Urbanites Meet Urban Ants:

Ant Species Distributions across the Urban Matrix in Ann Arbor, Michigan

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Abstract

Urban Ecology is an increasingly important field as we look to preserve biodiversity and ecosystem services in urban spaces. In this thesis, I review the literature on diversity, abundance and species composition of ants in urban areas and through ant surveys examine questions of ant species richness and composition in the urban landscape.

This study examines the effects of various urban matrix features at the habitat, local, and landscape levels on ant species richness and community composition. I surveyed ant richness at both the landscape and local scales by baiting and searching at twenty-seven equidistant sites within Ann Arbor city limits (landscape scale), and thirty sites within six city blocks northeast of Ann Arbor's urban core (local scale). Ant species richness and ant species community composition were compared to landscape features (site proximity to rivers, parks, or urban core), local features (site proportion of vegetation, streets, or buildings) and habitat features (observed substrate or street direction). Local and landscape features were identified with various tools in ARC Geographic Information Systems Desktop and habitat feature were identified on site.

A positive relationship was found between canopy cover and ant species richness. The composition of ant species within a sample site was more highly related to local habitat factors (such as bark or trash) than overall site composition, or proximity to urban or natural features. Furthermore, at the local scale species richness was associated with the nearest street city block. Our data suggest that small local changes in the habitat and block scale in urban landscapes are likely to alter ant species community composition. Specifically, changes in vegetation may increase species richness of ants and mediate the interaction between arboreal species and tramp species in the urban environments.

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Introduction

Wherever humans are in the world, they are impacting and exchanging resources in their local ecosystems. More than half of all human beings currently live in cities therefore it is essential to understand the impact and relationship of people to urban ecosystems (Seto, Güneralp, and Hutyra 2012). The pursuit of urban ecology is not only helpful as a way to better understand the impact of cities on global biodiversity loss (Pyle et al. 1981; Niemelä 1999; McIntyre 2000; Marzluff 2001; McKinney 2002; Miller and Hobbs 2002; Clark et al. 2007) but also practical for enhancing our decision making abilities, as land managers in urban areas. A system managed by humans, from individual citizens to urban planner, has the potential to impact habitat for other species in their parks, lawns, streets, and buildings, among others, and to influence the quality of life for themselves and their non-human neighbors.

Streets compose 30-50% of urban areas while parks in places like Manhattan occupy less than 5%. Places like Central Park are important green areas but, they are a small portion of the urban matrix area and small part of the urban planning agenda. In terms of total land areas in the city the areas of influence and management are often in public spaces such as sidewalks, right of ways, or medians. While city parks and natural areas are also a part of those city plans they are not a priority and often their own department such as Parks and Rec. In Ann Arbor, which has 297 miles of streets within the city, $30,826,852 is budgeted in 2017 for city street expenses (Major Street, Local Street, Street Repair, and Storm water maintenance), see Figure 1. This amount is much smaller than all park and open space related expenses combined, $6,918,724 (Bogan et al. 2017). Streets and the right of ways areas are entrenched across many city planning and maintenance departments. Complete streets are a design goal for urban planners worldwide that provides a framework for the ideal “win win” situation for city streets (Seskin, Stefanie (Smart Growth America); Kite, Hanna (Smart Growth America); Searfoss 2015). Complete street initiatives plan design streets that accommodate the many uses of streets from bike lanes to planter boxes. Urban planners oversee cities with a range of characteristics but 50% street area is considered a goal from a planning perspective as it stimulates desirable processes like, traffic flow, public transport, density, and prosperity (Mboup et al. 2013). As the main network for cities streets play a vital role in urban design. This provides opportunities described by cities such as Milwaukee who budget for street trees in every dollar of road improvement projects. The $0.02 for trees per $1.00 of improvements seems small but is powerful because of its connection to the many other essential urban features on that dollar, like water mains, drains, turf and sewers (Barker et al., n.d.). In the urban matrix the widely dispersed patches across the urban landscape, have

the potential to be “more complete” in their usefulness to species who may provide ecosystem services (such as ants). Seeing streets as avenues for species conservation and maintenance of species-mediated ecological functions is an expanded ecological view of “Complete Streets” (Seskin, Stefanie (Smart Growth America); Kite, Hanna (Smart Growth America); Searfoss 2015). I propose that for these city features, such as streets to be "complete" they will also need to be managed from an ecological perspective to improve ecological function of the urban system.

This study looks at patterns in ant species diversity and composition in the urban matrix using a review and field experiments focused on the street and right of way. A review of past studies looking at ant diversity in urban areas identified potential features in the urban matrix contributing to ant species distribution. Following the review, ant field studies conducted in Ann Arbor, Michigan are used to examine the factors that affect ant richness and composition at local and landscape scales. The field experiment covered all of the city of Ann Arbor.

All of Ann Arbor has been subjected to human disturbance of some kind in the form of logging, fires, agriculture, fragmentation, dam construction, invasive species and urbanization. This progression of land use towards urbanization is not unlike the history of many other urban areas. This study takes a snapshot that captures a time point in the trajectory of the development of an urban area. Each wave of human influence has brought a shift in land management to the area. Anthropogenic land use and management in the area began with the Ojibwa, Ottawa and Potawatomi Native Americans. Agriculture and logging expanded within Michigan generally in the 1600s and 1700s. However, Ann Arbor did not see significant colonization until a large number of migrants moved to Michigan in the early 1800s including Ann Arbor's founder, John Allen and Elisha Rumsey. The area was altered significantly again during World War II, with an influx in industrial infrastructure for the construction of B-24 Bombers causing a quick rise in urbanization, population, and industrial zones. Concurrently, logging and agriculture have been decreasing with increased urbanization in the area, but agriculture is still a major land use in Washtenaw County. That historical trajectory in urban development affects the biodiversity that is found in the city. What we observe today, and therefore, what is reported in this study, is not only a reflection of the current features of the urbanized landscape but also its history of land use and other anthropogenic processes characteristic of urban areas (Bogan et al. 2017; Natural Area Preservation Division 2002; Library 2015).

Figures

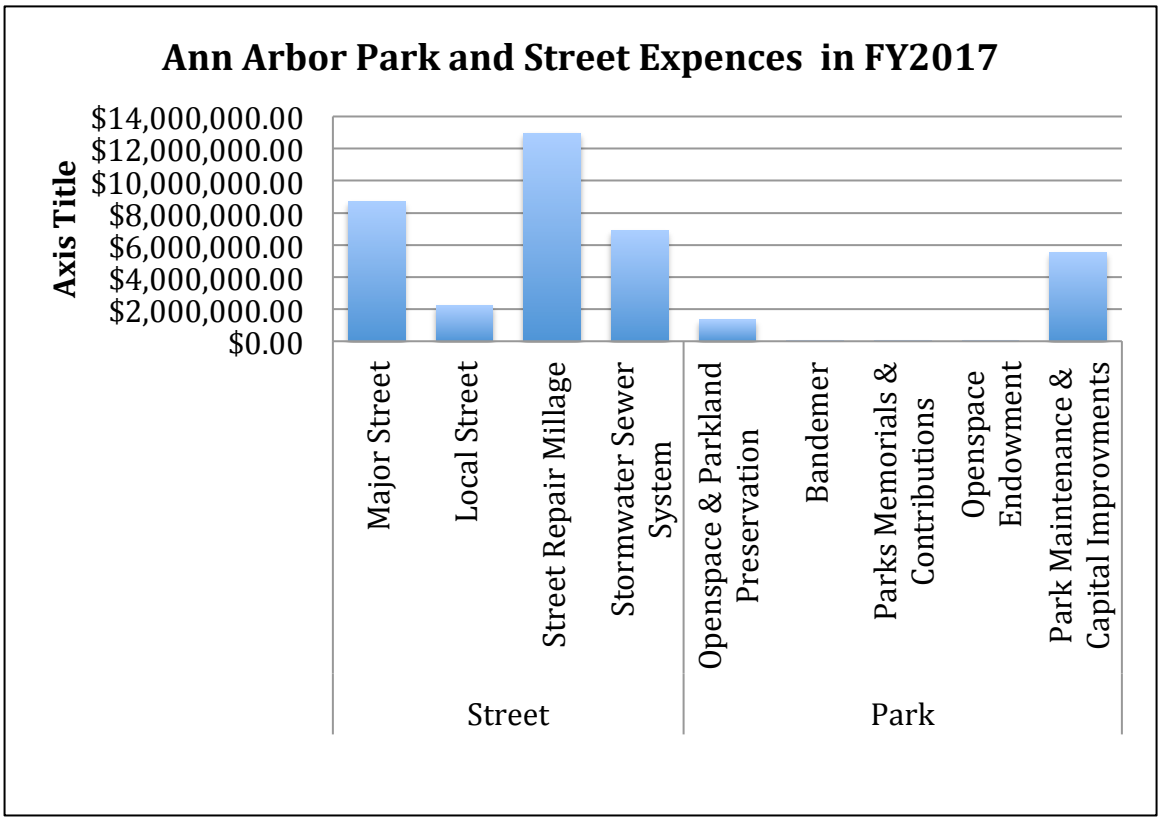


Figure 1: Ann Arbor park and street expenditures (Reported budget for fiscal year 2017).

Chapter I: Ecology of ants in urban landscapes, a review of urban ants

Abstract:

Urban landscapes are heterogeneous dynamic systems that have been explored with increasing interest and focus on biodiversity and conservation. This is a review of studies accessing ants in urban areas across the world so we can get an idea of what patterns are currently common, and what gaps are present in ant urban ecology. We looked at studies that accessed components of urbanization and the relationship of urbanization to ant species diversity, community composition, or ecosystem services. Just over half the studies found a decline in species richness with urbanization the remaining studies showed a range of patterns including a change in species composition and ecosystem function with urbanization. The primary conclusion was that ant species communities are responding variably to urbanization and incomplete sampling along the urban to rural gradient limits generalization. We suggest here potential themes and interpretations of current trends in ant species richness, community composition, and ant species role in urban ecosystem functions.

Introduction: What is an Urban Ant?

Urban studies across the globe have used a variety of methodologies to assess the impact of urbanity. McKinney in 2002 proposed a standardized urban-rural gradient that served the basis for reviews of urban species richness in 2008 and 2012 (McKinney 2008; McKinney 2006). However, the many studies with alternative gradients are useful in the characterization of the urban landscape beyond measures of impervious surface. (See tables 1 and 2). Alternative measures of urbanization are useful because of the amount of impervious surface -a key component of McKinney's gradient- is not always the mechanism for urban disturbance and rarely the mechanism for improved ecosystem function. In the fields of urban planning and landscape architecture, the use of static impervious surface percent cover thresholds leads to feedbacks that encourage urban sprawl as opposed to supporting integrative approaches that address the function of the entire urban matrix.

Urban areas comprise only 3% of the earth's surface but hold 54% of the human population; these altered landscapes created by the dense colonization of humans generate a unique ecological region (GRUMP 2011, World Bank 2015). Urban development is one of the leading causes of habitat loss producing high rates of local species extinctions and

reductions in native species (Czech, B., Krausman, P. R., and Devers 2000; McKinney 2008; Marzluff and Ewing 2008). Many of the native species are replaced by "weedy" non-native species constituting a process of biotic homogenization, which becomes more evident at the core of urban areas (Blair and Launer 1997; Kowarik 2008). Despite the evidence that urban areas are more similar to each other than to their surrounding rural landscapes (McKinney 2002; Pyšek et al. 2004; Pickett et al. 2008) within urban areas, the landscape is highly heterogeneous mainly due to fragmentation (Grimm et al. 2015; Cadenasso, Pickett, and Schwarz 2007; Irwin and Bockstael 2007) . As such, many distinct and small habitat patches exist within the urban matrix providing opportunities for biodiversity conservation.

As the world population becomes more urban and transforms the surrounding landscapes, it is essential for biodiversity conservation that we understand how this transformation impacts the abundance and distribution of species. Beta diversity is high, and species richness trends differ among plants, mammals, avian species, and invertebrates across this matrix (McKinney 2006; McKinney 2008). Furthermore, we must understand the potential consequences and opportunities in the changing urban landscape. The exploration of the urban ecosystem is an essential piece of successful transdisciplinary partnerships in urban managed systems. As ecologists learn to work with urban planners, landscape architects and citizens, our understandings of the urban system will be enhanced, and the potential for urban biodiversity conservation and the ecosystem functions it provides will be improved. In this review, we examine the diversity, abundance, and community composition of ants in urban areas, as well as the possible ecosystem services provided by ants in these areas.

Ants are a dominant taxon of terrestrial ecosystems, making up two-thirds of the biomass of all insects and contributing to a variety of ecosystem and cultural services. Ants are also a ubiquitous component of the arthropod fauna of almost all cities and play important roles (both positive and negative) in the ecology of cities (Youngsteadt et al. 2015). Over the last two decades, some studies have examined ants in the urban landscape with published studies doubling from 2008 to 2015. The number of publications showed steep growth after 2003 (Santos 2016).

The objective of this review is to explore both variation and consistencies in the existing urban ant literature in regards to biodiversity and ecosystem functions. A synthesis of the literature on the subject of ants in the urban landscape will help us better understand: (1) how ant assemblages are affected by urban development, and (2) how ants contribute to the functioning of urban ecosystems. Additionally, (3) an exploration of the variety of methods, experimental designs, and results will lead to a better framework for

the interpretation of the literature and future research innovations.

