundance of coyotes photo-trapped at the site, since it is known that the gray foxes avoid habitats where coyotes are abundant to evade interference (Fedriani *et al.* 2000). However, unlike red foxes, which are often displaced by coyotes, gray foxes' semi-arboreal behavior may provide an effective escape mechanism from coyote aggression (Chamberlain and Leopold 2005).

Between all four sites, the functional group that contributed the greatest average dissimilarity was the omnivores. A greater abundance of nine-banded armadillos, Virginia opossums, and raccoons were photo-trapped at Impacted 2, which was represented the long-term effect of urbanization. Although the nine-banded armadillo is an omnivore, it has a diet that consists of 90% animal matter; therefore, the Virginia opossums and raccoons represent the only true opportunistic omnivores (Golly 1962). Furthermore, both raccoons and Virginia opossum are known to coexist with one another without displays of territoriality, regardless of their mutual preferences for the same habitat and food sources (Kasparian *et al.* 2004). Besides access to anthropogenic food sources, Impacted 2 also included six of the nine preferred plant families, making it rich in resources for the omnivores.

The most abundant species photo-trapped, the white-tailed deer, are browse feeders that bite off new leaves and the tips of twigs, shrubs, and trees. This animal, which is known to be most active in the early evening and early morning, usually spends the remaining evening and daytime hours in a sheltered place (Golly 1962). Because of its known habitat and food preferences, the highest populations of white-tailed deer were expected to be found at the rural, protected sites. Although the highest number of white-tailed deer was found to be at Protected 1, the lowest abundance was photo-trapped at Protected 2. Similarly, cottontail rabbits were expected to be most abundant at the same two rural sites. Cottontail rabbits, which prefer old field communities with heavy grasses and thickets for cover, were found to be most abundant at Protected 1, where the highest number of preferred plant families were found. Protected 2, which had one less preferred plant family, had no members of this species photo-trapped. Eating many of the same plant families as cottontail rabbits, omnivorous gray squirrels were photo-trapped most often at Protected 2 despite the higher number of tree families present at Protected 1 that could be utilized for both food resources and cover.

When organisms were divided by the day versus night photo-traps a significant difference was found between species, between functional groups, between the total day versus night photo-traps for both species and functional groups, and the interaction between species and day versus night photo-traps; however, the interaction between day and night photo-traps and functional groups was not statistically significant. Gray squirrels were the only species to be photo-trapped during the day more often than the night throughout all of the locations. This was consistent with the expectation that more

gray squirrels would be seen during the daylight hours due to their known diurnal behavior (Whitaker and Hamilton 1998). White-tailed deer, nine banded armadillos, Virginia opossums, and raccoons were photo-trapped more often at night than during the day at all of the locations. According to both Golly (1962) and Whitaker and Hamilton (1998), raccoons, nine banded armadillos, and the Virginia opossums are typically nocturnal making the results of their higher prevalence during night photo-traps expected.

The effects of habitat fragmentation on population dynamics in which some populations are identified as sinks while others are identified as sources was a central concern in this study. In this model, individuals who are unable to locate a breeding site in the source emigrate to the sink where breeding sites are available (Donovan *et al.* 1996). An example of this model would be the portion of Impacted 2 that was utilized for the duration of this study. It was identified as a potential source population. The landscape, which was surrounded by potential sink populations found in the neighboring grass fields, yielded the greatest number of photo-traps than any other site. Because the complete or partial loss of a source subpopulation has long term effects on other subdivided populations it is important for conservation and management efforts to identify source habitats that produce large numbers of young per unit of area as they contribute a large number of individuals to the total population. This coupled with its urban surroundings make the mammalian species richness and abundance at Impacted 2 a possible interest for future research in order to assist in the maintenance of regional populations.

In the absence of human disturbance and urbanization, mammalian species richness and abundance at both protected sites was greater than that found at the impacted, urbanized sites. Shown in the comparison of the long-term sites, Protected 2 and Impacted 2, as urbanization increases further fragmenting a landscape, the available resources and habitat a species may utilize decreases. These sites, which demonstrate the negative effects of urbanization on mammalian species richness and abundance overtime, were the most dissimilar. With a greater number of mesopredators photo-trapped at Impacted 2 than any other site and the contribution of the greatest average dissimilarity from the omnivores, the progression of the mesopredator release theory was demonstrated. No longer constrained by a large, apex predator, the medium sized carnivores and omnivores were able to flourish even in the highly urbanized environment of Impacted 2 to exploit the habitat for resources. As urbanization and human expansion increase, the maintenance of native habitat becomes increasingly important to ensure the stability of mammalian species abundance and diversity. Therefore, future emphasis should be placed upon the management of original habitat patches to support native wildlife maintaining the trophic chain length to diminish the expansion of the mesopredators into urbanized environments.

