

ABSTRACT

HAMBLIN, APRIL LYNN. *Sizzling Cities: Native Bee Community Composition and Thermal Tolerances Related to Urban Heat.* (Under the direction of Dr. Steven Frank).

Bee communities provide ecosystem services as the most important pollinators. As urban areas expand and global climate change accelerates, temperatures become hotter, especially in cities. Unfortunately, it is poorly understood how temperature influences bee communities. Previous research has evaluated how urbanization and availability of floral resources affect wild bees, but most has neglected the effects of temperature. In Chapter 1, I asked how temperature and other urban environmental factors influence wild bee community attributes and species compositions. I hypothesized that temperature, impervious surface cover, and floral resources would predict bee abundance, diversity, and community composition. I used a map of surface temperature to select study sites at warmer and cooler sites in Raleigh, North Carolina, USA. I quantified environmental variables by measuring temperature, floral diversity, floral density, and percent impervious surface cover for 100 m and 1,000 m radii around each site. I determined that increasing impervious surface cover reduce bee abundance, floral density and diversity increased bee diversity, and temperature increased bee richness. Impervious surface cover altered species community compositions.

In Chapter 2, I measured the thermal tolerances of 16 bee species to first determine how they differed in CT_{max}, and thus, their potential responses to environmental warming. I then used the thermal tolerances to predict community composition and distribution responses. I found that a species' critical thermal maximum (CT_{max}) predicted species distribution as related to mean maximum temperature and percent impervious surface ground cover (1,000 m radius from study site). Mean maximum temperature of study sites decreased

as species CTmax increased. This was only shown with phylogenetic correction, so only closely related species showed this relationship. It is likely that local measurements of temperature in a shaded tree or shrub did not accurately measure the temperatures bees experienced throughout the study sites. Percent impervious surface cover at study sites over (1,000 m radius) increased as species CTmax increased, and impervious surface cover likely more accurately measures the large-scale temperature that bees experienced throughout study sites.

Together these results suggest that bees are currently within their thermal ranges, but may experience warming beyond their thermal tolerances in the near future. This could alter bee communities. More research should utilize temperature as a predictive variable and conduct manipulative studies to better understand thermal tolerances.

© Copyright 2015 April Lynn Hamblin

All Rights Reserved

Sizzling Cities: Native Bee Community Composition and Thermal Tolerances Related to
Urban Heat.

by
April Lynn Hamblin

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Entomology

Raleigh, North Carolina

2015

APPROVED BY:

Dr. Steven Frank
Committee Chair

Dr. Elsa Youngsteadt

Dr. David Tarpy

Dr. Hannah Burrack

DEDICATION

To my sister, Stacey Hamblin. Thank you for always encouraging me and saving my life, physically when I was younger, and mentally as I grew older.

I am blessed to have you as a sister.

To my parents, Cynthia and Thomas Hamblin, for going with me through my life struggles and joys as if they were your own. I wouldn't be who I am today without the both of you.

Thank you.

To all my family and friends—especially my grandmothers, Uncle Jody and Jennifer Hamblin, and Courtney Tomasello—who have supported me throughout my entire life journey, pursuing my dreams even though you sometimes would not understand or agree with them. I hope I have made as much of an impact on your lives as you have mine.

To God/Jesus/Holy Spirit, without whom I could do nothing.

BIOGRAPHY

April Hamblin was born February 10th, 1991, named after the month April because that was when she was supposed to be born. She grew up in Mullica, NJ, reading books and exploring the world outside for creatures of any kind (when her parents told her to stop reading and get some exercise, of course). As she watched her teachers inspire her fellow students and felt the excitement of learning herself, her excitement for teaching blossomed. As she learned about and experienced nature, her care for the environment and sciences grew. As an undergraduate at Stockton University and a Student Conservation Association Intern at Yellowstone National Park, her love for bees and other insects developed. She completed her B.S. in Environmental Sciences from Stockton University in 2013 and was blessed to be accepted into the Steven Frank Lab in the Entomology Department at North Carolina State University where she studied wild bee communities and urban heat.

ACKNOWLEDGMENTS

I would start by acknowledging my advisor, Dr. Steven Frank, and members of my committee, Dr. Elsa Youngsteadt, Dr. David Tarpy, and Dr. Hannah Burrack for their constant support and guidance throughout my Masters research. From our meetings together, making decisions and discussing constructive criticisms, to their advice about my future career, my advisor and committee helped me develop into a confident scientist. Particular thanks and appreciation goes out to Dr. Steven Frank and NCSU for funding my research. I had my heart set on studying native bees in urban areas specifically. With your faith in me and funding for my research, I was able to do just that. Thank you.

I would like to show my appreciation to the City of Raleigh and all the volunteers who let me conduct research on their property, from parks and preserves to backyard homes.

Thanks so much to Dr. Holly Menninger for helping me come in contact with these kind volunteers, and Mrs. Sally Thigpen for helping me obtain permission to sample bees from natural areas.

I am very grateful for Dr. Elsa Youngsteadt who substantially helped me with statistical analysis, advice on bee identifications (specifically *Andrena* spp.), our native bee outreach, and personal development. This research would not have been complete without you and my time at NCSU would have been much harder without the friend I found in you. I would also like to thank Dr. Margarita López-Uribe for her generous help making the phylogenetic tree and participating in our native bee outreach as well. Not only were Dr. Youngsteadt and Dr. López-Uribe essential, but the entire Frank Lab supported and helped me throughout my Masters. Postdocs and graduate students who gave me advice and answered every one of my

questions: Dr. Warren Sconiers, Dr. Sarah Jandricic, Dr. Kevin McCluney, Adam Dale, Emily Meineke, Kristi Backe, Lawrence Long, Robert Appler, Amanda Anderson, Sarah Parsons, and Travis McClure. Lab technicians: Andrew Ernst, Greg Bryant, Erik Archer, and undergraduates who helped collect and maintain data: Laura Daly, Anna Holmquist, Karly Dugan, Morgan Duncan, Catherine Croft, Samantha Dietz, Nicole Bissonnette, Bobby Chanthammavong, and Danielle Schmidt. I would like to give a special thanks to Dr. Warren Sconiers for his advice on teaching and my teaching philosophy (and being a top notch officemate)! I also thank Dr. Sarah Jandricic for her initial guidance with statistical analyses and Andrew Ernst for his expertise rearing insects and help with characters for identifying Hymenoptera. I thank the Frank Lab for all the help, but also for their friendship, making my time in the lab even more joyful and meaningful.

Without supplies and expertise from Tyson Wepprich and Joel Gardner, I would not have been able to complete my research. Without guidance and instruction from many bee experts, I would not have been able to grow as a scientist and individual, especially Sam Droege who has been a constant role model in my life and helped with native bee verification and identification and Dr. Jason Gibbs who identified a collection of *Lasioglossum* for me as an education tool. I want to particularly thank Sam Droege, Dr. John Ascher, Dr. Jason Gibbs, and Dr. Adrian Carper for answering my emails and questions, helping me categorize *Lasioglossum* for sociality and life histories. All of your involvement has been crucial to my scientific growth, from attending The Bee Course and Sam Droege's bee workshop to talks on the phone or emailing. Thank you so much for being there for developing scientists such as myself.

I also need to thank Dr. Clyde Sorenson for his help as my Certificate of Accomplishment in Teaching advisor and an education pillar at NCSU. I have learned much from him and from his example. Also, thanks to Jeff Essic for helping me accumulate necessary GIS data, as well as Dr. Mohan Ramaswamy for his initial database guidance.

I admire and appreciate Dr. Wes Watson and all those, from faculty to students, who make the NCSU Entomology Department work like a productive community and feel like a family. I was never once mistreated or misguided by anyone in the department and always felt as though I belonged. When everything else is new in life, it means everything to feel accepted and respected by your peers. Thank you. I want to specifically thank Heather Moylett, Katie Swoboda Bhattarai, Dr. Sally Taylor, and Dr. Steph Gorski for their friendship and support, their guidance and fun times from ESA lunches to gym workouts. I also want to particularly thank Kristen Hopperstad for all her help with my personal and professional growth. Your advice was invaluable and your friendship even more so. Words cannot express my gratitude. I also want to thank all those in other departments that I collaborated with or who answered my questions of various topics. I'd particularly like to thank Jen O'Brien for discussions about research techniques and late night work outs. It was great to bounce ideas off each other and bounce around in Zumba class.