In the urban landscape, the prevalence of ants and the potential for impact on ecosystem services and disservices given the impact of better known terrestrial systems suggests that ants in urban areas are in need of further investigation. Hospital managers and builders across cities are already aware of the potential negative impacts and the risks posed by some ant species as disease vectors and pests. However, the ecology of the greater ant community in urban landscapes needs to be understood to assess better both the positive and negative impacts of the many different ant species that inhabit urban areas. Ants do have the potential to provide a variety of services beneficial to people, their gardens, and other organisms in urban systems.

Only two other reviews have examined the topic of ants in the urban landscape (Campos-Farinha et al., 2002; Santos, 2016) . Campos-Farinhas and colleagues (2002) wrote a retrospect on urban ants in Brazil with a focus on ants as pest species in the built environment almost 15 years ago. More recently, Santos (2016) published a comprehensive review that consisted of a quantification and classification of the published studies on urban ants worldwide. According to Santos (2016), only 3.6% of all publications on ants are related to ants in the urban environment. Furthermore, most of these studies were published after the early 1990s and come primarily from 4 countries: The United States, Brazil, Japan and Australia. Most of the studies of ants in cities are related to their role as pests in the human built environment, especially within houses, hospitals, and other buildings. Santos focused on the questions of how many and what topics have been published since 1945. According to this review, 37.96% of the studies were under the category "Ecology and Biodiversity," 85% of which focused on diversity (Santos 2016). With the growth of urban ecology in the last few decades, many studies have examined ant assemblages in specific habitats within urban areas outside buildings, such as parks, urban forests, gardens, yards, street median, etc. In this review, we synthesize the literature on the ecology and biodiversity of ants in urban areas with the goal to better understand how the various features of the urban landscape impact ant species richness and distribution and the ecosystem functions that they perform within urban areas.

This review was conducted by searching the Web of Science database on July 2, 2015, using search term "urban* ant". The search yielded 513 entries. Based on title and abstract we eliminated entries of papers about control of ants in urban structures (houses and hospitals) and entries of urban transit models based on ant colony efficiencies. That left 193 entries published from 1975 to 2015. Sixty-one of those entries were related to topics that were marginally related to the theme of the review (such as physiology of particular species, taxonomic revisions, molecular studies) and were subsequently deleted

from the data set leaving a total of 132 articles for the review. In August 2016, another search was conducted using the same term ("urban* ant") and 12 additional papers were added. The resulting 144 articles were complemented with articles cited in other papers that were not found through the Web of Science search. In total 215 papers were reviewed for this study.

Section 1: Ant Diversity and Composition in Urban Landscapes

In the context of widespread urbanization, an essential query for ecologists is the presence, function, and shifts in biodiversity of the various taxon. In the case of ants in urban areas, biodiversity has been explored by measuring responses of ants regarding richness and community composition. However, very few studies have investigated the potential causes and mechanisms contributing to the extensive variation reported in studies examining ants in urban areas. Most studies examined a variety of "urban" variables to explain or predict the changes in ant richness observed across the urban landscape. This review will focus on teasing apart those variables to explain the variation in richness and composition of ants found across the literature and group them into ecological categories (hereafter referred to as factors) that may be useful in framing future studies. A meta-analysis was not conducted as it can give non-significant results when studies find contradictory patterns, defusing the potential mechanisms that generate those patterns.

Assessing ant species richness is an essential first step in determining how ant assemblages may be changing with changes in the ecosystem (Buczkowski and Richmond 2012). It is therefore not surprising that richness has been the primary focus of urban ant studies thus far. Just over half of the studies we reviewed report a decline in ant species richness with urbanization (Table 2). The magnitude of the decline in species richness is not discernable given the methodological variation of the studies a range of study geography's. It is important to point out that an intermediate peak in richness along the urbanization gradient has also been reported (Sanford, Manley, and Murphy 2009), as well as no changes in richness along the urbanization gradient (Guénard, Cardinal-De Casas, and Dunn 2014) and others see Table 2. Of the variables measured in each study, some common factors have arisen as significantly contributing to species richness. Common factors were proximity to the urban core, size and shape of patch area, and the presence of forest fragments. Each of these factors has the potential to partially explain changes in species richness of ants in urban areas, Table 3.

Proximity to urban core includes variables such as, distance to urban core(MacGregor-Fors et al. 2015; Antonova and Penev 2006), distance to city outskirts (Vonshak and Gordon 2015; Carpintero and Reyes-López 2014; Lopez-Moreno, Diaz-

Betancourt, and Landa 2003), or distance to buildings (Vonshak and Gordon 2015; Edwards 2014), see Table 3 and Table 2. This factor, proximity to urban core, does not include distance to parks or vegetation within the city. The variables that we included in this factor assume there is a biological mechanism, loss of habitat, driving change in ant richness with respect to proximity to urban areas. While this is the most ambiguous of all the factors it is also the most common measurement of the urban to rural gradient described previously. Urban rural proximity may be biologically relevant when considering metapopulation and source-sink dynamics. For example, in regions where the city exterior or rural areas, represent sources of ant species, high distance to city center may limit queen dispersal from rural source populations to urban sinks (Carpintero and Reyes-López 2014).

Proximity to urban core has been shown to impact ant species richness, where richness was measured along a gradient from the urban core to the edge of the Atlantic forest in Brazil (Souza-Campana et al. 2012). While the results show a significant relationship between proximity to urban core and ant species richness the mechanisms for this variation may not be limited to source population dispersal, as discussed above. The measure of proximity to urban core is more likely a measure of other landscape characteristics associated with urbanization. It is not surprising that as distance increases from an urban core across the heterogeneous urban landscape a greater diversity of species is encountered since a greater variety of habitats will be present as we move away from the urban core. While proximity to urban core may be an important factor in predicting ant richness, it is not yet clear how distances between patches within and outside the urban matrix may play a role in the population ecology of those species.

Size and shape of patches vary greatly throughout the urban matrix. As McKinney has pointed out for all urban areas (McKinney 2008), it is likely that the species-area relationships are guiding richness trends as patches of habitat tend to be much smaller near urban cores. Ant richness has been significantly predicted by urban park size (Carpintero and Reyes-López 2014) but not urban garden size (Heterick, Lythe, and Smithyman 2013). Larger parks had higher diversity than smaller parks, as would be expected. It is not clear yet how species-area relationships may be guiding urban ant ecology but there is evidence to suggest that it should be investigated further as it is likely to contribute to the shifts in ant communities and has potential for informing urban planning policy. Shape has also been found to be is a significant predictor of species richness and diversity (Carpintero and Reyes-López 2014). Although no general patterns in the literature could be discerned at present, due to the rarity of shape reporting, there are some urban planning and urban greening practices that are likely to dictate habitat shape and therefore edge effects. Patches may need to fit within city blocks, or grid shaped roads, creating long linear patches, such as roadside trees or right of ways.

Presence of forest fragments, unsurprisingly, is an important factor in modeling both ant species richness and community composition. Forest and tree presence provide specialized habitat for a variety of arboreal ant species. It is not yet clear how individual trees may contribute to species richness differently from forest fragments. In one study, however, green areas bordering streets were found to be the least diverse, and the parks and wooded areas the most diverse (Slipinski, Zmihorski, and Czechowski 2012)This increase in diversity with vegetative density follows the expected trends of the urban-rural gradient. Native shrub vegetation regrowth along highways in Australia increases the provision of refuge to native ant species compared to neighboring gardens or lawns (Heterick, Lythe, and Smithyman 2013). The local of the highway vegetation and consequent increase in native species leads to a higher richness of ants in the suburbs. The function of wooded areas as a population source for less common woody, native species is not clear although many suggest the forest fragment measurements are predictive of ant species richness because they provide foraging habitat (Slipinski, Zmihorski, and Czechowski 2012; Souza-Campana et al. 2012).

Much of the decline in species richness is attributed to invasion of non-native species, replacing native species. Given the current homogenization of urban landscapes and ecological patterns of biodiversity loss due to invasion (Vonshak and Gordon 2015). The before and after residential construction shows old land without construction has high diversity, which plummets during construction, and then slowly rises in the years after construction but does not recover to previous richness (Buczkowski and Richmond 2012). While invasion of non-natives is present some native species show resistance to urbanization.

Resistance to urbanization includes studies that found both invasive and native species present over time, maintaining overall richness. In a 40 year comparison it was confirmed that exotic species increased around the North Carolina State University campus however native species were not reduced and total richness had increased. (Guénard, Cardinal-De Casas, and Dunn 2014) There may not be a direct relationship between the establishment of exotics and persistence of native species. This may be due to different conditions needed in the life history of these species. In some cases but not all, native species are able to persist in the natural areas and invasive species are able to establish in areas with more disturbance (Vonshak and Gordon 2015). Menke described persistence of forest specialist species across the urbanization gradient. In Menke's experiments in Raleigh, North Carolina species richness did not differ across the urbanization gradient but assemblage did differ. Furthermore Menke did not find higher species richness in urban forests than in rural forests, Figure 2. Menke show the changes in impervious surface and vegetation over the urban to rural gradient but this is not found to be related to the changes in

richness but instead to changes in community composition. “MRPP results confirmed that ant communities differed between habitats (T=−15.583, A=0.117, p<10−8). Pair-wise comparisons revealed that forest sites were the only sites to be distinct from all other land-use environment” (Menke 2010).. The impact of invasive ants on local ant species richness and community composition have generally been assumed to be negative however the results are inconsistent. It is not clear how metapopulations of ant communities function across the highly fragmented urban landscape however there is evidence that some sensitive native species are able to persist.

While urbanization, proximity to urban core, reduced habitat area, and forest fragment reductions are common descriptors of a decline in species richness across the urban to rural gradient inconsistencies in these patterns have lead to several alternative hypotheses: 1) a **peak at intermediate levels,** and 2) **nested species composition.** *Furthermore,* species composition shifts due to the **presence of invasive species** may explain, in some cases, why and how richness is changing (See Table 4). Invasive species and their impact of native and existing ant communities in urban areas make up a large portion of all urban ant studies. Studies focused on invasive exotic species made up 23.15% of all urban ant studies reviewed by Santos.

One such study showing a *peak of ant species richness at intermediate level of urbanity* investigated the important role of geographic scale. The study in Lake Tahoe California found that at the scale of 300meter and 500 meter radius 3-14% of the increase in richness was explained at 30-40% of intermediate urban development (Sanford, Manley, and Murphy 2009). While these results are significant and indicate the intermediate disturbance as a factor in urban ant diversity, it may be more important to notice the scale at which a pattern was seen, 300-500m. The same quadratic, peak, pattern was found between abundance and development at 300m scale despite all other significant abundance development trends at other scales being negatively correlated. We know scale and size are related to richness and amount of microhabitat availability, especially in urban settings. In examining the distribution of ants by functional groups the same pattern was not found at 300m (Sanford, Manley, and Murphy 2009). The results of this study suggest that while few studies have found a peak at intermediate richness, see Table 2, Table 2. Studies that addressed the impact of urbanization of species richness using some form of urbanization gradient. Urbanity was characterized in a variety of ways (Urbanity Experiments column) both positive, negative and intermediate responses were found.both positive, negative and intermediate responses were found. This may be a result of the scale of studies and not a reflection of the actual patterns. In addition to scale influencing the presence of these patterns species of community type also has played a role.

Specific functional groups within ant communities have shown an increase or

decrease at intermediate urban development levels. Sanford et al. found aerators and generalist exhibited quadratic proportional abundance while decomposers and compilers exhibited linear changes in proportional abundance across the urban gradient (Sanford, Manley, and Murphy 2009), Similarly McKinney's results in a review of all plant and animal taxa in urban areas, suggests that some taxa, plants mainly, peak at intermediate urban levels(McKinney 2008). However, this trend is likely to be more related to human management than intermediate levels of disturbance. For example, intermediate urban development areas like suburban lawns provide very different floral resources than natural parks or apartment patios. Generally McKinney found higher species richness at lowly-urbanized areas, and higher abundances at highly-urbanized areas. The dominance of certain, mostly invasive, species in particular urban habitats is a common phenomena that alters overall community composition, and at some scales this abundance seems to peak at intermediate levels. However, a peak in species abundance has also been attributed to local availability of food trash (Reyes-Lopez and Carpintero 2014). Peaks at intermediate levels explain a small amount of the community composition shifts (Passera, 1994; Holway et al., 2002; Ditchkoff et al., 2006; Shochat & Ovadia, 2011).

Nestedness of species was found at moderate levels in Manhattan (Savage et al. 2015). The nested concept assumes non-random distribution (Slipinski, Zmihorski, and Czechowski 2012). The expected pattern for nesting is that ant assemblages in more natural spaces will include native expected species as well as a few new species from more transformed areas and the transformed areas will have a subset of that assemblage. A similar approach was taken using zoological categories and found that a portion of the regional range of expected species was found in urban and semi-urban areas with the urban community having a higher frequency of generalist species than the surrounding region (Antonova and Penev 2006).These studies, while they do not test nestedness directly, suggest that ant community composition shifts could be used as indicators of urban pressure.

While larger theories like the intermediate disturbance hypothesis may not explain all changes in species composition, factors affecting ant composition in urban environments, like **environmental** stress, foraging quality (**forests**) and habitat age (**successional stage**), are similar to recognized patterns affecting richness in natural areas. When ant composition was compared to existing predictions of protected sites the results were congruent with the expected composition change(Savage et al. 2015; MacGregor-Fors et al. 2015). Savage et al. predicted an inverse relationship between chronic environmental stress and species diversity within the urban landscape based on Menge & Olson and Fitgerald et al's summary of these patterns in natural areas (Savage et al. 2015; Bruce A Menge, Olson, and Dahlhoff 2002; B A Menge and Olson 1990; Fitzgerald et al. 2011).