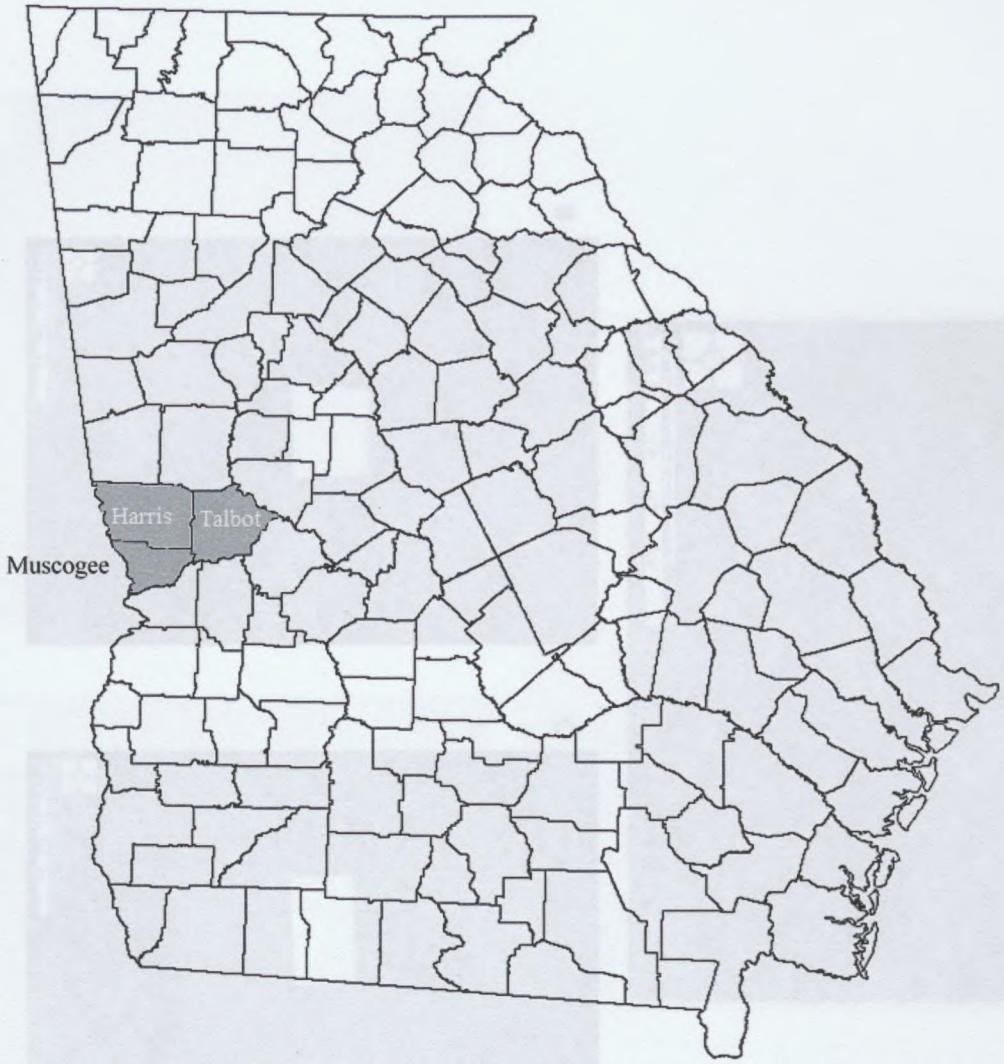

Figure 1 Map of Georgia with county divisions. Counties that are shaded include those in which a study site was located. These counties include: Muscogee, Impacted 2; Harris, Protected 2; and Talbot, Protected 1 and Impacted 1.