As an undergraduate, Dr. W. Jamie Cromartie gave me the chance to develop my love for entomology and Dr. Michael Geller and Dr. George Zimmermann (AKA Zim) helped me with career paths, realizing my passion for teaching. Even though this was years ago, your caring advice still influences me today. Thank you.

Last, but not least, I'd like to thank native bees for their pollination services, without whom I would have never been able to conduct this research.

TABLE OF CONTENTS

LIST OF TABLES	ix
LIST OF FIGURES	xi
CHAPTER 1 – Wild Bee Community Shifts along an Urban-Temperature Gradient ...	1
Introduction	1
Methods	6
Study Sites	6
Wild Bee Community Surveys	7
Specimen Preparation and Identification	8
Environmental Variables	8
Bee Community Variables	9
Data Analysis	10
Results	12
Discussion	15
References	20
CHAPTER 2 – Do Thermal Limits Predict Wild Bee Community Responses to Urbanization?	47
Introduction	47
Methods	50
Results	53
Discussion	54
References	59

LIST OF TABLES

Table 1.1. Results of general linear model analyses testing my hypothesis that temperature does not affect bee abundance, floral density increases bee abundance, and impervious surface cover reduces bee abundance. Bee abundance is unaffected by temperature, floral density, impervious surface cover, and their interactions.41

Table 1.2. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting bee abundance with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The final model has an adjusted R^2 of 0.2677.42

Table 1.3. Results of general linear model analyses testing my hypothesis that temperature does not affect bee diversity but floral diversity increases bee diversity. PIE is unaffected by temperature, floral diversity, and their interaction.42

Table 1.4. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting PIE with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The final model has an adjusted R^2 of 0.1748.43

Table 1.5. Results of general linear model analyses testing my hypothesis that temperature does not affect bee richness but floral diversity increases bee richness. Rarefied bee richness is significantly affected by temperature. Rarefied bee richness has a positive relationship with temperature; as temperature increases rarefied bee richness also increases.43

Table 1.6. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting rarefied bee richness with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The model has an adjusted R^2 of 0.2852.44

Table 1.7. Results of general linear model analyses of the effects of impervious surface (100 m radius) and nesting strategy on bee abundance. Impervious surface cover and nesting affected bee abundances in nesting categories, but they were changing at the same rate because the interaction is not significant.44

Table 1.8. Results of general linear model analyses of the effects of impervious surface (1,000 m radius) and nesting strategy on bee abundance. Nesting affected bee abundances in nesting categories, but they were changing at the same rate because the interaction is not significant. When cavity and ground nesting bees were analyzed separately, they were changing at a different rate. Cavity-nesting bees were unaffected by impervious surface cover at 1,000 m radius (p-value = 0.7970), yet ground-nesting bees declined as impervious surface cover increased at the 1,000 m radius (**p-value = 0.0347**).45

Table 1.9. Results of general linear model analyses of the effects of impervious surface cover (100 m radius) and life history categories on bee abundance. Impervious surface cover and life histories affected bee abundances in life history categories, but they were changing at the same rate because the interaction is not significant.46

Table 1.10. Results of general linear model analyses of the effects of impervious surface cover (1,000 m radius) and life history categories on bee abundance. Life histories and the interaction between life histories and impervious surface cover at 1,000 m affected bee abundances in nesting categories. This means the different life history categories were changing at different rates because the interaction is significant. Particularly, eusocial bees declined with increased impervious surface cover at 1,000 m radius (**p-value = 0.0249**).45

Table 2.1. Species with their life history, nesting, mean CTmax, mean CTmax standard error, mean size, and mean size standard error.72

Table 2.2. CTmax did not predict bee abundance or incidence based on temperature or impervious surface cover of study sites where the species was located. This table shows p-values for such models. CTmax is close to being able to predict incidence of bees based on impervious surface cover at the 1,000 m radius, although it is not significant. These results do not consider phylogeny.74

Table 2.3. CTmax and some other variables showed phylogenetic signaling.74

Table 2.4. CTmax did not predict species' response to warming, when response was measured as the change in bee abundance or incidence relative to temperature or impervious surface cover of study sites. Response to warming was the slope of the line for a graph of each species where the x-axis was one of the environmental variables listed in the table below and the y-axis was bee abundance or incidence. CTmax was then analyzed to see if it would predict these slopes. This table shows p-values for such models.76

LIST OF FIGURES

- Figure 1.1.** Thermal map of Raleigh, NC on August 18, 2007. Blue represents cooler areas and red represents warmer areas. White circles with C or H are the 19 study sites with C indicating the 9 coolest sites and H indicating the 10 hottest sites. Data source Meineke et al. 2013.29
- Figure 1.2.** A natural preserve (left) compared to an urban area (right). The natural preserve has 0% impervious surface cover at the 100m radius (yellow buffer) and 1.58% impervious surface cover at the 1,000 m radius (cyan buffer). The urban residential area has 48.11% impervious surface cover at the 100 m radius and 19.46% impervious surface cover at the 1,000 m radius. Impervious surface is pixel percentage. Data source 2011 National Land Cover Database.30
- Figure 1.3.** Wild bee abundance decreases as percent impervious surface increases at the 100 m and 1,000 m radii. Impervious surface is in pixel percentages. The inner city, with the most impervious surface cover, has lowest bee abundances. Data source 2011 National Land Cover Database.31
- Figure 1.4.** I used AIC_C to select this general linear model with impervious surface ground cover predicting bee abundance per study site. Bee abundance decreases with increasing impervious surface covers at the 100 m and 1,000 m radius buffers around study sites.32
- Figure 1.5.** I used AIC_C to choose this general linear model with floral diversity predicting PIE (probability of interspecific encounter). Higher PIE means the study site has higher probability of inter specific encounter.33
- Figure 1.6.** General linear model used without AIC_C model selection with temperature predicting rarefied bee richness. Higher rarefied bee richness means the study site has higher species richness.34
- Figure 1.7.** I used AIC_C to select this general linear model with floral density predicting rarefied bee richness. Rarefied bee richness increases as floral density increases.35
- Figure 1.8.** Model selection and db-RDA used to show species community composition related to the strongest predictor. Bee species community composition varies with impervious surface cover at the 100 m radius. Axis 1 represents the impervious surface cover, while Axis 2 represents explained variation in species composition.36
- Figure 1.9.** Ground-nesting bees (triangles) and cavity-nesting bees (circles). General linear model showing impervious surface cover predicting bee abundance based on nesting. Ground-nesting and cavity-nesting bees are decreasing at the same rate as impervious surface cover at the 100 m radius increases.37

Figure 1.10. Ground-nesting bees (triangles) and cavity-nesting bees (circles). General linear model showing impervious surface cover predicting bee abundance based on nesting. When ground-nesting and cavity-nesting bees were analyzed separately, ground-nesting bees declined significantly with impervious surface cover at 1,000 m radius (p-value = 0.0347) and cavity-nesting bees did not (p-value = 0.7970).38

Figure 1.11. Eusocial (triangles), solitary (squares), subsocial (circles), and parasitic bees (Xs). General linear model showing impervious surface cover predicting bee abundance based on life history categories. All life history categories are decreasing at the same rate as impervious surface cover at the 100 m radius increases.39

Figure 1.12. Eusocial (triangles), solitary (squares), subsocial (circles), and parasitic bees (Xs). General linear model showing impervious surface cover predicting bee abundance based on life history categories. Because the interaction between life histories and impervious surface cover at the 1,000 m was significant, the life history groups were not changing at the same rate. Because of this, I separated the life history categories and found that eusocial bees declined significantly with impervious surface cover (p-value = 0.0249), yet the other life histories did not (solitary p-value = 0.3874; subsocial p-value = 0.2297; parasitic p-value = 0.3205).40