Savage et al found a similar pattern in ant diversity across Manhattan's medians, parks, and forests. However, the results deviated slightly in the expected pattern of more exotics in more stress prone urban areas. Exotic ants were just as likely to occur in low stress and high stress environments, but some native ant species only occurred in lower stress habitats. Savage et al. found that medians, the highest chronic stress habitat measured, exhibited low diversity and minimal exotic species in comparison to lower stress urban parks and urban forests.

The **species-area** relationship in natural systems commonly explains diversity trends. Similarly in the urban landscape, park size and shape have been positively related to increased diversity (Carpintero and Reyes-López 2014). The effect of area itself may prove to be a crucial part of understanding urban heterogeneity and diversity. Composition may be changing in a variety of ways among urban centers and surrounding regions as well as within urban spaces. The proportions of generalists, specialists, zoological guilds, foraging strategies, natives, invasives, or functional groups may be changing. The continuation of the characterization of these community changes can help to describe the types of pressures urban development cause and respectively what species and community characteristics are beneficial to urban ant communities.

The most common explanatory factor of community composition change is **forest fragment** presence measured by individual trees, canopy cover, total area and proximity. While foraging and nesting in urban habitat may include more novel resources like trash and garden beds, foraging and nesting quality still affects ant community composition. Unsurprisingly parks near the forest were found to have more similar species than parks near the urban center(Souza-Campana et al. 2012)Urban green spaces did provide a refuge for rare species in Spain (Carpintero and Reyes-López 2014) but the network of forest fragments did not seem provide a habitat for specialist arboreal ant species in Alto Tiete. It is not clear yet if they are providing a refuge that functions as a gene source for arboreal ants found in urban areas.

Larger **time** scales and study designs that allow for an understanding of the direction and rate of ant species succession give evidence that time is likely to matter. In some studies, long term exposure of communities the invasive Argentine ant significantly reduced diversity. Suggesting that most urban ant studies that presently look at patterns from a single time point may be missing key information (Park, Hosoishi, and Ogata 2014). It is highly likely that species interactions overtime will change urban ant diversity. Park age influenced the composition of the ant fauna but not diversity (Carpintero and Reyes-López 2014). Similarly early generalists feeders were found in habitat under 10 years of age and specialists feeders found more often in older parks (Brown et al. 2013). However,

no significant change was found over 12 years in Japanese urban parks although the first measurement was found well after the initial building of the park (PARK et al. 2014).

The overbearing abundance of generalist invasive ant species leads to the question are **generalist and specialist** functional groups good predictors of ant community composition based on the advantage of opportunistic species in urban areas. In Spain, native opportunistic, generalist, and anthropophilic species were the dominant species in urban green areas (Reyes-Lopez and Carpintero 2014). Complementary results were found in urban parks near Atlantic forests, more forest specialists were found in those parks (Souza-Campana et al. 2012). In Tahoe, variation in the responses to variables among specialist and generalists made them ineffective community composition indicators alone (Sanford, Manley, and Murphy 2009). Generalist and specialist or invasive and native functional groups are useful in characterizing the urban ecosystem but are too coarse for predicting changes in ant community composition.

In assessing urban ant biodiversity, it is clear that dissecting the causes of community composition changes is needed. Several major questions remain. 1) Do these urban systems follow biodiversity patterns of existing ecosystems? 2) Who and what functional groups are driving community composition changes? 3) Which habitat characteristics are limiting factors for species richness?

Section 2: Ants on Urban Ecosystems

In a recent review on *ant mediated ecosystem services*, Del Toro (2012) showed that ants play a major role in all four categories of ecosystem services: provisioning, regulating, supporting and cultural (MEA, 2005). Since ant diversity and composition changes with urbanization, those changes can have important implications for the ecosystem services that ants provide in urban environment. Few studies have examined the ecosystem services provided by ants in urban landscapes, see Table 4, for the list of studies used for this review.

In one of the first studies of ecosystem services by ants in urban landscapes, Thompson and McLachlan (2007) documented the role of ants in seed dispersal of the myrmecochourus plant, *Viola pubescens,* in urban forest in Manitoba, Canada. Although ant species richness was lower in urban forests than in rural forests, the removal rate of seeds of *V. pubescens* was higher in the urban forests. The authors attributed the increase removal rate in urban forests to changes in the species composition of the ant community. The ant species that remain in urban forests tended to be the most competitively dominant species. Furthermore, members of the *Formica fusca* group, which tend to be among the

most effective foragers of the forest-dwelling ants in the region and remain within urban forests, exhibit competitive release when interference at food resources from superior competitors is removed (Sovalainen and Vepsäläinen 1988). Other studies have shown that invasive species can disrupt myrmecochory by displacing the ant species involved in a very tight myrmecochory interaction (Zettler et al., 2001; Carney et al., 2003). Myrmecochory is a geographically widespread phenomenon exhibited by at least 11,000 plant species (Lengyel et al., 2010). It has been estimated that in some temperate woodlands ants disperse up to 40% and the herbaceous plants, making myrmecochory an important ecological process for the maintenance of plant diversity in these ecosystems (Beattie, 1985). The role of myrmecochory in urban forests can be particularly critical for the spring flora and could be threatened by changes in ant species composition and, in particular, invasive species.

The role of ants in soil processes has received considerable attention in the literature (see reviews by De Bruyn et al., 1990; Folgarait, 1998; Vandermeer and Perfecto, 2007; Cammeraat and Risch, 2008). Ants have been shown to enhance soil structure and aggregate stability, lower bulk density and increase aeration and water infiltration due to their burrowing activities (Cammeraat and Risch, 2008). Generally, within or close to their nests, there is high concentration of soil nutrients and increased nitrogen and organic matter cycling (Cammeraat and Risch, 2008). However, very little is known about how these ant-mediated soil ecosystem services are affected by urbanization. Sanford and colleagues (2009) documented the changes of three groups of ants that have important soil-related ecosystem functions in forest landscapes as land development and urbanization increases. Aerator species built complex subterranean tunnels that aerate the soil and help with water infiltration as well as energy redistribution. Decomposer ants build tunnels within woody debris facilitating decomposition, and compiler (thatch) ants built mounds with vegetation increasing soil nutrient availability through higher mineralization rates of nitrogen and organic matter. This study, conducted in the Lake Tahoe basin in the border between California and Nevada, concluded that high levels of land development significantly reduce the diversity and abundance of aerators and decomposers, potentially reducing the ecosystem services that these species provide in urbanized landscapes. However, significant drops in species richness of these two groups were detected above 30-40% of land development, suggesting that the ant community can be robust to limited amounts of land development. Furthermore, thatch ants, were positively associated with urban development, although their overall abundance was low compared to all the other groups of ants.

Generalist ants, which tend to increase in abundance in urban environments, tend to be scavengers. Recent studies have demonstrated that urban ants are important in

removing food wasted in highly urbanized environments (Penick et al., 2015; Youngsteadt et al., 2015). The removal of food waste by ants can be an important ecosystem service because it reduces the amount of food available to rats and other arthropods that can be vectors of human diseases. In a study in Manhattan, NY city, it was shown that arthropods, primarily ants, removed on average 59% and 32% of small and large portions respectively of experimentally placed food (pieces of potato chips, cookies and hotdogs) within 24 hours. Surprisingly, street median, in spite of having lower species diversity than parks, had 2-3 time higher removal rates of food. The difference was attributed to the presence of the invasive pavement ant, *Tetramorium bicarinatum,* which occurs in high abundance in highly urbanized environments. Assuming a 5-8 month ant activity period and an average of 9 *Tetramorium* foraging territory on a single 400m^2 median, the authors estimated on the order of 4-6 kg per media per year being removed by arthropods, primarily ants, in Manhattan. Using isotope analysis another study showed that in urban areas *Tetramorium* had a C signature associated with human processed food and that the signal increased with the level or urbanization (Penick et a., 2015). The high scavenging rate in Manhattan median appears to be due almost exclusively to the presence of the 'pavement ant'. Cities without this species may show a very different pattern of scavenging by ants. For example, in a study conducted along a forest to urban gradient in Singapore, the pattern of dead insect removal was found to be the revers; high removal rate in forested sites as compared to urban parks and pavements (Tan and Corlet, 2012). In this study, the highly urbanized sites recorded the lowest rate of dead insect removal by ants, in spite of the fact that these areas had non-native trap-ants such as *Anoplolepis gracilipes*, *Monomorium pharaonis*, *Paratrichina longicornis*, *Pheidole megacephala* and *Tapinoma melanocephalum*. The main difference seems to be that the 'pavement ant' *Tetramorium* was absent from the sites in Singapore.

One of the best-documented ecosystem services provided by ants to humans is the service of natural pest control. This can be an important regulatory ecosystem service because it enables sustainable crop production without the reliance on toxic pesticides. Natural pest control by ants has been well documented in agricultural systems especially in the tropics (Way and Khoo, 1992; Perfecto and Castiñeiras, 1998; Philpott and Armbrecht, 2006) but few studies have examined this ecosystem service in the context of urban landscapes. Natural pest control can be particularly important in urban and periurban agriculture where high human population densities can be in close proximity to crop production sites.

The first documented case of biological control by ants in an urban setting was Pimentel's study of ants controlling fly populations in San Juan, Puerto Rico. After observations of the native fire ant, *Solenopsis geminata,* killing all of the nearly emerged

adults and full grown larvae of *Musca domestica* and blowflies near garbage bins, Pimentel (1955) conducted an experiment with all life stages of *M. domestica* and fund that ants were responsible for killing an average of 91% of the potential fly population between the egg and adult stages. Beside *S. geminata*, other species were observed retrieving larvae but in very low numbers. The only species capable of killing the pupal stage was the small *S. corticalis*, which was observed boring a hole in the wall of the puparia, entering and consuming the pupae inside. Pimentel attributed the low fly incidence in cities and towns in Puerto Rico to the high abundance of *S. geminata*. Twenty years earlier, Phillips had attributed *Pheidole megacephala* with keeping the house fly population to negligible levels in Hawaii (Phillips, 1934).

More recent studies of the biocontrol service of ants in urban landscapes have focuses on examining differences among a variety of urban habitats such as urban parks or forests, vacant lots and urban gardens. A study quantifying predation in artificial caterpillars along an urbanization gradient concluded that ant were responsible for only 4.7% of the attacks in forests, but that percentage increased to 11.3% in suburban and 16.4% in urban forest fragments (Ferrante et al., 2014). In a study comparing below ground predation of the last instar larvae of the lepidopteran *Galleria mellonella* used as a sentinel prey in two post industrial cities in Ohio, ants were reported to be responsible for 60% and 33% insect mortality after 48 h of exposure in vacant lots and urban gardens respectively (Yadav et al., 2012). The same study reported a slightly lower but non-significant difference in mortality of *G. mellonella* in younger (one year; 67% mortality) versus older (5-50 years; 78% mortality) gardens. Due to frequent irrigation, soils in urban gardens were consistently more moist and cooler than in the vacant lots and this may have contributed to lower predation activity by ants in gardens as compare to vacant lots (Kaspari et al., 2000; Yadav et al., 2012). However, a later study conducted in the same two cities and some of the same gardens and vacant lots found not difference in activity density of ants between the two types of habitat (Gardiner et al., 2014).

Through their association with hemipterans and other herbivores ants can protect pest species and/or interfere with biological control by other species. For example, in the Galapagos Islands, an otherwise successful classical biological control program of a scale insect with an introduced coccinellid beetle was found not to be effective in urban areas where pest colonies were heavily tended by invasive ant species (*Camponotus conspicuus zonatus*, *Solenopsis geminata*, and *Monomorium floricola*) (Hoddle et al., 2013). In Yaoundé, Cameroon, maize plants planted next to houses we reported to have a higher incidence of the corn delphacid, *Peregrinus maidis*, a vector of a viral disease, as compared to maize in vacant lots, farther away from houses and, those plants, in turn, had higher incidence of the pest than maize in rural fields. The difference was attributed to the abundance of ants

tending the delphacids. The areas next to the houses were rarely ploughed and had higher densities of ant colonies, while maize plots in vacant lots and fields outside the city were ploughed.

Table 4 presents a summary of the studies on ant-mediated ecosystem services in urban areas. An important conclusion to derive from the few studies that are available at this time is that the potential for ants to provide ecosystem services in urban areas depend of how the ant community is affected by urbanization and the resulting species composition. In some cases, the remaining species are highly effective, like in the case of the pavements ants scavenging on waste food in New York City (Youngstead et al., 2015) and the ants dispersing the myrmecochorous violets in urban parks in Manitoba (Thompson and McLachlan, 2007). However, sometime, the most efficient species decline or are replaced by less efficient species as urbanization proceeds. That is he case of the replacement of aerators and decomposer species by more generalist ant species in the urban forests in the Lake Tahoe basin (Sanford et al., 2009).

Climate change is not only predicted to increase the mean global temperature by 1.7 to 4.8 C by the end of the century (IPCC, 2014) but also the extremes, variability and seasonality. Warmer temperature will tend to influence ant populations directly though effects on survival, fecundity, generation time, and dispersal. Although individual species responses will depend on their geographic ranges and natural history, it is expected than ant populations in mid to high latitudes will benefit the most from a warmer climate. Since urban environments tend to be warmer than their surroundings (heat island effect), ants in cities may be indicators of future changes in the ant community associated with climate change.

Applying generalized linear models to a global data set of local ant assemblages Jenkins and colleagues (2011) found temperature to be the most important single predictor of ant species density, suggesting that climate change could have important consequences for ant species richness and the structure of ant communities. Using predictive models for physiological thermal tolerances in ants based on current and future climates Diamond and colleagues (2012) found that tropical ants will have lower warming tolerances to climate warming, than temperate ants. Refining their model with climatic, ecological and phylogenetic data they found that ants occupying warmer and more mesic forested habitats at lower elevations, in particular those that live in canopies of tropical rainforests, were the most at risk, globally, from climate warming (Diamond et al., 2012).