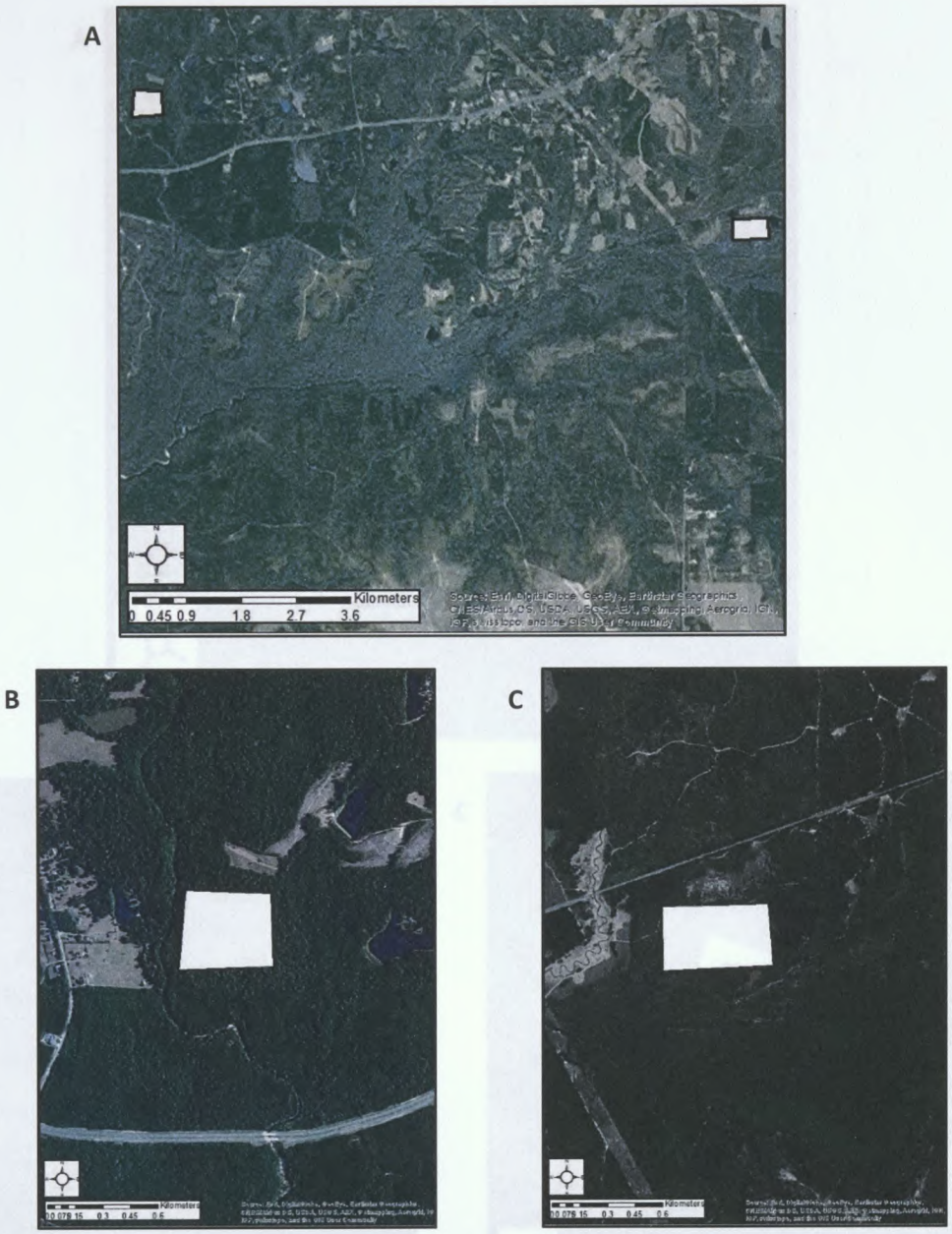

Figure 2 Satellite images of Protected 1 and Impacted 1, which were paired with one another for an analysis of the effects of urbanization on mammalian species richness and abundance. (A) The two sites in relation to one another and close up images of (B) Protected 1 and (C) Impacted 1.

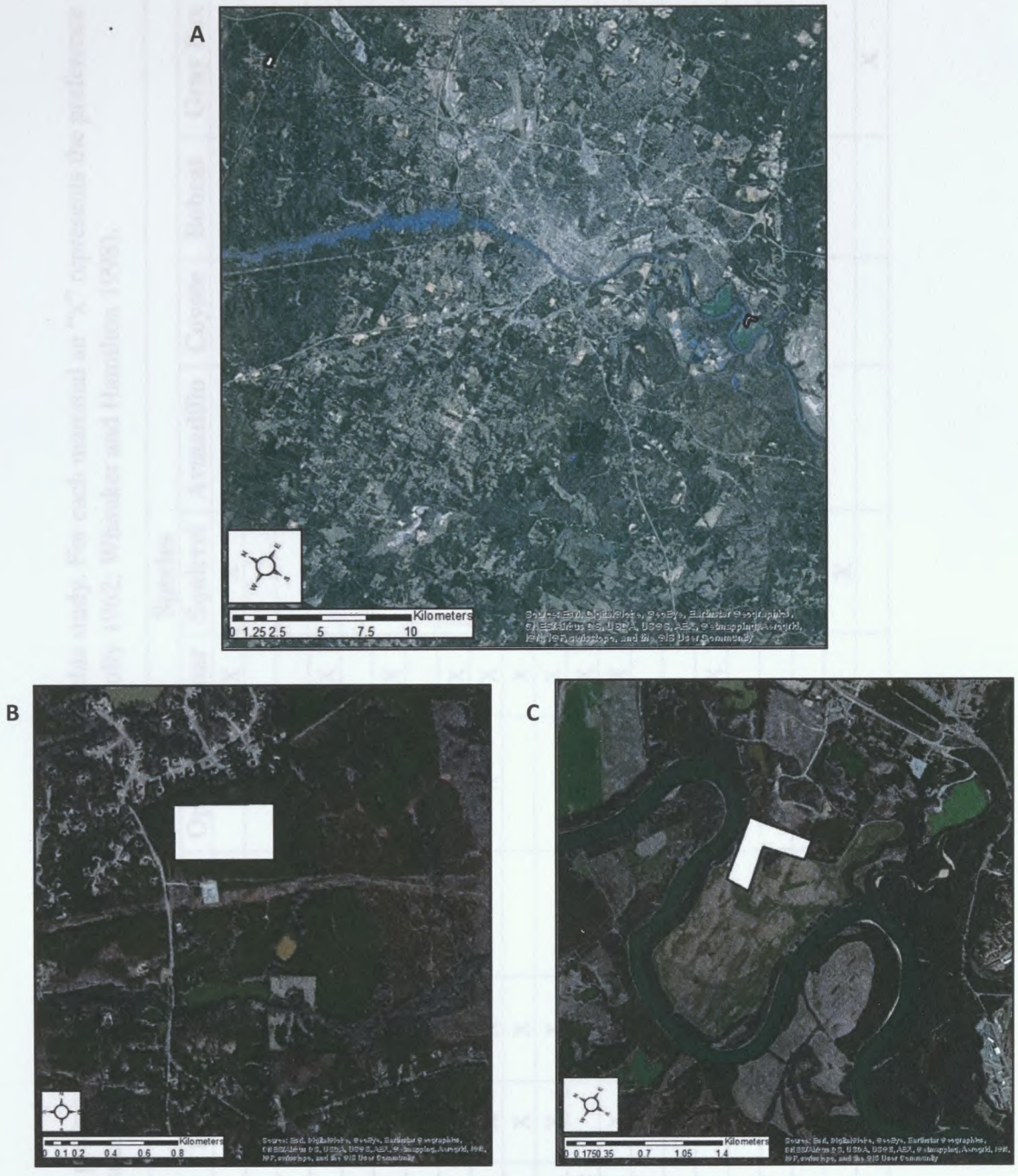

Figure 3 Satellite images of Protected 2 and Impacted 2, which were paired with one another for analysis of the effects of urbanization on mammalian species richness and abundance. (A) The two sites in relation to one another and close up images of (B) Protected 2 and (C) Impacted 2.