Figure 2.1. Species in phylogenetic tree and their CTmax. If a species on the CTmax graph y-axis did not have a phylogeny available, the next closest related species was used for the phylogeny. Species differ based on ANOVA ($p < 0.001$). Species with the same letter have CTmax that do not differ based on Tukey’s Honest Significant Difference test.64

Figure 2.2. Ground-nesting bees and cavity-nesting bees CTmax do not differ general linear models with or without phylogenetic correction.65

Figure 2.3. Each point on the graph is a species. Size is the mean intertegular distance of each species. Mean critical thermal maximum is the mean CTmax of each species. Bee size was not able to predict bee CTmax with or without phylogenetic correction.66

Figure 2.4. Each point on the graph is a species. Mean critical thermal maximum is the mean CTmax of each bee tested averaged by species. Temperature is the mean of the degree hours averaged across all study sites where the species occurred. CTmax did not predict bee species distribution based on temperature with or without phylogenetic signaling.67

Figure 2.5. Each point on the graph is a species. Corresponding symbols in the graph represent more related species. Mean critical thermal maximum is the mean CTmax of each bee species. Temperature is the mean of the maximum temperature average across all study sites where the species occurred. Without phylogenetic correction, CTmax did not predict species distribution based on mean maximum temperature. Once the data is phylogenetically corrected, CTmax then predicted species distribution based on mean maximum temperature. Lambda is 0.975, meaning that related species diverged more than expected under the Brownian motion model of evolution. The CTmax parameter estimate is -0.101775. As species CTmax increased, the mean maximum temperatures of the study sites where more related species were found decreased.68

Figure 2.6. Each point on the graph is a species. Mean critical thermal maxima is the CTmax of each bee tested averaged by species. Percent impervious surface cover is the mean of the percent impervious surface cover (100 m radius) averaged across all study sites where the species occurred. CTmax did not predict bee species distribution based on impervious surface cover (100 m radius) of the study sites with or without phylogenetic correction.69

Figure 2.7. Each point on the graph is a species. Mean critical thermal maxima is the mean CTmax of each species. Percent impervious surface cover is the mean of the percent impervious surface cover (1,000 m radius) averaged across all study sites where the species occurred. Without phylogenetic correction, CTmax predicted species distribution based on impervious surface cover (1,000 m radius). When I transformed the data with lambda, lambda was then 0, or independent of phylogeny. With phylogenetic correction, CTmax also predicted species distribution. The CTmax estimate is 1.37696. As species CTmax increased, the impervious surface cover (1,000 m radius) of the study sites where the species were found increased also.70

Figure 2.8. Bee CTmax predicted species distribution based on impervious surface cover (1,000 m radius). Bees with higher CTmax were present in areas with higher impervious surface cover. Data above are relative abundances shown for two species with the highest CTmax (*Xylocopa Virginia* and *Ceratina strenua*) and two species with the lowest CTmax (*Bombus bumaculatus* and *Agapostemon virescens*). Data source 2011 National Land Cover Database.71

CHAPTER 1 – Wild Bee Community Shifts along an Urban-Temperature Gradient

Introduction

A ubiquitous feature of cities is that they are warmer than the surrounding natural areas (Gago et al. 2013). This phenomenon, called the urban heat island effect, is driven largely by impervious surfaces that absorb and reradiate solar radiation (He et al. 2007). Urban warming can increase or reduce insect fitness and population growth (Colinet et al. 2015; Dale & Frank 2014; Meineke et al. 2013; Musolin & Saulich 2012; Nooten et al. 2014; Youngsteadt et al. 2015a; Youngsteadt et al. 2015b). For example, rural leaf-cutter ants (*Atta sexdens rubropilosa*) die when exposed to hot urban temperatures even though urban populations can adapt to the heat; this creates two populations of the same species with different thermal tolerances based on their thermal exposure during development (Angilletta et al. 2007). Spring-emerging bees have also showed reduced fitness due to warmer winter temperatures. Spring-emerged bees which overwinter as adults lost more weight than summer-emerged bees which overwinter as larvae, likely due to higher metabolic responses to warming (Fründ et al. 2013). In contrast, the urban heat island effect can increase the fitness of scales insects by increasing their fecundity and survival (Dale & Frank 2014; Meineke et al 2013). Since the effect of urban warming varies by species the effects on entire communities are difficult to predict. Predicting the effects of urban warming in the short term and global warming in the long term will be critical to conservation of beneficial species like wild bees.

I studied the effects of urban warming and impervious surface ground cover on urban wild bee communities compared to the well-known effects of floral density and diversity.

Wild bees are critical for pollination of many crops and wild plant species. However, evidence suggests that the abundance and range size of some wild bees are declining (Bates et al. 2011; Cameron et al. 2010; Kerr et al. 2015). By studying the effects of warming and impervious surface cover I hope to provide insights into how future climate change and urbanization may affect bees inside and outside of cities.

Insects use behavioral strategies to avoid or mitigate high temperatures (Colinet et al 2015; Hill et al. 2015). Some insects move to cooler locations in a habitat, forage at cooler times of day, or thermoregulate to avoid hotter body temperatures (Barton & Schmitz 2009; Rader et al. 2013; Stabentheiner et al. 2010). Honey bees cope with overheating by distancing themselves from each other, fanning the hive, and collecting water to spread on the combs (Evans & Butler 2010; Stabentheiner et al. 2010). Although these behaviors help the hive keep cool, they are time consuming and take energy away from other activities such as foraging and cleaning the hive, thus reducing fitness. Many bee species have optimal thermal ranges and times of day suitable for flight. Although bees often increase activity at flowers in warmer temperatures, warming decreases the amount of time available for the bees to forage because they need to spend more time cooling (Rader et al. 2013). Less foraging means less food provisioned for the young. This likely leads to fewer or smaller offspring. For some wild bees greater floral activity reduces fitness by reducing life span (Straka et al. 2014).

If temperatures remain too hot to mitigate behaviorally, insects will die or relocate (Hill et al. 2011). Thus, less tolerant species decline or disappear from unsuitable habitat but more tolerant species remain or colonize so that long-term warming can change insect

species community compositions (Banaszak-Cibicka 2014; Bartomeus et al. 2013b; Bates et al. 2011). Most insect species that cannot survive in hotter locations shift their geographical ranges poleward or upward in elevation from their previous habitat or range (Bennie et al. 2013; Hill et al. 2011; Kerr et al. 2015; Wilby & Perry 2006). Thus species' ranges often contract in the south and expand north as they move toward more suitable habitat or thermal conditions. However, if suitable habitat or thermal conditions cannot be reached a species range will only contract in the south. Kerr et al. (2015) analyzed historical bumble bee data from the past 110 years in Europe and North America to assess species response to climate change. Bumble bees are disappearing from the south, but not expanding northward. This is an example of a contracting geographic range where temperature and other conditions may be changing too fast for the species to adapt or colonize new ranges.

When species disappear from a habitat other species often colonize in response to open niches or to escape unsuitable conditions in their own habitat. In these cases insect diversity and abundance would remain the same but community composition would change. Because of this, community composition is often more sensitive to change than diversity or abundance (Winfree et al. 2011). In other cases tolerant species become more abundant while intolerant species disappear leading to lower diversity and evenness in the community (Bartomeus et al. 2013a). Some studies have found that wild bee abundance and diversity remain constant but community compositions change along an urban gradient or between distinct urban and wild areas (Banaszak-Cibicka & Zmihorski 2011; Wojcik & McBride 2012). In some cases, urban insect communities contain southern-ranged species that moved north (Banaszak-Cibicka 2014; Diamond et al. 2012; Kerr et al. 2015; Menke et al. 2011).

Menke et al. (2010) surveyed ants in North Carolina parks, forests, and throughout the city to observe ant response to land-use change. The ant species common in urbanized sites had southern and western native ranges allowing them to tolerate the warmer temperatures in cities.