Very few studies to date have examined the potential effect of climate change on urban ants specifically. In a study in Raleigh, NC, Menke and colleagues (2011) tested if the

city had a higher proportion of ants from warmer/dryer environments than the surrounding areas. They found that native ant assemblages in open environments within the city have more southwestern (i.e., warmer/drier) distributions than forest assemblages outside the city. The subset of species adapted to warmer/dryer environments suggest that urban areas may facilitate the movement and perhaps spread of species adapted to warmer conditions. It is also possible that species with tolerance to climatic extremes may be favor by urban environments. These findings are supported by a study that directly measure high and low temperature tolerance or urban ants as compared to ants from the surrounding cooler habitats. A study, conducted with the leaf cutter ants, *Atta sexdens rubropilosa,* collected from the city of Sao Paulo and its surroundings, found that ants from the city tolerate heat stress better than ants from their surrounding and that this did not come to the expense of tolerance to lower temperatures. (Anguilleta et al., 2007). However, an alternative explanation for the results of Menke and colleagues could be that cities favor soil nesting species rather than cavity nesters (Freidrich and Philpott) or species that nest in rotten wood (Vapselainen et al 2008). Since species form warmer and drier environments tend to be soil nesters, one may expect a higher proportion of those species in the city as compare to the forested surrounding habitats.

A study of the black garden ant, *Lasius niger*, which is a common ant in urban areas in northern and temperate Europe showed lower survival rates of workers at lower overwintering temperatures but no effect of higher or lower overwintering temperatures on queens (Haatanen et al. 2015). This suggests that urban areas could be acting as refuge for this species in higher latitudes and could be contributing to its northward expansion (Vepsalainen et al 2008). Warm urban areas and fluctuating snow cover due to climate change could affect the energetics of ants that overwinter beneath the snow (Leather et al 1993). But the ability of founding queens of *L. niger* to tolerate temperature variation present in urban environments suggest that this species may be one of the winning species in a warmer climate (Haatanen et al. 2015).

It has been speculated that climate change could facilitate establishment and expansion of invasive species. However, in a recent review Bertelsmeier and colleagues (2016) concluded that it is unlikely that global warming will systematically increase ant invasions. What is clear is that several ant species will benefit from more and higher climate suitability and therefore have the potential for further spread, as what seems to be happening with *L. niger* (Haatanen et al., 2015).

The ability of invasive species to increase their long-term fitness will depend on their phenotypic plasticity and their ability to cope with climate change. Invasive species with narrow phenotypic plasticity will experience decrease in fitness, while more plastic

species will be able to cope better with climate changes (Pelini et al. 2012). However, ants that are exposed to higher fluctuations in climatic conditions, as is the case in most urban environments, could be selected for higher phenotypic plasticity, enhancing their ability to cope better to a changing climate. The urban heat island effect can offer opportunities for exotic ants adapted to warmer climates (Bertelsmeier et al., 2015).

Tramp species common in urban areas have been shown to have a broad range of temperature tolerance. For example *Monomorium floricola*, and *Tetramorium bicarinatum* have been reported to tolerate temperatures up to 30-50^{0}C (Russ Solis and Correa Bueno, 2012). These species also show a high tolerance to low temperatures. In another study, *Solenopsis invicata* had a LT50 of 43.5^{0}C after one hour exposure (Xu et al. 2009). However, even though opportunistic species may be more tolerant to heat stress or other stressful conditions, they may not outcompete native species adapted to temperature extremes (Walters and Mackay 2004). For instance, comparing *Linepithema humile* in Australia with two native species Walters and Makay (2004) found the two native species to tolerate higher extreme temperatures. Likewise, Hollway et al. (2002) comparing the temperature tolerance of *L. humile* with 5 native species found it to be least tolerant to high temperatures.

Of course, physiological tolerance is not the only response that ants can have to changing climate, many species respond behaviorally, including changing foraging time, building nests deeper into soil, and other strategies. In California, *L. humile* invades riparian forest and costal sage scrub fragments of natural habitat from the urban edge but penetrates dryer costal sage scrub to a distance of only 200 – 250 m. It has been hypothesize that increased soil moisture near edges due to urban runoff allows expansion into dryer natural habitat (Suarez et al 1998; Menke et al 2006). However, Bolger (2007) did not found support for this hypothesis since there were no differences in downslope edges versus upslope edges, which would be expected if urban runoff was the main mechanism facilitation spread. Instead he did find that soil type had an influence. Soils that retain more moisture supported Argentine ant invasion more than well-drained coarse soils. There is no question that humid conditions facilitates Argentine ant invasion in dried environments. Argentine ants have been shown to have less resistance to desiccation than native ants in arid regions of California (Holway et al., 2002) and Australia (Walters and Mackay, 2003). El Niño events, which increase total rainfall in the San Diego area, have been increasing in frequency since the 1970 (Trenbeth and Hoar 1997) and climate change models also predict increase El Niño frequency (Timmerman et al. 1998). Taken this into account recent niche modeling analyses suggest that predicted climate change will lead to increases in introduce ranges of Argentine ants worldwide (Roura Pascual et al., 2004). However, in some regions were dryer conditions are predicted, lower soil moisture may

prevent invasion or further expansion.

It is well know that changes in microclimatic conditions can alter competitive interactions among ants (Perfecto and Vandermeer, 1996). Climate mediated changes in ant interactions could also facilitate some invasive species. For example, Argentine ants remain active throughout summer afternoons in Northern California while competing indigenous ants, less tolerant of high temperatures become inactive (Human and Gordon 1996). This can provide a competitive advantage to the Argentine ant under global warming scenarios. Furthermore, temperature along with disturbances that affects native species in urban environments, could create appropriate conditions for invasive species to get first establish and this could be hasten by climate change.

To our knowledge no study have examined the impact of climate change on ant mutualisms in urban landscapes. However, since ant-plant protective mutualisms and ant-hemitperan mutualisms are ubiquitous and occur also in urban environments, climate-mediated changes on these mutualisms would be expected to also occur in urban environments. Belatrix and colleagues (2013) argue that most ant-plant symbiotic interactions are evolutionary unstable and they easily appear in evolutionary time but changes in environmental conditions, including climate fluctuations, are likely to breakdown these interactions. Examining abrupt climate change during evolutionary time (mainly the Quaternary), Belatrix et al (2013) show that an ant-plant obligate mutualism in the rainforest in Africa was affected by past climate change that show contraction of forest areas creating fragmentation. Interestingly, while the plant partner showed evidence of remnants of distinct refugia during the Pleistocene (though molecular genetics), the ant partner showed no signal of this. On the other hand, in the ant fungus mutualism in the leafcutter ant, *Trachimymex septentrionalis*, the ant showed strong population fragmentation following cycles of quaternary glaciation but their microbial symbionts (fungus and bacteria) showed a different pattern (possible based on the ability of the symbionts to disperse independently). This study shows that even in these very tight symbiotic associations, the ant can show a different pattern than its symbionts. Since these interactions in the urban landscapes tend to be more opportunistic and generalists, it is possible that climate change can have an even stronger effect in the formation as well as breakdown of these interactions.

Conclusions

Overall ants are a taxa that, relative to some other taxa, are surviving the shift towards urbanization without major losses to biodiversity. The persistence of ant populations across the landscape present an opportunity to better understand urban

ecosystems and what it takes to make it in the city. One of the most consistent features of the urban landscape that explained variation in a range of studies was trees, as percent canopy or proximity to a forest. Forest fragment remnants and urban forests could be sources for generalist and specialist species as richness has been positively associated with proximity to greater canopy and forest. Urban forests had more unique species as compared to urban parks or medians (Savage et al. 2015, 2016). Additionally, minimal overlap between the community compositions suggests forest fragments could be a source only for only a fraction of the urban ant community. Proximity to impervious surface or buildings and the scale at which these factors are included in the study also mattered in predicting richness. A few have found peaks at intermediate disturbance, but it was not common (Sanford, Manley, and Murphy 2009). Moreover, Additionally a few studies have begun to unravel the ecosystem services of urban ants, and over the course of this review it became clear that urban ants are not only persisting in the urban environment but are also participants in the urban cycles of streets, sidewalks, garbage bins, and lawns.

In the synthesis of study themes and creation of tables the studies were divided by topic but also divided by urban gradient methodology. While all studies we examined were "urban" the degree of urbanity was highly variable. In looking at the various study designs it was clear the the portion of the urban intensification present could provide greater information to the functionality. For example urban parks, forest fragments, and natural areas were all used as the least disturbed end of the gradient by (Reyes-Lopez and Carpintero 2014; Souza-Campana et al. 2012; Lutinski, Lopes, and Morais 2013) respectively. All of these studies found a decline of diversity along the gradient but each of them tells us something different about the role of vegetation in urban ecosystems.

The variety of methods used for defining this gradient reflect the underlying assumptions of the studies, the hypotheses being tested, and the factors that have been found to influence other organisms along the gradient. Common factors used for comparing urban ants along the gradient have included vegetation (Menke et al. 2010; MacGregor-Fors et al. 2015; Souza-Campana et al. 2012), distance to urban center (Reyes-Lopez and Carpintero 2014; MacGregor-Fors et al. 2015; Sanford, Manley, and Murphy 2009), disturbance such as stress a development index (Sanford, Manley, and Murphy 2009) and percent of impervious surface cover (McKinney 2008; Savitha, Barve, and Davidar 2008). Vegetation abundance such as amount of canopy cover(MacGregor-Fors et al. 2015, 635) is used in comparisons of forest fragments within urban areas as well as across the gradient from street trees, to lawns, to city parks, to rural areas and forests in the periphery of cities. Distance or proximity to urban centers (MacGregor-Fors et al. 2015) is a geographic measure of the gradient that assumes that the urban core is the epicenter of disturbance in cities and further away in space are the more rural, natural, less disturbed

areas. Urban levels of disturbance can also be directly assessed through measures of anthropogenic stressors such as insecticide frequency, traffic frequency or temperature. Percent impervious surface is a very common tool in urban ecology literature as a measurement for urbanity, however, it has not been heavily used in ant studies. An alternative to a geographic gradient is a temporal gradient, where a historically rural or natural state is compared to the present developed or urban area. These studies are logistically challenging but have been used to study urban ants using, before and after sampling of construction sites (Buczkowski and Richmond 2012), a comparison to historical data (PARK et al. 2014), and observations of parks and buildings across the landscape of various ages (Carpintero and Reyes-López 2014).

All places along the gradient are likely to be managed or altered by human presence and in this way urban to rural gradients resemble management intensity (like agricultural intensification or land use intensification) scales used in agroecology or conservation biology studies (Philpott et al., 2008; Flynn et al., 2009; Ottonetti et al., 2010; Neoh et al., 2015). These intensification gradients are useful frameworks but also challenging in their wide human variation, urban spaces are no different. The magnitude of the unintentional transportation of ants by humans across the urban landscape is not known. Environmental disturbance and resources supplementation (from human food waste) in these areas could be very different than in areas with lower human density. For these reasons as well as causes of variation in environmental conditions across urban areas, the use of distance as a gradient can be misleading since within the urban core you can still find urban forests and other semi natural areas. Describing the gradient of each study with time, vegetation, stress agents, distance, and impervious surface can shed light on potential patterns across gradients and urban landscape types.

Regardless of what variable was taken as a measurement of urbanization, the majority of studies find a decrease in ant species richness with increased urbanization, (See Table 2 and Table 3) a conclusion congruent with the urban homogenization hypothesis (McKinney 2002). However, the negative trend is certainly not consistent and a number of studies have seen significant increases in richness; in most cases these neutral or positive findings are attributed to changes in community structure. This may be related to the introduction of non-native species, persistence of rare species, or opportunities in the heterogeneous landscape. We did not find evidence that metapopulation dynamics have not been studied. In this review we encountered 30 studies using an urbanization gradient that examined the effect of urbanization on ant richness, and of these, 16 found a significant reduction in ant species richness with increased urbanization (Table 2).

There is a great deal left to investigate in the function, trends, communities,

behaviors and population dynamics of urban ants. We have only just begun to explore the extent of urban hydrology such as flooding, regarding, sewer and stormwater systems on urban ant species (Youngsteadt et al. 2015, Brown et al. 2013). The successional stages of the urban landscape such as age of an area were not well supported. Park et al. found no change in ant richness over 12 years in urban parks but there was insufficient historical data to compare communities (PARK et al. 2014). A key direction of future studies should be metapopulation dynamics and species interactions. The effect of area and space could be explaining some of these patterns, however it is clear that in the urban landscape heterogeneity is a driving force and that matrix structure and condition is likely to be an essential part of understanding the larger urban landscape and the impact of global homogenization on species assemblages (Vonshak and Gordon 2015, 259). It is not yet clear what conservation efforts would be advised if a rare species was reliant on the urban system.

The overlap between local and landscape factors in the urban to rural gradient can make ecological generalizations of the results tempting but impractical (Savage et al. 2015; Philpott et al. 2014; Lutinski, Lopes, and Morais 2013; Ives et al. 2013; Souza-Campana et al. 2012). Given that urban spaces are highly heterogeneous any local changes may result in patterns different from the landscape scale. This is not to say that local factors are not important, in fact local factors have been found to be stronger indicators of richness than landscape factors (Philpott et al. 2014). However, viewing the entire urban network is essential in characterizing ant community composition and ecosystem function. Urban sprawl and urban infill are different landuse changes that can be occurring across the urban space and are likely to affect disturbance and vegetation patterns (Heterick, Lythe, and Smithyman 2013). As the relationship between ant functional groups and urban ecosystem drivers is untangled we will be better positioned to characterize the urban landscape qualities that affect diversity, composition and function of ant communities.