Table 1 Floral dietary preferences of species photo-trapped during this study. For each mammal an "x" represents the preference for consumption of the associated plant family found on study plots (Golly 1962; Whitaker and Hamilton 1998).

	Species									
	Deer	**Rabbit**	**Raccoon**	**Opossum**	**Boar**	**Squirrel**	**Armadillo**	**Coyote**	**Bobcat**	**Gray Fox**
Aceraceae	X	X			X	X				
Arecaceae		X								
Asteraceae	X	X								
Betulaceae	X	X			X	X				
Caprifoliaceae	X	X		X						
Cornaceae	X	X			X	X				
Cyperaceae										X
Ericaceae	X	X	X	X	X	X				
Euphorbiaceae	X	X		X	X	X				
Fabaceae	X	X			X	X		X		X
Fagaceae	X	X			X	X				
Hamamelidaceae		X			X	X				
Juglandaceae	X	X	X	X	X	X				
Lamiaceae		X								
Liliaceae	X	X								
Moraceae	X	X	X	X	X	X				
Oleaceae		X								
Passifloraceae		X								
Phytolaccaceae			X							
Pinaceae		X				X				
Platanaceae										X

Table 1 (Cont.)

	Species									
	Deer	**Rabbit**	**Raccoon**	**Opossum**	**Boar**	**Squirrel**	**Armadillo**	**Coyote**	**Bobcat**	**Gray Fox**
Poaceae	X	X						X		
Pteridaceae	X	X								
Rosaceae	X		X	X	X	X		X		
Salicaceae	X	X		X	X					
Smilacaceae	X									
Tiliaceae	X	X								
Ulmaceae	X	X			X	X				
Vitaceae	X	X	X	X	X	X				

Figure 4 A photograph of a game camera that was mounted to a tree after understory vegetation was cleared away. Bait was placed on a paper plate approximately 3m away from the camera and secured in place by a stakes.

Table 2 Mammals successfully identified from photo-traps during phase 1. Each of the four sites, Protected 1 (P1), Impacted 1 (I1), Protected 2 (P2), and Impacted 2 (I2), is separated into replicates. For each replicate, total number of each species of mammals is indicated; blank entries represent zero photo-traps.

Site	Replicate	Deer	Raccoon	Armadillo	Opossum	Rabbit	Boar	Coyote	Squirrel	Bobcat	Gray Fox
P1	1	6	2	2	3						
P1	2	1	2		7						
P1	3	5	1	2	4	2					
P1	4	2	2		7	1	1				
I1	1	4			1						
1	2	3		7	4						
I1	3	3	1		4						
I1	4	1	2		1						
P2	1	3	1								
P2	2	1	1	1	3						
P2	3				6						
P2	4	3	2	1	7			1			
I2	1	2	5	2	7						
I2	2		10	4	12						
I2	3		13	3	10		1		1		
I2	4	2	5	7	11						

Table 3 Mammals successfully identified from photo-traps during phase 2. Each of the four sites, Protected 1 (P1), Impacted 1 (I1), Protected 2 (P2), and Impacted 2 (I2), is separated into replicates. For each replicate, total number of each species of mammal is indicated; blank entries represent zero photo-traps.

Site	Replicate	Deer	Raccoon	Armadillo	Opossum	Rabbit	Boar	Coyote	Squirrel	Bobcat	Gray Fox
P1	5	7	2					1	1		
P1	6	8	2		1	2			2	1	
P1	7	3							1		
P1	8	12		1	2	1			2		
I1	5	5				1		1			
1	6	2	6							1	
I1	7	3	2								
I1	8	3									
P2	5	1	1							1	
P2	6	1	4		3				7		
P2	7	3	1		3			1	3	1	1
P2	8	2									
I2	5	3	7		2			2	1		
I2	6	3	9		5				1		
I2	7	13	4	1	2	2					
I2	8	9	12	1		2		1			

Table 4 Combined data from phase 1 and phase 2 of mammals successfully identified from photo-traps. Each of the four sites, Protected 1 (P1), Impacted 1 (I1), Protected 2 (P2), and Impacted 2 (I2) is listed with the total number of each mammal; blank entries represent zero photo-traps.

Site	Deer	Rabbit	Armadillo	Opossum	Raccoon	Boar	Squirrel	Coyote	Bobcat	Gray Fox
P1	44	6	5	24	11	1	6	1	1	0
I1	24	1	7	10	11	0	1	1	1	0
P2	14	0	2	22	10	0	10	2	2	1
I2	32	4	18	49	65	1	3	3	0	0