Other studies have found bee abundance and diversity to decline with urbanization (Bates et al. 2011; Hennig & Ghazoul 2011). In many cases changes in bee communities have been related to floral abundance or diversity that typically benefit bees but change inconsistently along urban gradients (Hernandez et al. 2009; Pardee & Philpott 2014; Winfree et al. 2011). Some of this inconsistency may be accounted for by unmeasured abiotic factors such as temperature. I predict that bee abundance and diversity will remain similar across a temperature gradient, but that community composition will change. Bees with higher thermal tolerance will replace bees with lower thermal tolerance in hotter city locations. I also predict that floral abundance and diversity will increase bee abundance and diversity, respectively (Bennett & Gratton 2012; Wojcik et al. 2008).

In many cases the species that decline in urban areas have common life history traits. Guild or life-history diversity may be more telling in this instance and are often more important than diversity per se for preserving ecological functions (Williams et al. 2010). In addition, animals of some guilds, trophic levels, or life history strategies may be more susceptible or responsive to environmental changes than others (Fortel et al. 2014; Williams et al. 2010). Wild bees are primarily either ground-nesters that live in subterranean burrows or cavity-nesters that live in hollow twigs, wood, or hives. As ground-nesting bees live below ground and most cavity-nesting bees live above ground, it is likely that these bees experience

different temperatures during development. Some researchers have found that cavity-nesting bees are more common in urban areas (Fortel et al. 2014; Milagros 2010), while others found that ground-nesting bees are more common in urban areas (Banaszak-Cibicka & Zmihorski 2011; Fetridge et al. 2008). I predict that bee abundances will decline with increased impervious surface cover (Fortel et al. 2014). I also predict that ground-nesting bees will decrease at a faster rate with increasing impervious surface cover because impervious surface cover directly eliminates available soil for nesting (Ahrné et al. 2009; Cane et al. 2006; Matteson et al. 2008; Neame et al. 2013).

Wild bees may be eusocial, subsocial, solitary, or parasitic. These life history strategies have such different behavioral traits it is likely that they respond differently to urbanization as well. I predict social bees will be more negatively affected by urbanization than solitary bees (Winfrey et al. 2009). It is likely that solitary bees are able to better utilize the reduced amount of resources available under urban conditions because they live alone and only need enough resources for their offspring. Parasites are also often the first to respond to land-use change (Fortel et al. 2014). I predict that parasitic bees, eusocial bees, and subsocial bees will decline with more impervious surface cover and that solitary bees will remain stable or increase in abundance because of lower rates of interspecific competition.

Temperature may be an overlooked environmental variable that is playing an important role in shaping wild bee communities. Other insect communities that occur on the same plants in similar environments differ because of temperature (Nooten et al. 2014). I predict temperature is an influential variable on wild bee communities. By investigating

different aspects of urbanization over an urban-temperature gradient, I measured how temperature and other environmental variables (impervious surface cover, floral resources) influence wild bee communities and their species compositions.

Methods

Study Sites. I surveyed bee communities at 17 residential yards and 3 natural areas in and around Raleigh, NC. I compiled a list of potential volunteers and natural areas and I chose sites based on temperature, geographic distribution, and distance from each other. I used a heat map of Raleigh constructed from surface temperature measurements in 120-m thermal band (Band 6) of Landsat-5 World Reference System 2 (WRS-2) path 16, row 35 on August 18, 2007 (Meineke et al. 2013) to select sites within a range of thermal conditions. I overlaid this map with the coordinates of each potential study site in ArcMap (ArcGIS Desktop 10; ESRI, Redlands, California, USA), and chose 8 relatively warm urban sites, 2 relatively warm natural sites, 9 relatively cool urban sites, and 1 relatively cool natural site (Figure 1.1). To measure site temperatures during my observation period, I recorded hourly temperature with iButton thermochron temperature loggers (Maxim Integrated, San Jose, CA). IButtons were placed in shaded areas in tree canopies rather than out in the sun where more flowers are growing and more bees are foraging (Matteron & Langellotto 2010). I did this to protect the iButtons from overheating, but they still experienced direct sunlight in 2014. I then placed the iButtons under radiation shields in 2015 to protect them from overheating from direct sunlight, so temperatures used in analyses are only from that year (Hubbart 2011).

Urban sites were located in residential yards that ranged from 0.1 acres (~405 sq. meters) to 1.85 acres (~5,686 sq. meters). Natural sites included Annie Louise Wilkerson Preserve (35.92605, -78.60036), Prairie Ridge Ecostation (35.81264, -78.71596), and William B. Umstead State Park (35.87117, -78.76354). Although the natural areas were much larger than the residential areas, I limited sampling to 1 acre (~4,047 sq. meters) of each. To ensure independence of samples, all study sites were at least 1,000 m apart, which is the maximum foraging range for most wild, native bees (Greenleaf et al. 2007; Winfree et al. 2007).

Before beginning my second field season, I eliminated one cool urban study site due to low bee collection numbers. I created a species accumulation curve and found that the curve leveled off at five sampling dates (Gotelli & Colwell 2001). Based on this, I sampled five times in 2015 instead of six times.

Wild Bee Community Surveys. I visited 17 residential and 3 natural study sites 6 times each from May to August, 2014 and 16 residential and 3 natural study sites 5 times from May to August, 2015. On each sample date, I visited four study sites (two relatively hot and two relatively cool) and rotated the order of visitation throughout the season. At each site, I used 12 pan traps (4 blue, 4 white, and 4 yellow), 1 blue vane trap, and 20 minutes of netting to maximize sampling effort and limit collection technique biases (Ascher 2015; Cane et al. 2006; Droege 2005; Droege 2011; Droege 2015; Sardinas 2013).

I placed pan traps 5 m from each other and floral resources in two X patterns throughout the study areas when possible (Droege 2005), but site shape and size ultimately determined pan trap pattern. The blue vane trap was placed at least 5 m from the pan traps.

Because most bees forage from 9:00 to 16:30 (Albretch et al. 2012), traps were left out for 5 to 7 hours between 8:00 and 17:30. I collected bees with aerial netting between 10:00 to 17:00 for 20 minutes at each site.

Specimen Preparation and Identification. I pinned netted bees without washing them and washed and dried specimens from pan traps and blue vane traps (Droege 2005). I identified species using the online Discover Life key (<http://www.discoverlife.org/>), by comparison to reference specimens in the North Carolina State University Insect Museum, and by consulting experts. In 2014, experts verified bee identification and identified *Lasioglossum*. In 2015, I identified bees to species, but separated difficult to identify genera *Lasioglossum* and *Sphecodes* into morphospecies. I included morphospecies in analyses, but did not include 30 unidentifiable bees in the analyses (most were male *Lasioglossum*). As an indicator of body size, I also measured bee intertegular distances (Fortel et al. 2014; Greenleaf et al. 2007).

Voucher specimens will be deposited in the North Carolina State University Insect Museum. Other specimens were donated to the natural study sites as documentation of species found and outreach materials for visiting guests or sent to other scientists as supplemental data to their research.

Environmental Variables. For each site, hourly temperature recordings were averaged into mean hourly temperature and converted to cumulative degree hours by subtracting 15°C base temperature from the hourly recordings and summing any number greater than zero. I chose 15°C as the base temperature for degree hours because most bee species are foraging by then (Batra 1985; Heinrich & Raven 1972; Heinrick 1975; Rader et

al. 2013; Stone 1994). Hourly mean site temperature ranged from 23.74°C to 28.03°C. Degree hours ranged from 15752.25 to 19133.50. Temperature data are from 2015 because 2014 temperature data was compromised. I analyzed percent impervious surface cover (2011 National Land Cover Database) within buffers of 100 m and 1,000 m radii surrounding each study site using ArcMap (ArcGIS Desktop 10; ESRI, Redlands, California, USA). Impervious surface cover ranged from 0% to 48.11% at the 100 m radius and 0.62% to 40.14% impervious surface cover at the 1,000 m radius from study sites (Figure 1.2).