It has been proposed that urban habitats are undergoing a process of large-scale homogenization across many taxa (McKinney 2006). It is highly likely that a similar process is occurring regionally, if not globally, for ants, although individual studies have a wide range of results for overall biodiversity changes. Most studies reviewed here find a decreasing richness in the most urban locations, which supports the hypothesized homogenization trends. Some studies reviewed here found peak diversity at intermediate levels of disturbance, or increasing diversity reverse trends driven by resilient or opportunistic species present in urban areas. In some of these cases the community composition shifts towards tramp species supporting the homogenization hypothesis. The findings across all studies reviewed were not consistent and the sample siting methodology was highly variable.

Future research of ants in urban ecosystems should address the gaps in sampling methodology and explicitly address ecosystem processes when possible. The intra urban landscape has been poorly sampled and many studies lack enough locations across the urban to rural gradient to adequately ask if urban ecosystems play by their own rules or are they akin to other disturbed areas? The research thus far suggests that further investigation of the role vegetation across urban to rural sites could be fruitful, furthermore the investigation of shifts in community composition look to be a key part of understanding ecosystem responses to urbanization.

Figures

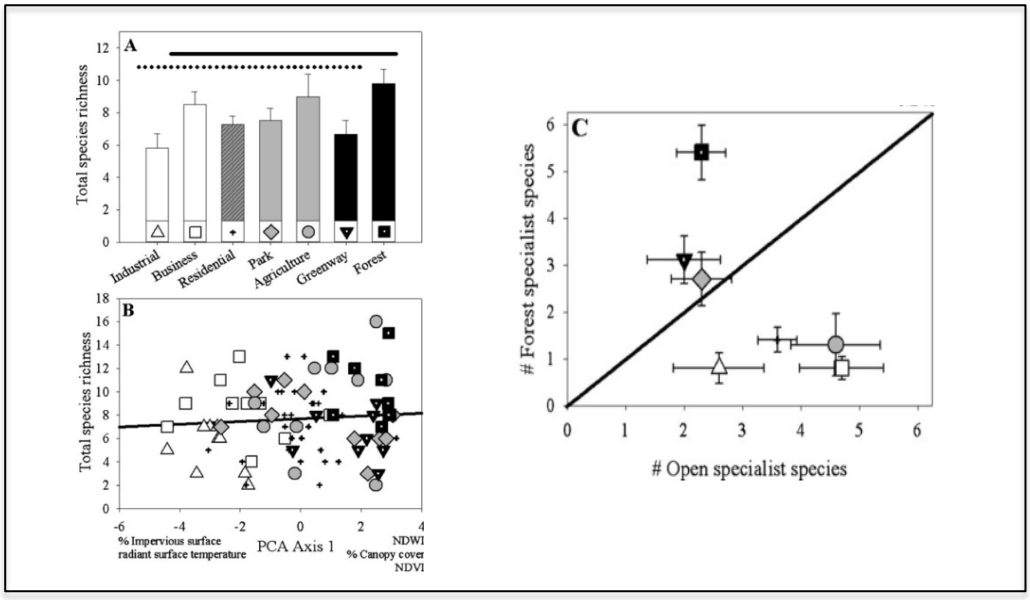


Figure 2. Menke show the changes in impervious surface and vegetation over the urban to rural gradient but this is not found to be related to the changes in richness but instead to changes in community composition. "MRPP results confirmed that ant communities differed between habitats (T=−15.583, A=0.117, p<10−8). Pair-wise comparisons revealed that forest sites were the only sites to be distinct from all other land-use environment" (Menke 2010).

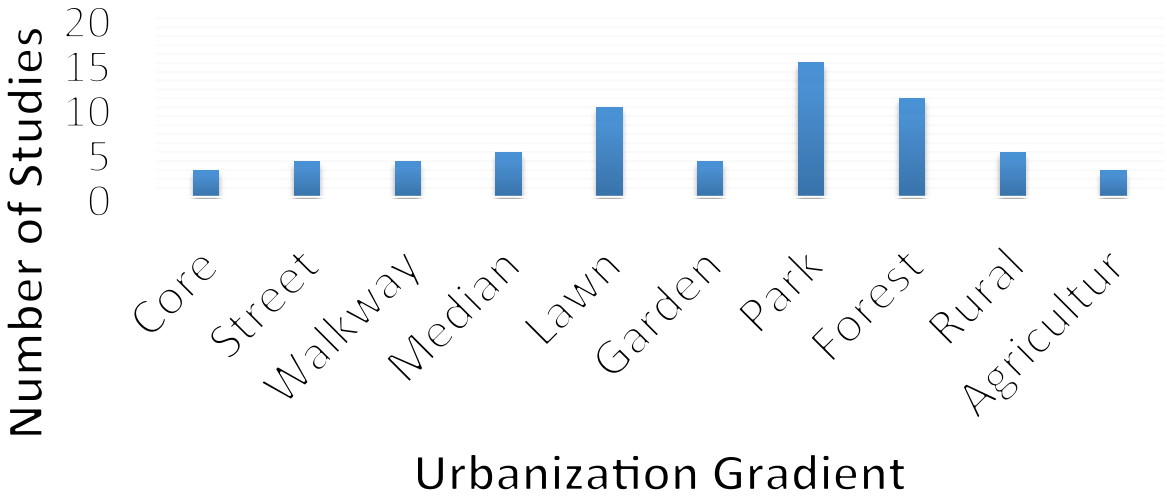


Figure 3. Number of studies that sampled the locations listed on the X axis representing various parts of the urbanization gradient.

Tables

Table 1. Key to Tables

Measure: *Ecosystem function measurement type*		Urban to Rural Gradient: *Where the study sampled along the gradient*		Methods: *Ant sampling methods*		Comparisons: *Type of experimental comparison *see also Urban to Rural Gradient*		Effects: *Direction of effect*	
I	INDERECT	U	URBAN	✪	BAIT	U	URBAN	-	NEGATIVE
D	DIRECT	C	CORE	✣	SEARCH	R	RURAL	+	POSITIVE
		S	STREET			-	TO	^	PEAK
		W	WALKWAY					V	BIMODAL
		M	MEADIAN	O	PITFALL		Examples (U-RF = urban to rural forest) (U-U = urban to urban)		
		L	LAWN						
		G	GARDEN						
		P	PARK						
		F	FOREST						
		R	RURAL						
		A	AGRICULTURE						

Table 2. Studies that addressed the impact of urbanization of species richness using some form of urbanization gradient. Urbanity was characterized in a variety of ways (Urbanity Experiments column) both positive, negative and intermediate responses were found.

Urbanity Experiments		Comparison	Effect	City, country	Methods			Urban to Rural Gradient										Reference	Year
					Search	Pitfall	Bait	Urban	Core	Street	Walkway	Median	Lawn	Garden	Park	Forest	Rural	Agriculture	
Urban Index	**Anthropogenic Disturbance**	U-U	-		✣	O		U								F	R		Savitha	2008
	Chronic Stress	U-U	-	Manhattan, New York City, USA	✣	O		U				M			P	F			Savage	2015
	Development	U-U	^	Lake Tahoe, central Sierra Nevada, California,		O		U	C	S	W	M	L		P				Sanford	2008
Distance to…	**Buildings**	U-R-A	v	Silicon Valley, California (Bay Area)	✣		✪	U	C		W	M	L		P	F	R	A	Vonshak	2015
	City Center	U-U	+	Xalapa de Enriquez, Mexico	✣		✪	U											MacGregor-Fors	2015
		U-R	-	Sofia, Bulgaria. 42.41 N 23.19 E	✣			U					L			F	R		Antonova	2006
	City Boarder	U-U	-	Spain		O		U							P				Carpintero	2014
	Concrete	U-U	-					U											Edwards	2014
	Forest	U-U	-	city of Mogi das Cruzes, Spain		O		U					L		P	F			de Souza	2012
	Forest	U-U		Southern Brazil				U							P	F			Lutinski	2013
	Impervious Surface	U-R	-	Veracruz, Mexico				U		S			L				R	A	Lopez-Moreno	2003
Presence of …	**Densification (HWY vs Garden)**	U-U	+	Austrailia		O		U		S				G					Heterick	2013
	Soil Contamination	U	-/+					U											Gramigni	2014
	Industry	U-U	-	Raleigh, North Carolina		O		U	C				L		P	F		A	Menke	2010
Landscape Location	**River Basin**	U-R	≠	Sydney, Australia		O		U							P		R		Ives	2013
	Island Mainland	U-U	≠					U							P				Iawata	2005
		U-U	-	Spain		O		U						G					Reyes-Lopez	2014
Simplification	**Simplification**	U-U	-	Warsaw, Poland		O		U			W	M	L		P	F			Slipinski	2012
Time:	**Age of Building**			Puerto Rico			✪												Brown	2013
	Age of park	U-U	≠	Fukuoka City, Japan	✣			U							P				Park	2014
		U-U	≠/+	Raleigh, North Carolina (NCSU campus)		O		U			W		L			F			Guenard	2015
		U-U	≠	Hiroshima Japan	✣			U							P				Park	2014
			+			O		U							P				Yamaguchi	2004
		U-U	≠		✣			U		P									Park	2014
	Pre/Post Construction	U-U	-/+	West Lafayette, Indiana, U.S.A.			✪	U					L	G	P	F			Buczkowski	2012
Urban	**Enviromental Conditions**	U-U	-	New York City, USA	✣	O	✪	U				M			P				Youngsteadt	2015
	Micro Climate	U-U	-	Toledo, Ohio		O		U					L	G		F			Philpott	2014
	Urbanization Scale	U-U	≠	Xalapa de Enriquez, Mexico	✣		✪	U											MacGregor-Fors	2015

Table 3. Common characterizing variables found to be significant factors in explaining ant species responses. Studies with multiple factors are repeated so that each factor from the study has a row.

Charicterizing Variables	Effect on Richness	Reference	Year
Area	+	Edwards	2014
Area	⦸	Heterick	2012
Area of Median	+	Pecarevic	2010
Building Area	+	Philpott et al	2014
Canopy Cover	⦸	Menke	2010
Canopy Cover	+	Savitha	2008
Canopy Cover	#	Youngstead	2018
Canopy Cover	+	Vonshack	2015
Concrete	-	Vonshack	2015
Concrete Structures (number)	⦸	Pecarevic	2011
Construction	-	Buckowski	2012
Cut and Fill	⦸	Yamaguchi	2004
Development 300m	-	Sanford	2008
Development 500m	^	Sanford	2008
Distance from Forest	+	Edwards	2014
Distance to Buildings	+	Vonshack	2015
Distance to habitat edge	#	Youngstead	2020
Distance to Urban Edge	⦸	MacGregor-Fors	2015
Elevation	⦸	MacGregor-Fors	2015
Forest Fragment	+	Slipinski	2012
Forest Fragment	+	Guenard	2014
Forest Fragment	+	Lutinski	2013
Forest Habitat Type	+	Philpott et al	2014
Garbage bins	⦸	Pecarevic	2011
Ground Cover (%mulch)	⦸	Pecarevic	2011
Humidity	#	Youngstead	2016
Impervous Surface	⦸	Menke	2010
Impervous Surface	#	Youngstead	2019
Insecticide+House age	-	Buckowski	2012
Lawn Neighbor	+	Edwards	2014
Litter	⦸	Ives	2013
Litter Depth	+	Savitha	2008
Litter Depth	#	Youngstead	2017
Local Factors	+	Philpott	2014
Lowland	+	Yamaguchi	2004
NDVI	⦸	Menke	2010
NDVI	+	Savitha	2008
NDWI (wetness)	⦸	Menke	2010
Nearest Street	+	Pecarevic	2010
Park Shape	+	Carpintero	2014
Park size	+	Carpintero	2014
Park size	+	Yamaguchi	2004
Percipitation	-/+	Sanford	2008
Reclimation	-	Yamaguchi	2004
Shrub abundance	+	Philpott et al	2014
Soil Clay	-	Edwards	2014
Soil Tillage	-	Edwards	2014
Surface temperature	⦸	Menke	2010
Temperature	#	Youngstead	2015
Upland	-	Yamaguchi	2004
Vegetation height*	-	Ives	2013
Vegetation Natives	+	Heterick	2012
Vegetation Richness	⦸	Heterick	2012
Vegitaion Charicteristics	+	Philpott et al	2014
Vegitaion Charicteristics	-	Sanford	2008
Vegitation (perenial groundcover)	+	Pecarevic	2011
Vegitation (rank low/high)	⦸	MacGregor-Fors	2015
Vegitation Complexity	+	Unoetal	2010
Vents (subway)	⦸	Pecarevic	2011

Table 4. Ecosystem Services found in the review to have direct or indirect relationships to ecosystem functions done by ants. Most studies also compared the function of these services in and outside of urban areas to examine change in effect.