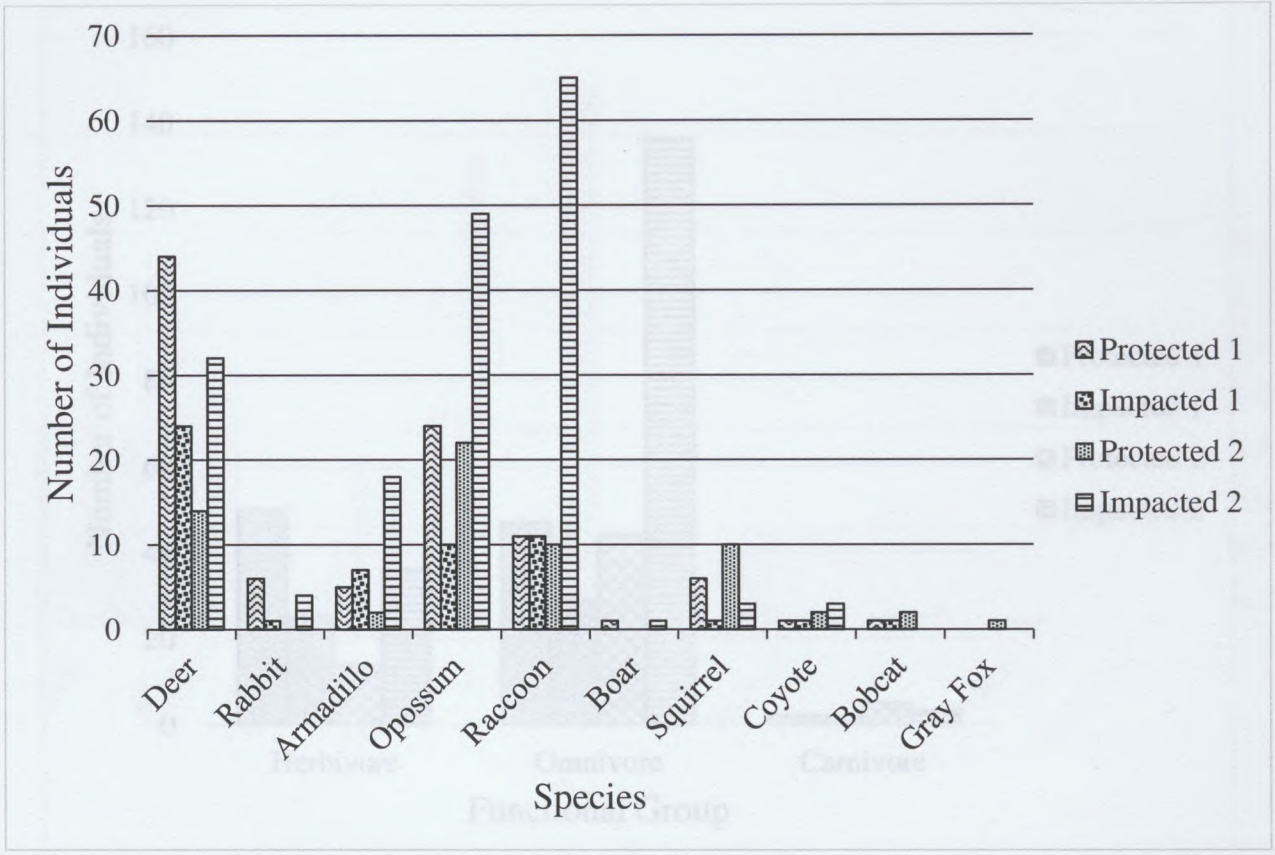

Figure 5 The total number of species photo-trapped for each of the four sites included in this study. The most abundant species for all four sites were the raccoon, opossum, and white-tailed deer.

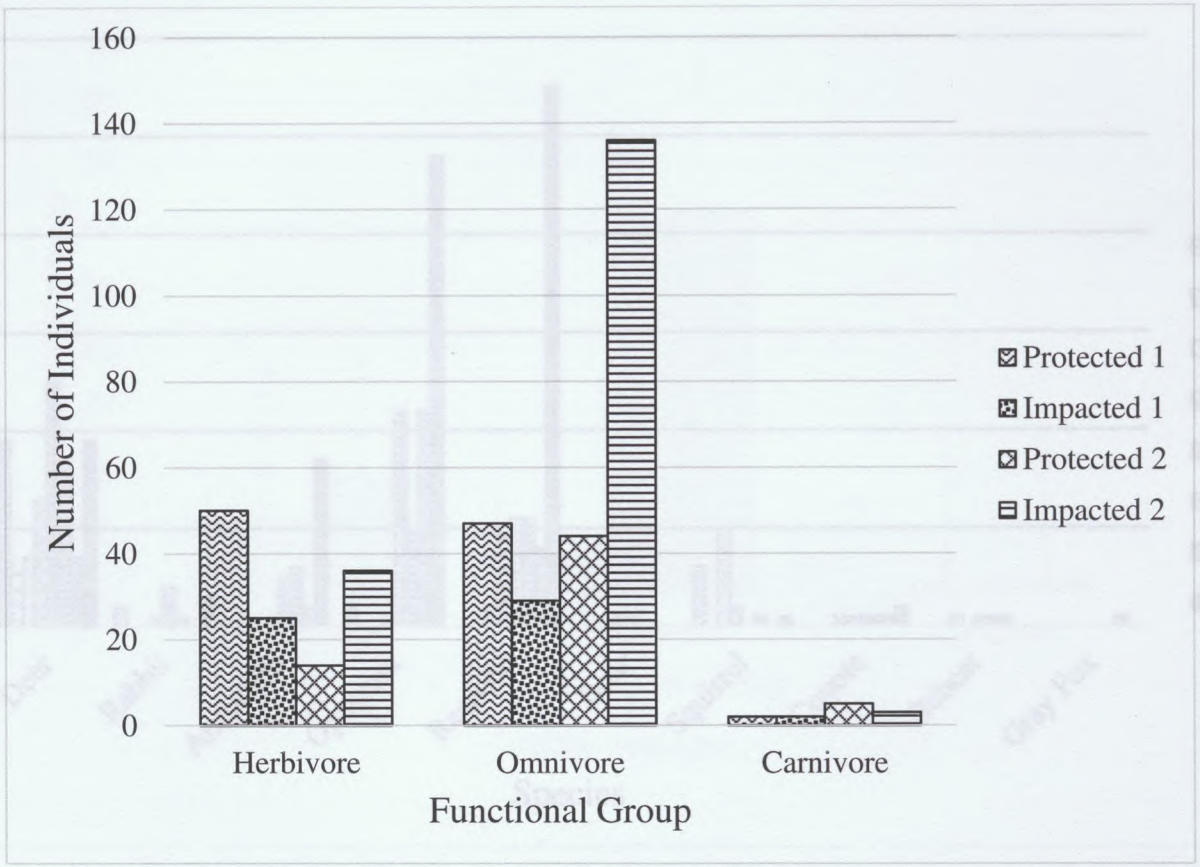

Figure 6 Total number of herbivores, omnivores, and carnivores photo-trapped during the study among all four sites.