To measure floral diversity at each site, I photographed every blooming flower type on each sampling date in 2014 and 2015. Plants were identified to the lowest taxonomic level possible from pictures which provided a measure of species richness at each site. Mean 2014 and 2015 floral richness was calculated for each site. In 2015, I estimated floral resource abundance by placing a 1 m pvc pipe square where I observed the lowest and highest floral densities. This was to calibrate my eyes for estimating total floral bloom abundance on a logarithmic scale at each site on each date (Bates et al., 2011). I took the most common floral abundance for each site based on the five sampling dates and divided it by site area to obtain a measure of floral density which ranged from 100 flowers to 60,000 flowers per acre.

Bee Community Variables. The number of bees collected by pan traps (not netting or vane traps) from each site was considered bee abundance to avoid collector biases. I calculated two estimates of bee diversity for each study site: PIE (probability of interspecific encounter, eq. 1) and rarefied species richness.

$$PIE = (N/N-1)(1 - \sum_{i=1}^s p_i^2)$$

Where N is the total number individuals in the sample, s is the total number of species, and p is the proportion of the entire sample represented by species i to investigate species richness and evenness in one biologically relevant variable (Gotelli et al 2013; Hamilton 2005; Hurlbert 1971). To estimate species richness independently of bee abundance, I used EstimateS (Colwell 2013) to rarefy samples to 100 bees from each study site. PIE and richness calculations included bees collected with all methods: pan traps, vane traps, and netting.

Species community compositions were based on bee species abundances from only pan traps to reduce sampling bias and eliminated species found at one study site. I also assigned bees to nesting and life history categories I based on previous studies with similar categories and by consulting experts (Ascher 2015; Carper 2015; Droege et al.; Droege 2015; Fetridge et al. 2008; Gibbs & Griswold 2014; Gibbs et al. 2014; Gibbs et al. 2013; Gibbs 2015; Gibbs 2011; Gibbs 2010; Gibbs; Linsley et al. 1980; Michener 1974; United State Department of Agriculture).

Data Analysis. To test my specific predictions about the relationships between environmental variables and bee abundance and diversity, I constructed a series of linear models using PROC GLM in SAS (SAS 9.4; SAS Instituted, Cary, NC, USA). I predicted bee abundance and diversity would remain the same across a temperature gradient. I also predicted bee abundance would decrease with increasing impervious surface cover and increase with floral density and bee diversity would increase with floral diversity. To improve distribution of residuals in these linear models, I $\ln(x+1)$ transformed bee abundance

and rarefied bee richness and arcsin(sqrt) transformed PIE. I hypothesized that temperature would influence species community composition.

To consider the possibility that other combinations of environmental variables might better predict bee abundance and diversity, I explored all possible combinations of predictors in SAS. To choose the strongest combination of predictor variables, I compared AIC_C (Akaike information criterion corrected for small sample size) for all models and predictor variables (Symonds & Moussalli 2011). Specifically, I explored temperature, floral density, and impervious surface cover (100 m and 1,000 m radii) as predictors of bee abundance, PIE, and rarefied bee richness.

Before using statistics to analyze community composition, I $\ln(x+1)$ transformed the abundance of each species to increase linearity of relationships between species abundances and environmental variables. I did not transform present/absent data of each species where abundance of the species was disregarded. To test my prediction about temperature changing species community composition, I used a db-RDA (Bray-Curtis distance based redundancy analysis) in R (R Core Team 2013) using Vegan package Version 2.2-1 (Oksanen et al. 2015). Db-RDA is a multivariate multiple regression where the environmental variable is the predictor (temperature in this case) and the species are the response variables.

To investigate how species composition changed relative to all measured environmental predictor variables, I used AIC-based stepwise model selection to choose the strongest predictors of species community composition for two models, one describing $\ln(x+1)$ species abundances and the other species incidence. To examine variation in

community composition, I used db-RDA in R Vegan package with the selected variables (Gugger 2012).

To determine whether bees with different nesting strategies responded differently to impervious surface cover, I used JMP (JMP Pro 11.2.0; SAS Instituted, Cary, NC, USA) to fit mixed models. I $\ln(x+1)$ transformed the total abundance of bees in each nesting category to increase linearity and normality. I used a model where natural $\log(x+1)$ bee abundance was the response and nesting, impervious surface cover, and their interactions were predictors. I used two separate models to test 100 m and 1,000 m radii of impervious surface cover. I also added sites as a random effect to account for multiple bee abundances categorized into different nesting histories for the same study site. The same methods were used for life histories replacing nesting as a predictive variable.

Results

I collected a total of 3,755 bees from 119 species (including 7 morphospecies) at 19 sites over 2 years. Of these, 53% were in the genus *Lasioglossum*. I caught ~35% of bees with netting, ~62% bees with bee bowls, and ~3% of bees with vane traps. Of the total count, ~91% are ground-nesting, ~9% are cavity-nesting, ~74% are eusocial, ~5% are subsocial, ~20% are solitary, and <1% are parasitic species.

Over all study sites, bee abundance ranged from 40 to 302 individuals from total pan trap sampling. Bee abundance was unaffected by temperature, floral density, impervious surface cover at 100 m and 1,000 m radii, and their interactions (Table 1.1). On the basis of the AIC_C -based model selection procedure, the model that best predicted bee abundance had impervious surface cover at the 100 m and 1,000 m radii as predictor variables (Table 1.2;

Figure 1.3 and Figure 1.4) with an adjusted R^2 of 0.2677. Bee abundance decreased with increasing impervious surface cover (100 m and 1,000 m radii).

Over all study sites, PIE ranged from 0.73 to 0.96. PIE was unaffected by temperature, floral diversity, and their interaction (Table 1.3). The model that best predicted PIE had floral diversity as the predictor variable (Table 1.4; Figure 1.5) with an R^2 of 0.1748. PIE increased as floral diversity increased.

Over all study sites, rarefied bee species richness ranged from 17.74 to 38.99 species per 100 bees. Rarefied bee richness was significantly affected by temperature ($p = 0.0331$) (Table 1.5). This showed that, as temperature increased, rarefied bee richness increased (Figure 1.6). The AIC_C -based model that best predicted rarefied bee richness had floral density as the predictor variable (Table 1.6; Figure 1.7) with an R^2 of 0.2852. Rarefied bee richness increased as floral density increased.

Community composition was unaffected by temperature with bee abundance data and incidence data (p -value = 0.129; p -value = 0.491, respectively). The species composition db-RDA model selection using species abundance as the response variable selected impervious surface cover at the 100 m radius to explain the most variance within the model (Figure 1.8). When model selection was used with the species incidence data as a response variable, no predictor variables were selected, although impervious surface cover at 100 m was nearly significant (p -value = 0.065).

The abundance of most species were negatively related to impervious surface cover at 100 m radius (Figure 1.8). A few species responded strongly and contribute the most to the significant changes in community composition across impervious surface cover at 100 m

radius. *Lasioglossum pilosum*, *Lasioglossum tegulare*, and *Lasioglossum zephyrum* were more abundant in locations with higher percent impervious surface cover. *Lasioglossum bruneri*, *Augochlorella aurata*, and a few other *Lasioglossum* species are more abundant in locations with lower percent impervious surface cover.

Impervious surface cover at the 100 m radius (p-value = 0.0017) significantly predicted bee abundances of cavity-nesting and ground-nesting bees with an adjusted R^2 of 0.8264 (Table 1.7; Figure 1.9). Ground-nesting and cavity-nesting bees decreased at the same rate as impervious surface cover at the 100 m radius increases. In the second model, impervious surface cover at 1,000 m radius was not significant (p-value = 0.3377), but there was a nearly significant interaction between nesting and impervious surface cover (p-value = 0.0555) with an R^2 of 0.8923 (Table 1.8; Figure 1.10). Because the interaction was almost significant, I analyzed ground-nesting and cavity-nesting bees separately. Ground-nesting bees significantly declined with impervious surface ground cover at the 1,000 m radius (p-value = 0.0347). Cavity-nesting bees were unaffected by impervious surface cover at the 1,000 m radius (p-value = 0.7970).