Ecosystem Services	Measure	Comparison	Effect	Example	Species	City, country	Reference
Seed dispersal	I	U-R	+	Removing seeds of the myrmecochorous plant *Viola pubescens*	*Formica glacialis, Lasius pallitarsis, Myrmica detritinodis*	Winnipeg, Manitoba, Canada	Thompson & McLachlan, 2007
Soil aeration & infiltration	I	U-R	-	Building subterranean tunnels that facilitate soil aeration and water infiltration	*"aerators" Formica cf. sibilla, F. sibilla, F. lasioides*	Lake Tahoe Basin, Nevada and California, USA	Sanford et al., 2009
Decomposition	I	U-R	-	Building tunnel networks in woody debris facilitating decomposition and nutrient release	*"decomposers" Camponotus modoc, F. accreta*	Lake Tahoe Basin, Nevada and California, USA	Sanford et al., 2009
Nutrient addition	I	U-R	+	Built thatch mounds that increase nutrient availability and adds heterogeneity to soil	"compilers" *F. obscuripes, F. ravida*	Lake Tahoe Basin, Nevada and California, USA	Sanford et al., 2009
Food scavenging	D	U-R	+	Retrieving food waste from urban areas	*Tetramorium bicarinatum*	New York City, New York, USA	Penick et al., 2016
	D	U-U	+	Retrieving food waste from median in the city	*Tetramorium bicarinatum*	New York City, New York, USA	Youngstead et al., 2015
	D	U-R	-	Retrieving dead arthropods	*Anoplolepis gracilipes, Monomorium pharaonis, Paratrichina longicornis, Pheidole megacephala, P. parva, Tapinoma melanocephalum*	Singapore (within the University of Singapore)	Tan & Corlett, 2012
Pest control	D	U-U	?	Predation on house fly eggs, larvae and nearly emerging adults	*Solenopsis geminata*	San Juan, Puerto Rico	Pimentel, 1955
	I	U-R	+	Predation attempts on artificial caterpillars	No data taken on ant species	Sorø, Denmark	Ferrante et al., 2014
	D	U-U	+	Underground predation on sentinel prey	No data taken on ant species	Akron and Cleveland, Ohio, USA	Yadav et al., 2012
Interference with Biological Control	D	U-R	+	Ant interference with biological control of a hemipteran pest by other species	*Camponotus conspicuus zonatus*, *Solenopsis geminata*, *Monomorium floricola*	Santa Cruz, Galapagos	Hoddle et al., 2013
	D	U-R	+	Ants tending hemipterans that are disease vectors of maize	*Camponotus acvapimensis, Crematogaster* sp., Pheidole megacephala	Yaoundé, Cameroon	DeJean et al., 2000
	D	U-U	-	Invasive ant tending invasive pest species in citrus	*Linepithema humile*	Several cities in southern California	Tena et al., 2013

Chapter II: Characterizing the Ants of Ann Arbor, a Midsized Temperate City

Abstract

Urban landscape classifications are the precursor to understanding the variety of spatial stratification patterns in urban areas that are essential to predicting ecological processes. Furthermore, the debate of which scale, local and landscape, is the most important in driving ecosystem changes in urban environments needs further investigation. This study in Ann Arbor Michigan examines the relationship between urban characteristics at habitat, local, and landscape scale and ant community composition and richness. Microhabitat features were the most predictive scale of ant community shifts in composition. Vegetation was also associated with increased species richness.

Introduction

This study explores the ecological context of urban areas from the perspective of a different urban resident: ants. The state of ants in urban areas is useful because ant species are good indicators of ecosystem change (Andersen 1997, Anderen and Majer 2004). By understanding the changes in ant species richness and community composition we can better assess changes in the ecosystem. Ants are great subjects for exploring the impacts of urbanization on biodiversity because they are a prevalent component of almost all cities, are very abundant and easy to measure and respond to environmental changes (Andersen 1997, Anderen and Majer 2004)

In a variety of urban areas arthropods, including ants, have been found to be affected by urbanization through altered biodiversity, abundance, community structure, and trophic interactions (Turner et al. 2004; Shochat et al. 2006; McKinney 2008, Phillpott 2012). Throughout the past decade, studies began to explore the underlying mechanisms that cause changes in the ant community within urban landscapes or along an urban to rural gradient (Table 3). Features of the urban ecosystem that have been found to influence ant distribution in urban landscapes include: vegetation, forest fragments, proximity to built environment or natural features, impervious surface area, anthropogenic food inputs (i.e. trash), leaf litter, and habitat connectivity, see tables two and three.

There is evidence for effects on arthropod diversity and composition at the local

scale (McKinney 2008; Uno et al. 2010,) and at the landscape scale (Rudd et al. 2002; Yamaguchi 2004; Pacheco and Vasconcelos 2007; Magura et al. 2010). Some studies have also compared the relative effect of these scales on arthropods generally (Philpott 2014, Bates 2011, Bennett and Gratton 2012; Wojcik and McBride 2012; Shwartz et al. 2013). In particular, Philpott found that arthropod community shifted towards more carnivorous species in disturbed areas at the local scale(2014).

The study of ant community structure and function in the urban matrix is growing, but it is still a limited field of research. It is not clear under what conditions ant communities in urban landscapes would be clustered, nested, or exhibit niche partitioning. In this study I hypothesize that vegetation in the urban landscape (inside and outside of designated parks, forest fragments or yards) will determine the diversity and composition of ant species and that an increase in vegetation will correspond to an increase in native species.

In this study, I will expand on the on the literature by examining the effect of urban matrix characteristics on ant richness, abundance and community composition at three scales. I looked at features of the urban landscape at the habitat, local and landscape level. Microhabitat characteristics were measures of substrate, local characteristics addressed area of relevant features within the foraging range of the sample, and the landscape variables were defined by proximity of key features to the sample area. I explore the shift in the ant community across urban features at habitat, local and landscape scales. The following questions are addressed:

(1) Do ant species richness, abundance, and community composition respond to habitat, local and landscape conditions differently?

(2) What features of the habitat, local, and landscape levels are most important in determining ant species richness, abundance, and community composition in the urban matrix?

Due to the negative effects of urbanization on biodiversity, the richness of ant species in Ann Arbor will likely be a small subset of those known to be present in the region. I hypothesize that natural features of the landscape that improve habitat quality, such as vegetation, will increase ant species richness at the local scale. This hypothesis is congruent with studies showing that local factors are likely to be the driving forces of diversity in urban systems (Phillpott 2012).

Materials and Methods

Study Site

The city of Ann Arbor, currently home to approximately 113,900 residents, is

located in Southeast Michigan in the Northern Midwest United States. Ann Arbor's environment is characterized by a seasonal climate, temperate forests, proximity to the freshwaters of the Great Lakes, and an elevation between 700-900 feet above sea level. Major features of the city include six miles of the Huron River and associated watersheds and glacial deposits shaped by continental glaciers 14,000 years ago. Steep and moderate hills from moraines and kames as well as flat outwash plains from melting glaciers give Ann Arbor its current topography. The variety of glacial deposits across Ann Arbor result in a range of soil types that allow for a variety of ecosystem types. The various soil types affect everything from plant composition in natural areas to building codes and storm water infiltration potential. Outwash plains tend to be sandy and drain well while moraines tend to have more clay mixed into the soil resulting in moisture retention. The slope and elevation of these features can also affect local moisture levels found in 631.4 acres of managed city-owned natural areas along the river (Natural Area Preservation Division 2002).

Several policies, historical events, and community demographics have affected the city's land use history. Most recently, in the 2000s, the Green Belt Project was voted in by residents to reduce urban sprawl(Bogan et al. 2017). Controlled burns, a management practice once very common in this landscape when it was maintained as an oak hickory forest by first nation people, is now becoming a more frequent practice in Ann Arbor's natural areas, some rain gardens, and a few residential areas. It is still unclear how controlled burns or other management practices in the city landscaping in urban areas could impact native ant communities(Houdeshell, Friedrich, and Philpott 2011). Overall, Ann Arbor has a history of land use change towards increased urbanization (Library 2015; Bogan et al. 2017).

Ant Sampling

Over the course of two months in the summer of 2015, ant species richness was surveyed using baits and visual searches. Field collection sampling was done in a grid formation across the city of Ann Arbor, approximately one square mile apart. Twenty-seven sites were sampled at 1256.64 square meters each (a circle with a 10 meter radius). Sampling occurred on whatever landscape was present at the site including city streets, sidewalks, medians, parks, intersections, or driveways.

At each site, four types of samples were taken: ant baiting and three types of visual searches with time limits. For both bait and search samples, the sampling was divided up onto each side of the road to included the street, sidewalk, right of way, and medians if present. For the ant baiting, nine small pieces of canned tuna in oil were placed on the ground trying to cover as many different kinds of habitats as possible within the 10 meter

radius of the central point. Baits were checked after ten, twenty, and thirty-minutes and any ants present at the bait was collected by hand or with an aspirator. The abundance of ant species was recorded as bait occupation. Solitary foragers were counted as equal to a group of swarming foragers.

The first timed search type was for sidewalks: which involved walking slowly along the sidewalk ten meters in each direction of the central sample point and identifying and recording any ant that was encountered during a 10 minute period. The second type of visual survey addressed vegetation and trees present at the site; each tree and woody vegetation was searched for ants for a total of 10 minutes. The third visual survey occurred under any present rocks, logs, or other large debris and it also lasted 10 minutes. If the species of an ant found during the survey was not known or had not been seen yet on that site, the specimen was collected and search time was paused.

Microhabitat and Environmental Characteristics

Microhabitat features were recorded at the time of sampling for each collected specimen. In this study the microhabitat is defined as the substrate directly beneath where the ant sighting was recorded. Ants often did not come to baits, only substrates with siting of ants were used in analysis. Similarly all trees, vegetation, paths, and roads were always searched for species but occurrences were rare; only substrates at successful sitings were recorded. Microhabitat features captured the observed habitat during the species search and bait sampling. Additionally, environmental conditions were recorded such as temperature, substrate type, the occurrence of garbage bins, and concrete features such as signs, drains or platforms.

Landscape and Local Characteristics

Geographic Information Systems (GIS) and remote sensing, processed with ArcGIS Desktop, was used to characterize the landscape and local level factors in separate processes. These analyses were separated due to the variation in sampling scale used for each. The landscape factors measured were distance to the urban core, distance to urban parks, and distance to the river. These distances were defined as the Euclidean (shortest linear) distances from predefined prominent landscape features. The landscape features, were chosen based on features identified as important in previous studies. Using ArcMap (version 10.4.1) the distance between the nearest edge of the sampling circle and the nearest edge of the polygon landscape feature: parks, the Huron River, or the urban core, were recorded. In this way, the shortest possible distance in any direction to the feature of interest was captured. Parks and river boundaries were defined by a data layer provided by

the City of Ann Arbor. The urban core was defined as the region with high metropolitan features relative to the surrounding area. Metropolitan features included a high impervious surface cover, low vegetation area, reduced lot size, dominance of retail, restaurant, public parking and city-owned buildings. These features created a distinct two by three block region used to create the urban core polygon.

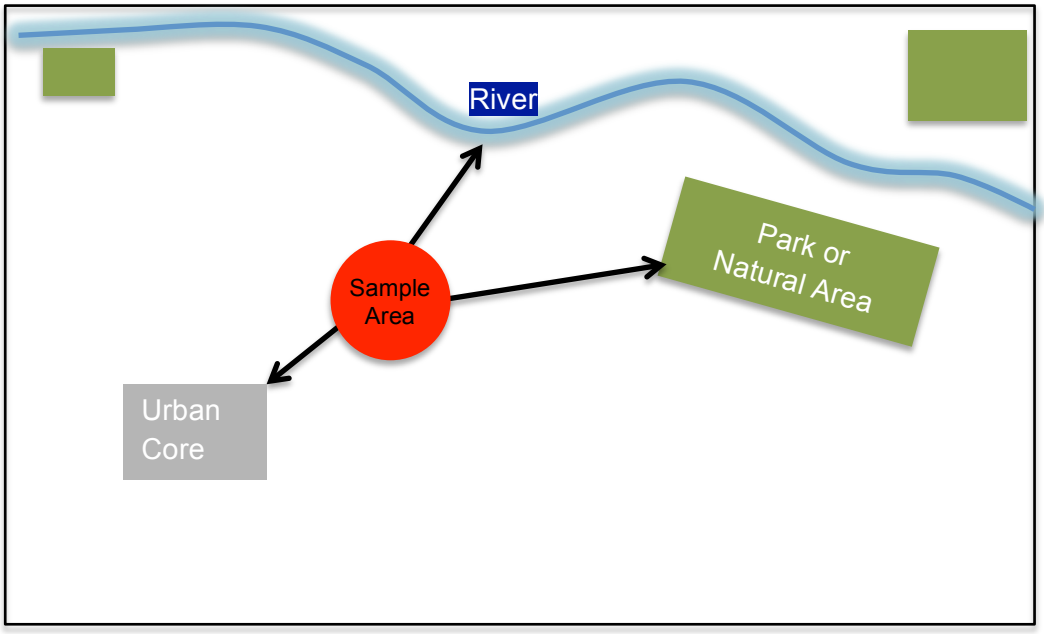


Figure 4. Landscape Features: Measured as shortest Euclidean distance to nearest park, nearest river intersection, and urban core edge.

While landscape factors measured features of the urban matrix that surrounded the sampling sites, local factors measured the conditions within the sampling site. Local factors were a measured as a proportion of the sampling location, defined by a 10-meter radius, covered by vegetation, streets, or buildings. In addition, the average elevation of the site was calculated. All of the local factors were calculated with ArcGIS Desktop using the buffer tool and raster sum tool. The vegetation layer was created using Light Detection and Ranging (LIDAR) data to produce a Normalized Difference Vegetation Index (NDVI) layer. Similarly, the LIDAR data set was used to create a Digital Elevation Model (DEM) used to calculate site elevation. Buildings and streets were defined by city land use data that originated from the same LIDAR data set.