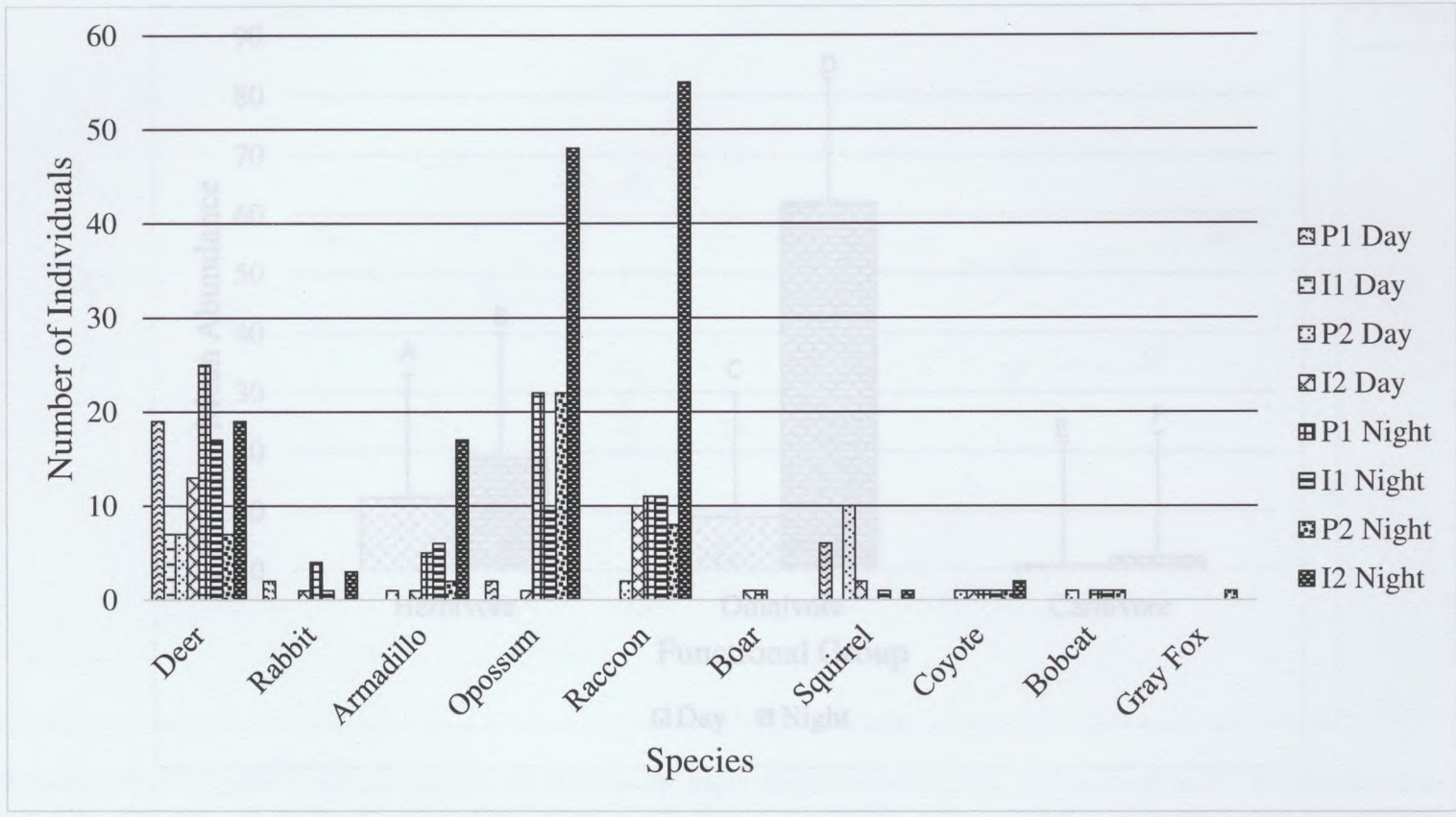

Figure 7 Total number of individuals photo-trapped at each of the four sites, Protected 1 (P1), Impacted 1 (I1), Protected 2 (P2), and Impacted 2 (I2), divided by day and night photo-traps.