Impervious surface cover at the 100 m radius (p-value = 0.0355) significantly affected the bee abundances of eusocial, subsocial, solitary, and parasitic bees with an adjusted R^2 of 0.8154 (Table 1.9; Figure 1.11). All life history categories are decreasing at the same rate as impervious surface cover at the 100 m radius increases. In the second model, impervious surface cover at 1,000 m radius was not significant (p-value = 0.4412), but the interaction between life history categories and impervious surface cover at 1,000 m radius

(p-value = 0.0479) significantly affected the bee abundances of eusocial, subsocial, solitary, and parasitic bees with an adjusted R^2 of 0.8474 (Table 1.10; Figure 1.12). Because the interaction was significant, I analyzed the life history categories separately. Eusocial bees significantly declined with impervious surface ground cover at the 1,000 m radius (p-value = 0.0249). Solitary, subsocial, and parasitic bees were unaffected by impervious surface cover at the 1,000 m radius (p-value = 0.3874; p-value = 0.2297; p-value = 0.3205; respectively).

Discussion

Urban areas are expanding at unprecedented rates as the population grows and people move from rural to urban homes (Seto et al. 2011). This means that impervious surface cover and concomitant effects on temperature and habitat quality are also increasing. My goal was to determine how temperature and impervious surface cover affected wild urban bee communities.

Impervious surface cover has direct and indirect effects on habitat temperature (Xiao et al. 2007; Yuan & Bauer 2007), floral abundance and diversity (Cane 2005; Fortel et al. 2014; Hernandez et al. 2009; Marco et al. 2008; McKinney 2006), connectivity (Alberti 2005; Bierwagen 2007; Winfree et al. 2009), nesting resources (Chace & Walsh 2006; Fortel et al. 2014; Hernandez et al. 2009), pollution, and even bee health (Appler 2014; Goulson et al. 2012; Grimm et al. 2008; Huang 2012; Jha & Kremen 2013). Perhaps because it can affect so many different aspects of habitat quality I found that impervious surface cover reduced the overall abundance of bees in the community and strongly affected bee community composition. In fact, the effects of impervious surface cover in my study was

stronger and more consistent than the effects of floral diversity or density that are often implicated as driving urban bee community composition.

Impervious surface cover reduced the abundance of many bee species but increased a few that may be urban adapters. *Lasioglossum pilosum*, *Lasioglossum tegulare*, and *Lasioglossum zephyrum* abundances increased with impervious surface cover. Most bees decreased with impervious surface cover, but *Lasioglossum bruneri* and *Augochlorella aurata* decreased the most. Although these species respond differently to increasing amounts of impervious surface cover, all of these species are small, eusocial, ground-nesting bees. This is interesting and important because it suggests that bees with similar roles in the bee community are replacing each other along an impervious surface cover gradient.

In my study, impervious surface cover also affected cavity-nesting and ground-nesting bee abundances. Some studies found cavity-nesters to be more common in the urban areas (Fortel et al. 2014; Milagros 2010), while others found ground-nesters to be more common (Banaszak-Cibicka & Zmihorski 2011; Fetridge et al. 2008). These differences may result in part from how ‘urban’ was defined and the scale at which it was measured. I found that the effects of impervious surface cover around study sites differed at the 100 m and 1,000 m radii. At the 100 m radius, both cavity-nesting and ground-nesting bee abundances declined. At the 1,000 m radius, ground-nesting bees declined, yet cavity-nesting bees were unaffected. It is likely that impervious surface cover directly eliminates ground-nesting resources. More research needs to manipulate bee nesting resources so that we can learn how to appropriately add nesting resources to urban areas to buffer some of the negative effects of impervious surface cover on wild bee communities.

The effect of impervious surface cover on bees in each life history category also differed at the 100 m and 1,000 m spatial scales. At the 100 m radius of impervious surface cover, eusocial, subsocial, solitary, and parasitic bees all declined at the same rate. At the 1,000 m radius of impervious surface cover, eusocial bees declined while subsocial, solitary, and parasitic bees were unaffected. Studies have found eusocial bees decline with increasing impervious surface cover (Zanette et al. 2005) and tended to be more negatively affected by urbanization than solitary bees (Winfree et al. 2009; Winfree et al. 2011). Eusocial bees require more resources due to their larger populations that form larger nests so it makes sense that they would decline with increasing impervious surface cover.

Winfree et al. (2009) reviewed bee response to anthropogenic land-use change and found that pollinators respond more consistently to the change of floral resources than other variables of land-use change. Bee diversity and bee abundance tend to be positively related to floral richness, floral abundance, or both (Grundel et al. 2010; Hopwood 2008; Matteson et al. 2013; Matteson & Langellotto 2010; Pardee & Philpott 2014; Wojcik et al. 2008). Although some urban areas can have the floral resources required for wild bees, most urban areas have increased floral diversity from invasive, ornamental species (Hinners & Hjelmroos-Koski 2009; McIntyre 2000; Quintero et al. 2010). Native bees are usually more attracted to native flowers, but some can also be attracted to and eat exotic, ornamental flowers (Hinners & Hjelmroos-Koski 2009; Masierowska 2006). Other studies have found that many exotic flowers do not necessarily feed native bees (Bergerot et al. 2010; Faeth et al. 2011). I did not separate native from exotic flowers. PIE, the probability of interspecific encounter, gives the probability that two individuals from a community will be two different

species and measures species evenness and richness (Hamilton 2005). Rarefied bee richness measures the number of species found at each study site based on a bee community of the same abundance or size. I found that PIE increased as floral diversity increased and rarefied bee richness increased as floral density increased. Of course impervious surface cover and floral availability are not mutually exclusive and it is clear that floral diversity and floral density are both important for a diverse bee community.

Contrary to my prediction rarefied bee richness increased with site temperature. This could indicate that urban areas have not yet reached temperatures near species thermal tolerances (Diamond et al. 2012). Bees also prefer warm, sunny locations (Matteson & Langellotto 2010), so warmer locations could be supporting more diverse bees. The temperature data loggers were positioned in shady areas out of direct sunlight. Thus, an alternative explanation is that my data loggers did not provide an appropriate measurement of site temperature. Percent impervious surface cover is linearly related to land surface temperature (Dale & Frank 2014; Yuan & Bauer 2007). Impervious surface cover may be a reliable measurement of large-scale temperature and may be a better proxy for the temperatures bees experience while foraging. Also, the natural study sites were all open meadows. Other studies have found lower bee abundance and diversity in natural sites but in these cases natural sites were forests where temperature and floral resources were low (Carper 2013; Fetridge et al. 2008; Liu & Koptur 2003; Quintero et al. 2010; Sattler et al. 2010; Winfree et al. 2007). I studied three natural sites, two of which were some of the hottest of the study sites. This could also be influencing my results with temperature increasing rarefied bee richness and other results as well.

I believe temperature should still be considered when studying communities in ecology. Insects have thermal ranges for their survival (Colinet et al. 2015). Temperature has already been shown to affect bumble bees by contracting their geographic ranges (Kerr et al. 2015). Temperature will also likely influence plant-pollinator interactions and potential phenological shifts (Harrison & Winfree 2015). Global temperature is predicted to increase 1-3°C in the next 50-100 years (Pachauri et al. 2014) and urban areas are expanding at unparalleled rates (Seto et al. 2011). More research needs to be conducted that involves temperature in observational studies and manipulative studies to help us continue to understand how insect communities, especially bee communities, respond to warming.