Data Analysis

Richness and frequency of ants were compared to site characteristics using general linear models using R (Version 3.1.2 2014-10-31). The variation in species richness was

compared in a series of three ANOVAs that compared environmental variables at three scales: landscape, local and microhabitat. Microhabitat was converted to proportions using the number of habitats where ants were sited compared to all habitats sampled at the site. The microhabitat proportions were analyzed using the primary and secondary principal components from a Principal Component Analysis (PCA) and cluster matrix from the nMDS in a mixed model.

Clustering of ant species composition was tested with the non-metric multidimensional scaling (NMDS) (Young 1987) method using the Bray-Curtis Index (Bray and Curtis 1957). For the cluster analysis, I first created distance matrix with Bray-Curtis-dissimilarity index distances. Clusters were generated using the agglomerative clustering method with furthest-neighbor joining (MASS package). The isoMDS permutations were done 100 times at 100 random starting points, to confirm the ideal clusters. Then, Kmeans was used to identify clusters from one to six groupings. The elbow method determined the best number of clusters as three clusters (Goutte et al. 1999; Thorndike 1953).

Four Principal Component Analysis (PCA) were completed, one for all environmental factors combined and three PCAs for a subset of environmental factors pertaining to each scale, landscape, local, and microhabitat. Using the Index of Reliability (Tucker, L.R & Lewis, C. 1973) a reliability coefficient for maximum likelihood factor analysis was done before using the PCA axis and primary components in regressions comparing the environmental gradients to richness and cluster category by the site.

To compare the ant community clustering pattern to the environment, pairwise and grouped urban features were used. Using each scale specific PCA, the principal components were used in PerMANOVAs to compare the Bray-Curtis dissimilarity distance matrix, to the three scales of urban features. ANOVAs were used to compare individual types of urban features to clusters assigned by the Kmeans test. The characteristics of each cluster found in the kmeans test were compared in a series of three ANOVAs looking at environmental variables at three scales, landscape, local and microhabitat. These analyses allowed to look at the response of ants to characteristics of the urban environment as isolated features and grouped by scale.

Results

Species Richness and Abundance

Overall richness of all sites within the large scale grid sites was 11 species with an average of 4.48 species per site. The richness ranged from two to ten species per site. Richness was significantly and positively related to the amount of vegetation in a simple linear regression model comparing NDVI, within the sample site to site richness ($p = .0352$,

R^2 = 0.127). Elevation, proportion of building area, proportion of impervious surface, and temperature of sampling site were not significantly related to the richness or abundance of ants at the sites. See tables 8-10

In the comparison of the ant species richness to landscape factors, distance to parks, distance to the river, and distance to the urban core were not related. We would have expected a measure of urbanization, distance to urban core, to reflect changes in environmental gradient and therefore richness. However, no relationship was found between any landscape factors and species richness.

Similarly, in the model of local level environmental factors, no relationships of ecological consequence were found. Elevation, NDVI, building area, and street area of the site did not predict site richness.

However, at the microhabitat level, 58% of the variation in species richness was explained by microhabitats, especially the presence of bark, gravel, organic litter, rocks, sidewalk, streets, trees, and non-woody vegetation (p-value = <2.2e-16). The presence of some species was related to the overall species richness of the plot. In a comparison of all ant species present to the ant species richness of the site 13% of the variation in richness was explained by the presence of these five species: *Camponotus castaneus, Lasius neoniger, Mermica, Prenolepis imparis, and Tepinoma sessile* (p-value = 1.748e-06).

The average abundance of species was 9.04,. There was a large range of the number of successful encounters, 3-22 records, with anywhere from 20% to 100% of the baits or search attempts resulting in encounters. There was no significant difference between species frequencies or abundance across sites.

Community Composition and Distribution (Clusters)

The community composition of ants found in Ann Arbor was congruent with common urban ant species from the region such at *Tetramorium caespitum* and *Camponotus pennsylvanicus*. The most common species found at sites was *Tetramorium caespitum* and *Formica subsericea* making up an average of 21.31% and 20.9% of ant samples per site, respectively.

In examining the ant community composition differences between sites in Ann Arbor three separate communities, referred to here as clusters, were identified (See figure 6). The three clusters were determined in a NMDS using the Bray-Curtis index with a stress of 20.29 (indicating good clarity of the two dimensional cluster output). The clustering pattern of three groups was compared to a variety of landscape, local, and microhabitat factors to determine if any of these factors contributed to the formation of the clusters (Table 6). Distance to the river was the only landscape factor related to the clustering pattern, with the Tetramorium dominated cluster occurring closer to the river (F

value 9.83, P .0019). Distance to the urban core and distance to parks were not related to the clustering pattern. Among local factors measured, the vegetation (NDVI) and elevation were both significantly related to the clustering pattern (F values 6.8620 and 12.2869, P values .0093 and .0005). Where there was more vegetation there was more richness of species, and cluster Two was also associated with Higher NDVI. Building area was not related to the clustering pattern. See Figure 10 and Table 6.

At the microhabitat level, the occurrence of garden, gravel, lawn, rock, sidewalk, and tree were significantly related to the clustering pattern. Microhabitats such as trees occurred more in Cluster Two, lawns occurred most in Cluster Three, and several disturbed habitats, drains, dirt, gravel, and gardens, dominated Cluster One. The most important species related to community cluster patterns was species *Formica subsericea* (F 18.06, p-value 3.087e-05), it did not occur in Cluster One, it appeared with other species in Cluster Two, and occurred alone or dominant in Cluster Three.

Cluster One included 46 of the total 350 observations and was characterized by a community dominated by *Tetramorium caespitum* (47.83%) the highest of all the clusters. *Prenolepis imparis* was the next most common species at an average of 13%, much less than its occurrence in other clusters. The landscape environmental characteristics of sampling sites associated with Cluster One included the shortest average distance to the Huron River (2029.47 meters). The dominate local environmental characteristics found in Cluster One sites were high building area. This was echoed in microhabitat observations with the highest proportion of drain occurrences (13.04%) and lowest percentage of lawn occurrences (17.39%). However, Cluster One's sites also had above average observations of ants on gardens, dirt, and wood (4.35%, 19.57%, and 4.35% respectively).

Cluster Two included the largest number of observations, 126, and was composed primarily of three species, *Prenolepis imparis*, *Camponotus pennsylvanicus* and *Formica subsericea* (averaging 20.63%, 26.67%, and 29.84% of all ants per site respectively). *Tetramorium caespitum* was very uncommon in Cluster Two (0.07% on average per site). The landscape environmental characteristics associated with Cluster Two included an average 2490.82 meter distance to the river[1].

Cluster Three included 74 observations and is characterized by an ant community dominated by *Formica subsericea* (34.72%) and accompanied by an average occurrence of *Tetramorium caespitum* 29.17%; compared to its average across all sites, 21.31%. [2] The most dominant microhabitat feature of Cluster Three is lawn with an average occurrence of

[1] The local factors of Cluster Two were characterized by high NDVI. The microhabitat factors were similarly dominated by above average occurrence of trees, 16.67% ant occurrence on trees in cluster three compared to below 7% of ant occurrences on trees in Clusters One and Cluster Two.

[2] The landscape environmental characteristics associated with Cluster Three included the smallest average of distance to parks (715 feet), an average 12451-foot distance to the urban core, and an average 9,539.55 foot distance to the river. Local landscape factors of Cluster Three sites were characterized by the high street area but had moderate NDVI, building area, and elevation relative to other clusters.

31.94% far above the average 23.77% lawn per site. The most ubiquitous microhabitat feature across clusters was the sidewalk, with an average occurrence range of 19.67% to 23.61%.

Discussion

The overall richness of ant species in Ann Arbor is comparable to other urban sites in the temperate zone. For example, 14 species were recorded in Manhattan medians and parks, Table 5. However, regionally 23 ant species have been historically documented across the state of Michigan. The 11 species found in this study of Ann Arbor's right of ways, is much lower than the potential total richness of ants in Michigan (123) (Wheeler et al 1994). While this suggests a decreased richness of ants in urban areas, it also shows that 11 species are able to persist within the urban matrix, explicitly in the right of way, a very high disturbance area of the urban matrix. The 11 species found do not include the potential of forests or natural area parks within the city to sustain ant species diversity. This suggests that Ann Arbor has reduced species richness compared to all the possible species found in the state, which is likely a result of the city's urbanization.

The habitat features of the urban landscape were found to be more important than local or landscape factors in determining ant species richness and community composition. The importance of habitat level features on ants in the urban landscape echoes the relationships that are found with other small arthropods in urban landscapes. Our results suggest that in the urban landscape, especially along the right of way, the habitat, forage resources, and matrix substrate (i.e. lawns or sidewalks) are much more likely to determine the richness or community composition of ants than the landscape features. This is in contrast to a number of studies suggesting proximity to forest fragments explained patterns in community composition and richness.

The lack of evidence for a relationship between many natural or urban features measured such as impervious surface and the ant species community suggest that although urbanization is a physical transition of the landscape, ants may reflect that change in behavior. In other words, species interactions may be dictating ant community composition more so than physical or abiotic features that change with urbanization. This is perhaps not surprising given the fragmentation of the urban landscape which may cause in increased competition in isolated areas.

My results suggest that habitat substrate and microhabitat factors are more related to community composition and richness than factor at larger scale (local and landscape). It is also clear however that microhabitat substrate alone is not enough to dictate community composition or else we would have seen a response from NDVI at every scale, showing the importance of the amount of overall vegetation in each site area and in proximity to the

sites. The use of vegetation as a resource by urban ants may be mediated by species interactions and vegetation type. The results of this study give some indication that the differences in use of lawns, gardens, and trees by species need further exploration as we look into the interaction of species at local urban sites.

Clustering shows the persistence of species that forage on trees and vegetation in some communities in the urban landscape, Clusters two and three had a much greater species richness and prevalence of these semi-arboreal species, such as *Prenolepis imparis, Camponotus pennsylvanicus, and Formica subsericea*. Given that this study did not did not included some important urban habitats for ants, such as community gardens or parks, it is not clear what about the urban environment allows for the persistence of these species. However, the results of this study do not suggest, contrary to some studies, that proximity to parks may be mediating the persistence of arboreal species as a source of species. As have been shown in other studies, ants nesting in wooded areas forage outside those wooded areas (Edwards, 2016), but it is not clear if those forest species are able to form permanent colonies in the urban environment. Again we suggest that future research is needed to understand the role of behavior in ant-establishment of colonies which may prevent proximity to forest fragments from being a successful population source.

In regards to vegetation, the original hypothesis was partially supported as there was a positive relationship between vegetation (NDVI) and species richness as well as ant community composition. However, there was no relationship between richness, abundance or clustering and distance to parks or natural areas suggesting forest fragments may not be source populations, or that once a queen arrives in the urban environment, it cannot succeed in establishing a colony. Whether this is because of the habitat characteristics or the presence of other species that do not allow the establishment of the new queen, is a question for further research. These results suggest that presence of vegetation, especially trees, matter more than the impervious surface in determining ant species composition. None of the key urban features, such as buildings or streets, were found to be negatively related to species richness or community composition. The urban matrix quality for urban ants seems to be determined in part by the areas that have high NDVI despite also having high street surface area. This is likely due to trees which can be very high in density along the otherwise impervious area. Trees provide resources to ants, especially food resources such as honeydew from hemipterans and protein from other insects, and then can also reduced water logging in rainstorms, and in some cases provide nesting resources.

The implications of this study for urban land management and policy are positive in that impervious surface was not the determining factor for species richness. The influence of habitat factors on ant species diversity suggests that small-scale management changes to increase vegetation, especially trees, have the potential to be positively impactful on overall ant species diversity. In the case of Ann Arbor where many natural areas are within the city, we have learned that it is likely not good enough to have patches of forest fragments or

natural areas across the city. Maintenance of urban biodiversity will also require an understanding of the urban matrix between those patches. Furthermore, in the case of ants, small scale improvements in presence and complexity of vegetation in the right of ways is likely to improve the ability of the semi-arboreal species to persist and may influence overall urban ant species diversity more so than urban forests or parks.

Tables

Table 5. Ant Species Richness in the Region

Study	Location	Habitat	Richness
This study Jackson (2017)	Ann Arbor, Michigan	Right of way	11
Edwards(2003)	Ann Arbor, Michigan	Garden, park	19
Uno et al (2010)	Detroit & Toledo, Michigan	Garden	14
Uno et al (2010)	Detroit & Toledo, Michigan	Vacant Lots	20
Perfecto (peronal commnuiication)	ES George Reserve, Michigan	Natural Area	88
Wheeler (1994)	Michigan	All	123
Pecaravic 2010	Manhattan, NY, USA	Medians and parks	14

Ants diversity in in the region has been documented as high as 88 species found in a research preserve in south east Michigan. However, this study's richness is comparable to other locations sampling similar habitat, such as medians. Edwards found 19 species in the same city, Ann Arbor, but was sampling in a garden within park.

Table 6. Summary of Key Cluster Characteristics. Above average or below average characteristics (relative to the other clusters) are listed. Any significant defining characteristics are marked (*).