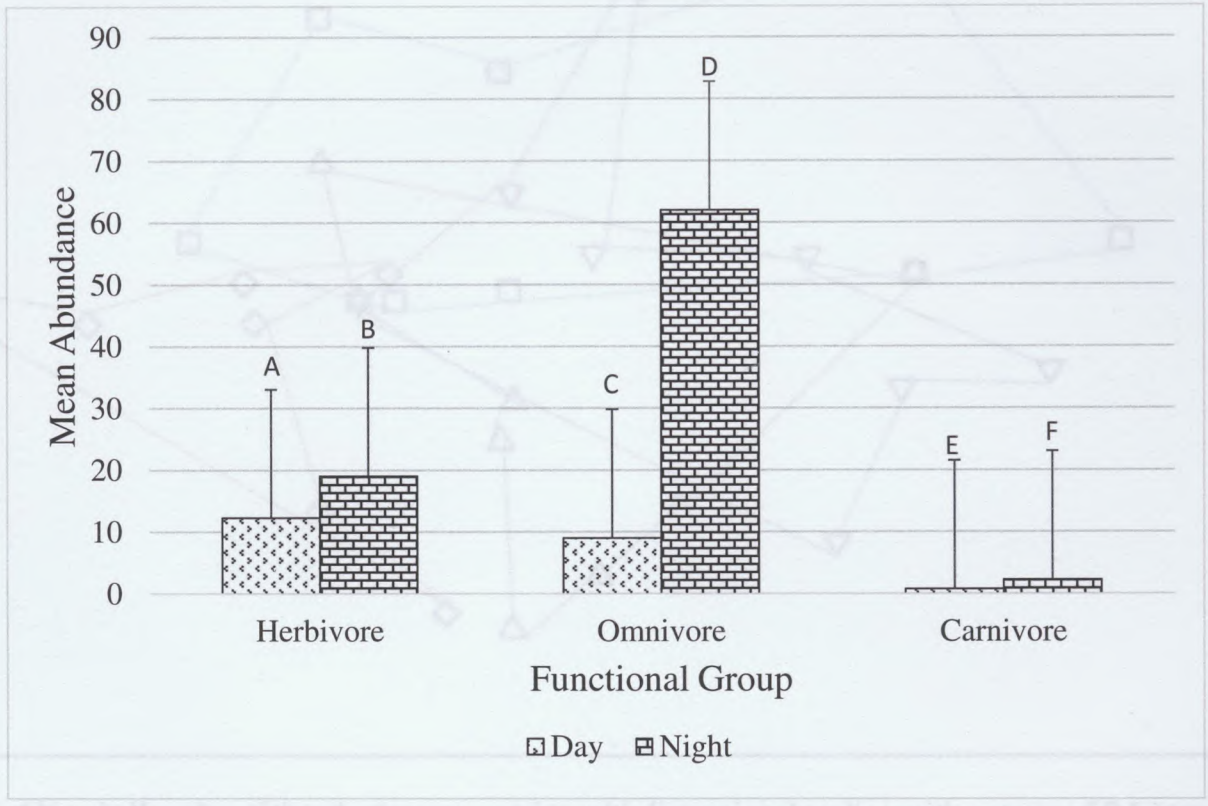

Figure 8 The mean abundance for day and night photo-traps among the three functional groups is displayed with standard deviations (20.798). From the analysis of variance, this data was found to be statistically significant between day and night captures (p=0.05) and between functional groups (p=0.04). The analysis of variance of the interaction between functional groups during day and night captures was found to be statistically not significant (p=0.09).