References

- Ahrné, K., J. Bengtsson, T. Elmqvist. 2009. Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. PLoS One. e5574. doi:10.1371/journal.pone.0005574.
- Alberti, M. 2005. The effects of urban patterns on ecosystem function. Inter. Reg. Sc. Rev. 28(2): 168-192.
- Angilletta, M. J. Jr., R. S. Wilson, A. C. Niehaus, M. W. Sears, C. A. Navas, and P. L. Ribeiro. 2007. Urban physiology: City ants possess high heat tolerance. PLoS One. e258. doi:10.1371/journal.pone.0000258.
- Appler, R. H. 2014. The effect of urbanization on the immunocompetence and pathogen pressure of managed and feral honey bees (*Apis mellifera* Linnaeus). North Carolina State University Thesis.
- Ascher, J. S. 2015. Personal communication.
- Banaszak-Cibicka, W. 2014. Are urban areas suitable for thermophilic and xerothermic bee species (Hymenoptera: Apoidea: Apiformes)? Apidologie. 45: 145-155.
- Banaszak-Cibicka, W. & M. Zmihorski. 2001. Wild bees along an urban gradient: Winners and losers. J. of Insect Cons. 16: 331-343.
- Bartomeus, I., J. S. Ascher, J. Gibbs., B. N. Danforth, D. L. Wagner, S. M. Hedtke, & R. Winfree. 2013a. Historical changes in northeastern US bee pollinators related to shared ecological traits. Proc. of the Nat. Aca. of the United State of America. 110(12): 4656-4660.
- Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth A. N. Lakso, & R. Winfree. 2013b. Biodiversity ensures plant-pollinator phenological synchrony against climate change. Eco. Letters. 16: 1331-1338.
- Barton, B. T. & O. J. Schmitz. 2009. Experimental warming transforms multiple predator effects in a grassland food web. Eco. Letters. 12(12): 1317-1325.
- Bates, A. J., J. P. Sadler, A. J. Fairbrass, S. J. Falk, J. D. Hale, & T. J. Matthews. 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. PLoS One. 6(8): e23459. doi:10.1371/journal.pone.0023459.
- Batra, S. 1985. Red maple (*Acer rubrum* L.) an important early spring food resource for honey bees and other insects. J. of the Kansas Ent. Soc. 169-172.

- Bennett, A. B. & C. Gratton. 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. *Landscape and Urban Planning*. 104: 26-33.
- Bennie, J., J. A. Hodgson, C. R. Lawson, C. T. Holloway, D. B. Roy, T. Brereton, ...R. J. Wilson. 2013. Range expansion through fragmented landscapes under a variable climate. *Eco. Letters*. 16(7): 921-929.
- Bergerot, B., B. Fontaine, M. Renard, A. Cadi, & R. Julliard. 2010. Preferences for exotic flowers do not promote urban life in butterflies. *Landscape and Urban Planning*. 96(2): 98-107.
- Bierwagen, B. G. 2007. Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. *Urban Eco*. 10: 29-42.
- Cameron, S. A. et al. 2010. Patterns of widespread decline in North American bumble bees. *PNAS*, Early Ed. 1-6.
- Cane, J. H. 2005. Bees, pollination, and the challenges of sprawl. *Nature in Frag. The Legacy of Sprawl*. Columbia University Press, New York. 109-124.
- Cane J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, & N. M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Eco. Appl*. 16(2): 632-644.
- Carper, A. 2013. Effects of suburbanization on plant-pollinator interactions. Dartmouth College Dissertation.
- Chace, J. F. & J. J. Walsh. 2006. Urban effects on native avifauna: A review. *Landscape and Urban Planning*. 74: 46-69.
- Colinet, H., B. J. Sinclair, P. Vernon, & D. Renault. 2015. Insects in fluctuating thermal environments. *Ann. Rev. of Ent*. 60: 123-140.
- Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at <http://purl.oclc.org/estimates>.
- Dale, A. G. & S. D. Frank. 2014. Urban warming trumps natural enemy regulations of herbivorous pests. *Eco. Appl*. 24(7): 1596-1607.
- Diamond, S. E., L. M. Nichols, N. McCoy, C. Hirsch, S. L. Peline, N. J. Sanders...R. R. Dunn. 2012. A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology*. 93(11): 2305-2312.

Droege, S. 2015. Personal communication.

Droege, S., S. Kolski, J. S. Ascher, & J. Pickering. Bee identification key. Retrieved from <http://www.discoverlife.org/>.

Evans, E. C., & C. A. Butler. 2010. *Why do bees buzz? Fascinating answers to questions about bees*. New Brunswick, NJ: Rutgers University Press.

Faeth, S. H., C. Bang, & S. Saari. 2011. Urban biodiversity: Patterns and mechanisms. *Ann. of the New York Aca. of Sc.* 1223: 69-81.

Fetridge, E. D., J. S. Ascher, & G. A. Langellotto. 2008. The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Ann. of the Ent. Soc. of America.* 101(6): 1067-1077.

Fortel, L., H. Henry, L. Guilbaud, A. L. Guirao, M. Kuhlmann, H. Mouret, ...B. E. Vaissière. 2014. Decreasing abundance, increasing diversity and changing structure of the wild bee community (ymenoptera: Anthophila) along an urbanization gradient. *PLoS One.* e104679. doi: 10.1371/journal.pone.0104679.

Fründ, J., S. L. Zieger, & T. Tschardt. 2013. Response diversity of wild bees to overwintering temperatures. *Oecologia.* 173: 1639-1648.

Gago, E. J., J. Roland, R. Pacheco-Torres, & J. Ordóñez. 2013. The city and urban head islands: A review of strategies to mitigate adverse effects. *Renewable and Sustainable Energy Rev.* 25: 749-758.

Gibbs, J. 2015. Personal communication.

Gibbs, J. Halictidae. Retrieved from <https://sites.google.com/site/dialictus/bees-of-tompkins-county/halictidae-halictinae-halictini>.

Gibbs, J. 2011. Revisions of the metallic *Lasioglossum* (Dialictus) of Eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa.* 3073: 1-216.

Gibbs, J. 2010. Revision of the metallic species of *Lasioglossum* (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). *Zootaxa.* 2591: 1-382.

Gibbs, J. & T. Griswold. 2014. Bee biology, ecology, evolution and systematics: The latest buss in bee biology. *J. of Melittology.* 29: 1-15.

Gibbs, J., S. Dumesh, & T. L. Griswold. 2014. Bees of the genera *Dufourea* and *Dieunomia* of Michigan (Hymenoptera: Apoidea: Halictidae), with a key to the *Dufourea* of the Eastern United States. *J. of Melittology*. 29: 1-15.

Gibbs, J., L. Packer, S. Dumesh, & B. N. Danforth. 2013. Revision and reclassification of *Lasioglossum* (Evyllaesus), *L.* (Hemihalictus) and *L.* (Sphecodogastra) in Eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa*. 3672: 1-117.

Gotelli, N. J., A. Chao, & S. Levin. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. *Encyc. of Biod.* 5: 195-211.

Gotelli, N. J. & R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Eco. Letters*. 4(4): 379-391.

Goulson, D., P. Whitehorn, & M. Fowley. 2012. Influence of urbanization on the prevalence of protozoan parasites of bumblebees. *Eco. Ent.* 37: 83-89.

Greenleaf, S. S., N. M. Williams, R. Winfree, & C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia*. 153(3): 589-596.

Grimm, N. B., D. Foster, P. Groffman, J. M. Grove, C. S. Hopkinson, K. J. Nadelhoffer, ...D. P. Peters. 2008. The changing landscape: Ecosystem responses to urbanization and pollution across climatic and societal gradients. *Fron.in Eco. and the Env.* 6(5): 264-272.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, & N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution - across an open-forest gradient. *Eco. Appl.* 20(6): 1678-1692.

Gugger, P. F. 2012. Redundancy Analysis Tutorial: Landscape Genetics. University of California, Los Angeles PDF Publication.

Hamilton, A. J. 2005. Species diversity or biodiversity? *J. of Env. Mngt.* 75: 89-92.

Harrison, T. & R. Winfree. 2015. Ecology of Organisms in Urban Environments: Urban drivers of plant-pollinator interactions. *Func. Eco.* 29: 879-888.