Cluster Characteristics		One	Two	Three
		46	126	74
Community	Dominant	T.c	P.I C.p. F.s.	F.s.
	Rare		T.c.	
Landscape Features	Near	River*, Core		Parks
	Far	Parks		
Local Features	High	Buildings	NDVI*	Street
	Low		Building	
Habitat Features *	Above	Drains,	Tree	Lawn

	Average	Garden, Dirt, Wood		
	Low	Lawn		

Table 7. Impact of individual species on clustering. Analysis of Variance Table, response to 3 Cluster types found in isoMDS a Kmeans cluster analysis. Formica species are significantly different between clusters and may be mediating species interactions.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Camponotus castaneus	1	0.517	0.5170	1.1692	0.28068	
Camponotus pennsylvanicus	1	0.322	0.3219	0.7281	0.39438	
Formica subsericea	**1**	**7.989**	**7.9889**	**18.0670**	**3.087e-05**	***
Lasius neoniger	1	0.163	0.1631	0.3689	0.54421	
lbi	1	0.240	0.2397	0.5421	0.46232	
Mermica	1	0.001	0.0012	0.0027	0.95867	
Prenolepis imparis	1	0.597	0.5972	1.3505	0.24638	
Solenopsis molesta	**1**	**1.774**	**1.7744**	**4.0129**	**0.04631**	*
Tetramorium caespitum	1	0.589	0.5886	1.3311	0.24980	
Tapinoma sessile	1	0.009	0.0091	0.0206	0.88611	

Table 8. Species Richness and Vegitated Area. Vegitation is positively related to richness.

lm(formula = Richness ~ AREA_NDVI)

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	1.673e+00	1.183e+00	1.414	0.1692	
AREA_NDVI	1.779e-04	8.007e-05	2.222	0.0352	*

Table 9. Species abundance was not related to vegitation area.

lm (formula = Abundance ~ AREA_NDVI)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	4.4775883	2.7816377	1.610	0.120
AREA_NDVI	0.0002897	0.0001883	1.539	0.136

Table 10. Proportion of habitat types in identified clusters.

Analysis of Variance Table

Response: BC_KmeCl3

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Bark	1	0.025	0.0249	0.0797	0.777907	
Garden	1	11.191	11.1906	35.8674	8.021e-09	***
Gravel	1	10.401	10.4014	33.3381	2.483e-08	***
Lawn	1	5.716	5.7165	18.3222	2.735e-05	***
Litter	1	0.003	0.0028	0.0090	0.924387	
Rock	1	9.254	9.2543	29.6615	1.314e-07	***
Sidewalk	1	3.182	3.1815	10.1973	0.001602	**
Street	1	0.660	0.6604	2.1166	0.147069	
Trash	1	0.209	0.2090	0.6699	0.413918	
Tree	1	1.688	1.6877	5.4095	0.020895	*
Vegetation	1	0.524	0.5244	1.6806	0.196132	
Wood	1	0.304	0.3045	0.9759	0.324255	

Garden, gravel, rock, sidewalk, and tree habitat types are corelated to shifts in communoty composition.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Habitat	1	0.1394	0.13945	0.65829	0.02489	0.684
Local	1	0.3367	0.33672	1.58956	0.06009	0.152
Landscape	1	0.2548	0.25484	1.20300	0.04548	0.319
Residuals	23	4.8722	0.21183	0.86954		

PerMANOVA using cluster distance matrix and first principal component from each scale.

Figures:

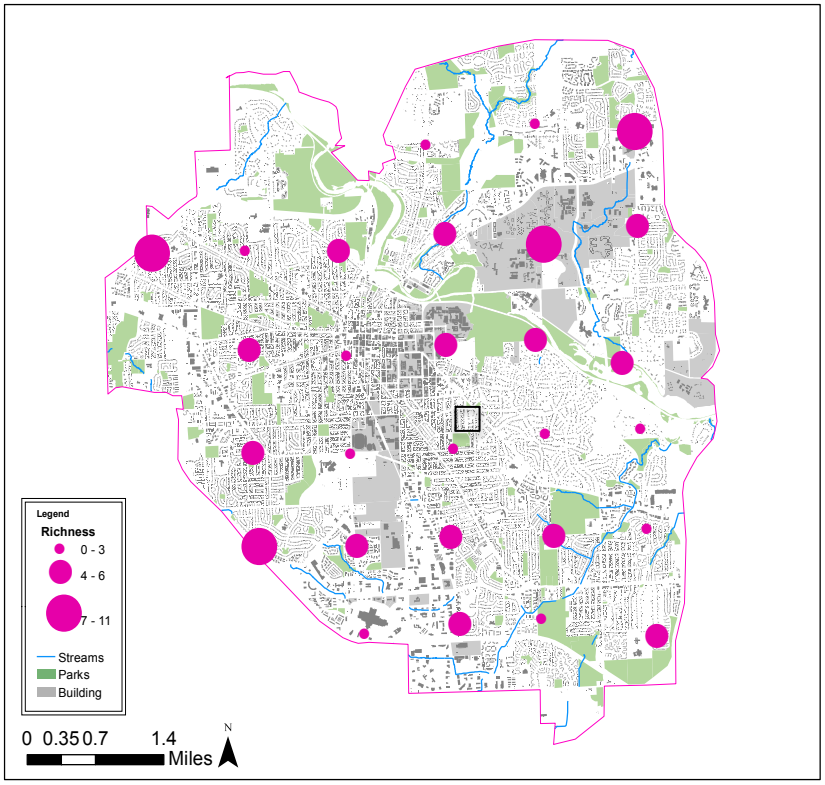


Figure 5. Ant species richness across Ann Arbor and the major landscape features (Huron River, Public Parks, Public Natural Areas, and Urban Core).

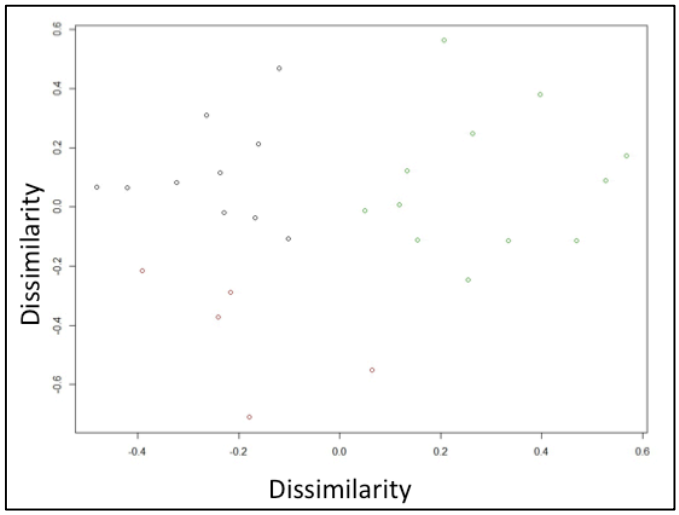


Figure 6. nMDS of ant community composition. This graph shows the dissimilarity of ant species found at each site (each point). Colors distinguish the three groupings determined by the K Means test (stress of 20.29).

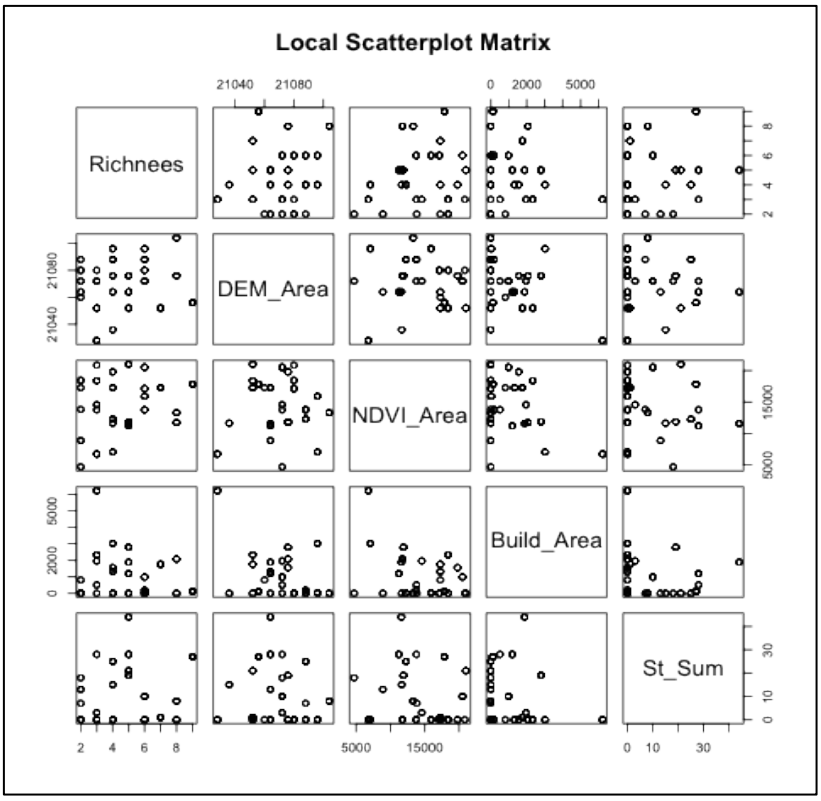
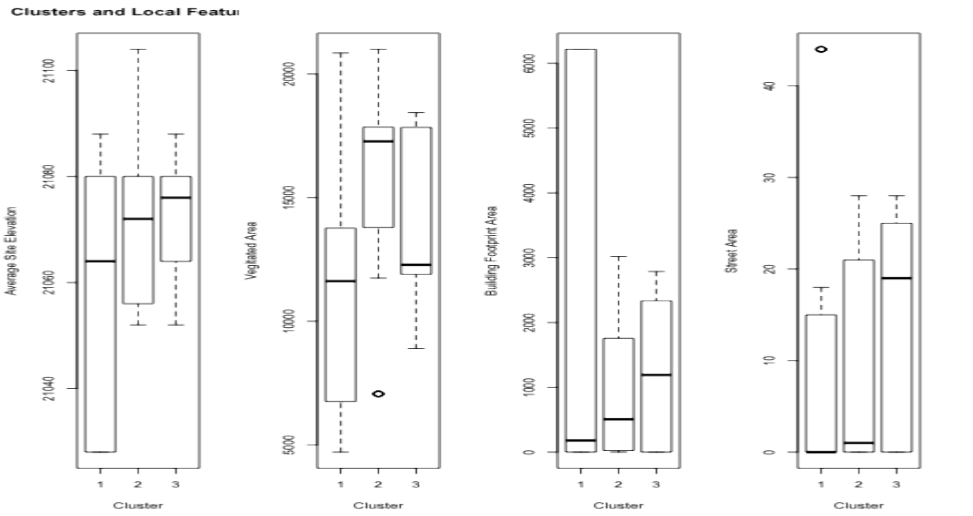
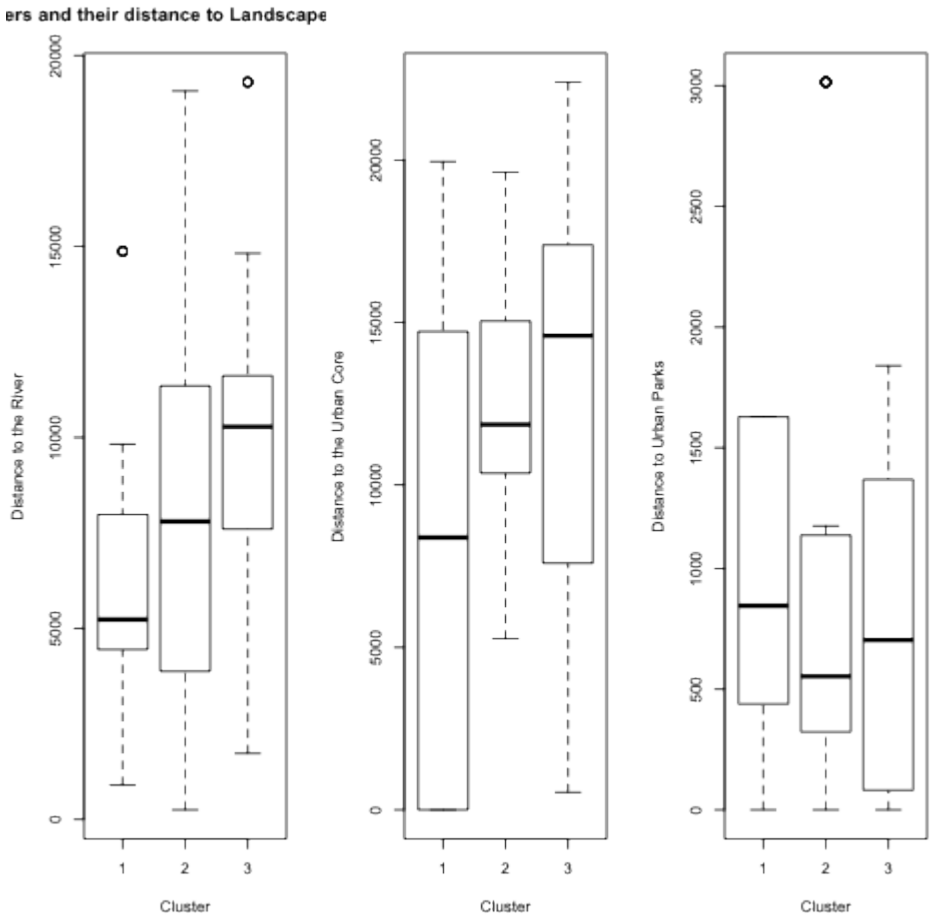


Figure 7. Pairwise comparisons of local level urban features. Building and street area are correlated however buildings and NDVI are not negatively correlated. Richness is significantly positively correlated with NDVI.



	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
DEM_Area	1	5.447	5.4466	12.2869	0.0005442	***
NDVI_Area	1	3.042	3.0418	6.8620	0.0093661	**
Built Area	1	0.353	0.3530	0.7964	0.3730610	

Figure 8. Box plots of local features and ant community composition clusters.



Cluster One, Two and Three and Landscape characteristics, ANOVA

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Distance to Park	1	0.538	0.5377	1.1819	0.278050	
Distance to River	1	4.476	4.4755	9.8383	0.001923	**
Distance to Core	1	1.039	1.0388	2.2835	0.132072	

Figure 9. Boxplots of Ant Community composition cluster types and landscape level features, distance to river, distance to urban core and distance to urban parks.

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