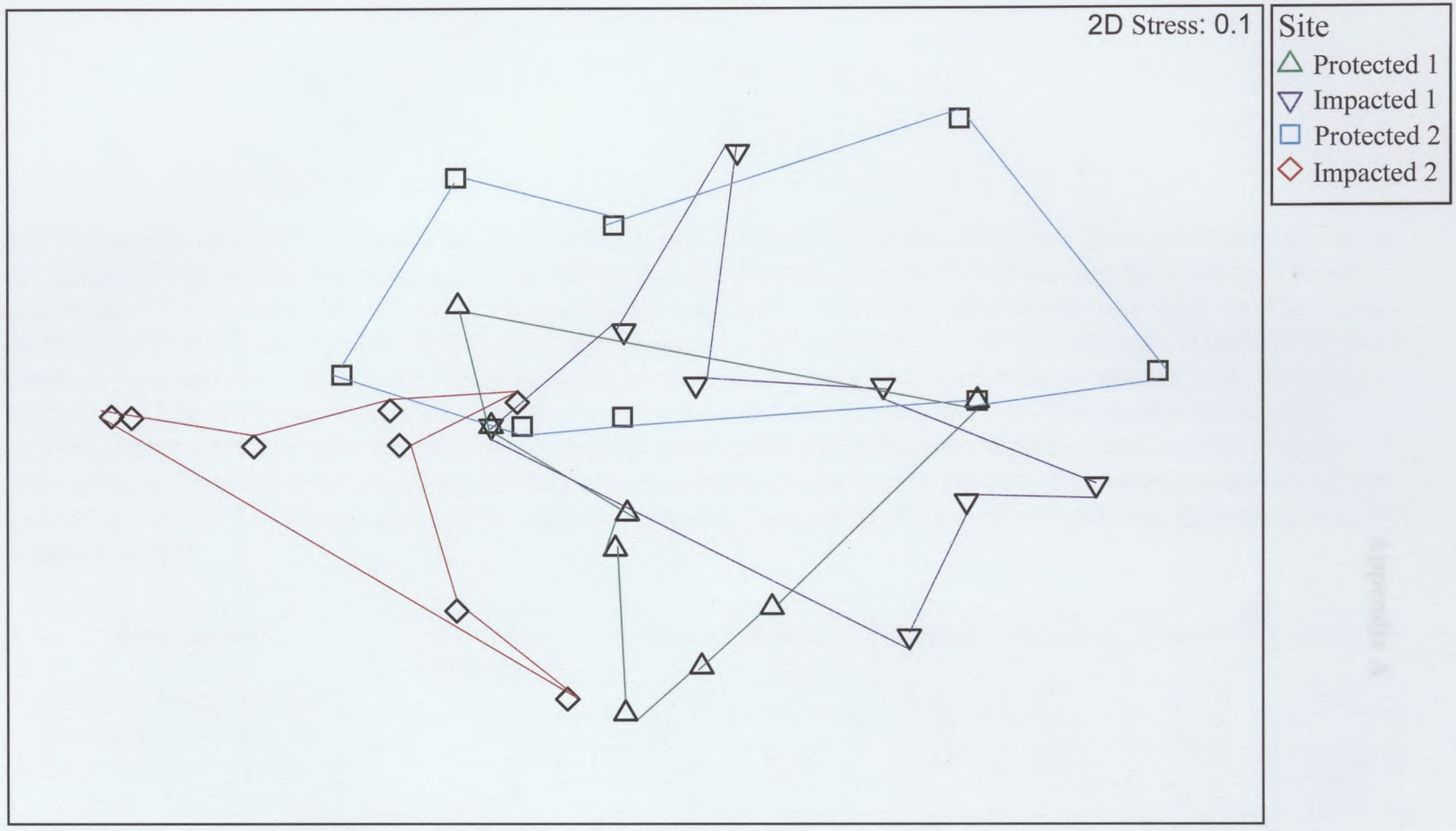

Figure 9 Based off of Kruskal's rules of thumb, the non-metric multi-dimensional scaling with a stress of 0.1 is considered to be a fair ordination. For each site, all eight replicates of the study are displayed. From this, it is possible to view the level of similarity between sites based off of the proximity of the replicates. For Protected 1, most replicates are located near the bottom center of the figure; however, its paired site, Impacted 1, has most of its replicates located on the right side of the figure. The replicates for Protected 2 are located mostly in the upper half of the figure towards the left side, while the paired site, Impacted 2, has replicates in the middle and bottom left side.

Appendix A

Table 5 The average dissimilarity between sites in which each pair of sites is broken down into the major contributing species for their dissimilarity. The percent that each species contributed is listed. The sites with the highest average dissimilarity is found between Protected 2 and Impacted 2 (68.43%). The species that contributed most to their dissimilarity was raccoons. The second largest dissimilarity was found between the two urban sites, Impacted 1 and Impacted 2 (67.81%). The major contributing species between these two sites was also raccoons. The third largest average dissimilarity was found between the rural sites, Protected 1 and Protected 2. Of their 61.09% dissimilarity, the highest contributor was the Virginia opossum. The average dissimilarity between Impacted 1 and Protected 2 was 60.06%. The highest contributing species between these two sites was the Virginia opossum. Between Protected 1 and Impacted 2, the highest contributing species was the raccoon. These two sites had an average dissimilarity of 59.89%. The average dissimilarity between Protected 1 and Impacted 1 was 56.61%. Of this, the highest contributor was white-tailed deer.

Site Number	Average Dissimilarity	Deer	Rabbit	Opossum	Raccoon	Armadillo	Squirrel
Protected 2 and Impacted 2	68.43	16.42		24.60	35.07	10.04	6.39
Impacted 1 and Impacted 2	67.81	16.20		27.50	35.25	12.27	
Protected 1 and Protected 2	61.09	32.99	5.64	26.04	10.58	5.56	12.24
Impacted 1 and Protected 2	60.06	21.10		26.86	19.27	9.26	10.93
Protected 1 and Impacted 2	59.89	21.92	4.19	23.41	33.10	9.74	
Protected 1 and Impacted 1	56.61	29.63	6.36	26.30	15.08	10.35	7.22

Table 6 The average dissimilarity between sites in which each pair of sites is broken down into the major contributing functional group for their dissimilarity. The percent that each functional group contributed is listed. The largest average dissimilarity was found between both urban sites, Impacted 1 and Impacted 2 (61.84%). The second largest average dissimilarity was found between Protected 2 and Impacted 2 (57.50%). The third largest average dissimilarity was found between the two rural sites, Protected 1 and Protected 2 (50.71%). Between Protected 1 and Impacted 2, there was an average dissimilarity of 49.82%. Impacted 1 and Protected 2 had an average dissimilarity of 48.58%. Protected 1 and Impacted 1, had an average dissimilarity of 44.04%. Among all site comparisons, omnivores were found to have contributed the most to the average dissimilarity, while carnivores contributed no value throughout.

Site Number	Average Dissimilarity	Herbivore	Omnivore	Carnivore
Impacted 1 and Impacted 2	61.84	20.82	76.03	
Protected 2 and Impacted 2	57.50	22.39	72.87	
Protected 1 and Protected 2	50.71	45.74	47.73	
Protected 1 and Impacted 2	49.82	30.82	65.93	
Impacted 1 and Protected 2	48.58	27.86	62.94	
Protected 1 and Impacted 1	44.04	43.81	51.73	

Appendix B

Figure 10 Deer photographed on August 1st at Impacted 2 during phase 1, plot 4.

Figure 11 Rabbit photographed on September 24th at Protected 1 during phase 1, plot 1.

Figure 12 Armadillo photographed on August 13th at Impacted 2 during phase 2, plot 2.

Figure 13 Opossum photographed on August 4th at Impacted 2 during phase 1, plot 3.

Figure 14 Raccoon photographed on November 4th at Impacted 2 during phase 2, plot 4.

Figure 15 Boar photographed on September 17th at Protected 1 during phase 1, plot 3.

Figure 16 Eastern gray squirrel photographed on November 4th at Protected 2 during phase 2, plot 1.

Figure 17 Coyote photographed on October 7th at Impacted 2 during phase 1, plot 2.

Figure 18 Bobcat photographed on November 21st at Protected 2 during phase 2, plot 4.

Figure 19 Grey Fox photographed on November 23rd at Protected 2 during phase 2, plot 4.

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