He, J. F., J. Y. Liu, D. F. Zhuang, W. Zhuang, & M. L. Liu. 2007. Assessing the effect of land use/land cover change on the change of urban heat island intensity. *Theo. and Appl. Clim.* 90(3-4): 217-226.

Heinrich, B. & P. H. Raven. 1972. Energetics and pollination ecology. *Sc.* 176(4035): 97-602.

- Heinrich B. 1975. Energetics of pollination. *Ann. Rev. of Eco. and Sys.* 139-170.
- Hennig, E. I. & J. Ghazoul. 2011. Plant-pollinator interactions within the urban environment. *Persp. in Plant Eco., Evo. and Sys.* 13(2): 137-150.
- Hernandez, J. L., G. W. Frankie & R. W. Thorp. 2009. Ecology of urban bees: A review of current knowledge and direction for future study. *Cities and the Env.* 2: 3.
- Hill, J. K., H. M. Griffiths, & C. D. Thomas. 2011. Climate change and evolutionary adaptations at species' range margins. *Ann. Rev. of Ent.* 56: 143-159.
- Hinners, S. J. & M. K. Hjelmroos-Koski. 2009. Receptiveness of foraging wild bees to exotic landscape elements. *The American Midland Naturalist.* 162(2): 253-265.
- Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. *Bio. Cons.* 141(10): 2632-2640.
- Huang, Z. 2012. Pollen nutrition affects honey bee resistance. *Terr. Arth. Rev.* 5(2): 175-189.
- Hubbart, J. A. 2011. An inexpensive alternative solar radiation shield for ambient air temperature and relative humidity micro-sensors. *J. of Nat. and Env. Sc.* 2(2): 9-14.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. *Eco.* 52(4): 577-586.
- Jha, S. & C. Kremen. 2013. Urban land use limits regional bumble bee gene flow. *Mol. Eco.* 22(9): 2483-2495.
- Kerr, J. T., S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, ...S. G. Potts. 2015. Climate change impacts on bumblebees converge across continents. *Sc.* 349(624): 177-180.
- Linsley, E. G., J. W. MaxSwain, & C. D. Michener. 1980. *Nesting Biology and Associates of Melitoma (Hymenoptera, Anthophoridae)*. Berkeley, CA; University of California Press.
- Liu, H. & S. Koptur. 2003. Breeding system and pollination of a narrowly endemic herb of the lower Florida Keys: Impacts of the urban-wildlife interface. *American J. of Botany.* 90(8): 1180-1187.
- Marco, A., T. Dutoit, M. Deschamps-Cottin, J. Mauffrey, M. Vennetier, V. Bertaudière-Montes. 2008. Gardens in urbanizing rural areas reveal an unexpected floral diversity related to housing density. *Comptes Rendus Biologies.* 331(6): 452-465.

- Masierowska, M. L. 2006. Floral reward and insects visitation in ornamental Deutzias (*Deutzia* spp.), saxifragaceae sensu lato. *J. of Apic. Res.* 45: 13.
- Matteson, K. C., J. B. Grace, & E. S. Minor. 2013. Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. *Oikos*. 122(5): 682-694.
- Matteson, K. C., J. S. Ascher, & G. A. Langellotto. 2008. Bee richness and abundance in New York City urban gardens. *Ann. of the Ent. Soc. of America*. 10: 140-150.
- Matteson, K. C. & G. A. Langellotto. 2010. Determinates of inner city butterfly and bee species richness. *Urban Eco*. 13(3): 333-347.
- McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. *Ann. of the Ent. Soc. of America*. 93(4): 825-835.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Bio. Cons.* 127(3): 247-260.
- Meineke, E. K., R. R. Dunn, & S. D. Frank. 2014. Early pest development and loss of biological control are associated with urban warming. *Bio. Letters*. 10(11): 1-4.
- Meineke, E. K., R. R. Dunn, O. J. Sexton, & S. D. Frank. 2013. Urban warming drives insect pest abundance on street trees. *PLoS One*. 8(3): e59687. doi: 10.1371/journal.pone.0059687.
- Menke, S. B., B. Guénard, J. O. Sexton, M. D. Weiser, R. R. Dunn, & J. Silverman. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerance species; an example from ants. *Urban Eco*. 14(2): 135-163.
- Michener, C. D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Cambridge, MA; Harvard University Press.
- Milagros, D. 2010. Diversity and biological aspects of wild bees in an urban and a natural environment in the central region of Santa Fe, Argentina. *Revista De La Sociedad Entomologica Argentina*. 69: 33-44.
- Musolin, D. & A. K. Saulich. 2012. Responses of insects to the current climate changes: From physiology and behavior to range shifts. *Ent. Rev.* 92(7): 715-740.
- Neame, L. A., T. Griswold, & E. Elle. 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. *Insect Cons. and Div.* 6: 57-66.

- Nooten, S. S., N. R. Andrew, & L. Hughes. 2014. Potential impacts of climate change on insect communities: A transplant experiment. *PLoS One*. 9(1): e85987. doi: 10.1371/journal.pone.0085987.
- Oksanen, J., F. Guillaume Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, & H. Wagner. 2015. *Vegan: Community Ecology Package*. R package version 2.2-1. <http://CRAN.R-project.org/package=vegan>.
- Pachauri, P. K., M. Allen, V. Barros, J. Broome, W. Cramer, R. Christ, ... P. Dasgupta. 2014. *Climate change 2014: Synthesis report. Contribution of working groups I, II, and III to the fifth assessment report of the intergovernmental panel on climate change*.
- Pardee, G. L. & S. M. Philpott. 2014. Native plants are the bee's knees: Local and landscape predictors of bee richness and abundance in backyard gardens. *Urban Eco*. 17(3): 641-659.
- Quintero, C., C. L. Morales, & M. A. Aizen. 2010. Effects of anthropogenic habitat disturbance on local pollinator diversity and species turnover across a precipitation gradient. *Biod. and Cons.* 19: 257-274.
- R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R. K. Reilly, I. Bartomeus, & R. Winfree. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Bio*. 19(10): 3130-3110.
- Sattler, T., P. Duelli, M. K. Obrist, R. Arlettaz, & M. Moretti. 2010. Response of arthropod species richness and functional groups to urban habitat structure and management. *Lands. Eco*. 25(6): 941-954.
- Seto, K. C., M. Fragkias, B. Güneralp, & M. K. Reilly. 2011. A meta-analysis of global urban land expansion. *PLoS One*. 6(8): e23777. doi: 10.1371/journal.pone.0023777.
- Stabentheiner, A., H. Kovac, & R. Brodschneider. 2010. Honeybee colony thermoregulation—regulatory mechanisms and contribution of individuals in dependence on age, location and thermal stress. *PLoS One*. 5: e8967. doi: 10.1371/journal.pone.0008967.
- Stone, G. N. 1994. Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body size. *Eco. Ent.* 19(2): 177-189.
- Straka, J., K. Černá, L. Macháčková, M. Zemenová, P. Keil. 2014. Life span in the wild: The role of activity and climate in natural populations of bees. *Func. Eco*. 28(5): 1235-1244.

Symonds, M. R. & A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioral ecology using Akaike's information criterion. *Behav. Eco. and Socio.* 65: 13-21.

United State Department of Agriculture. *Ptilothrix bombiformis*, the rose-mallow bee. Retrieved from <http://www.fs.fed.us/wildflowers/pollinators/pollinator-of-the-month/rosemallowbee.shtml>.

Wilby, R. L. & G. L. Perry. 2006. Climate change, biodiversity and the urban environment: A critical review based on London, UK. *Progress in Physical Geo.* 30: 73-98.

Williams, N. M., E. E. Crone, H. R. T'ai, R. L. Minckley, L. Packer, & S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Bio. Cons.* 143(10): 2280-2291.

Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, & M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Eco.* 90(8): 2068-2076.

Winfree, R., I. Bartomeus, & D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Ann. Rev. of Eco., Evo. and Sys.* 42: 1.

Winfree, R., T. Griswold, C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Cons. Bio.* 21: 213-223.

Wojcik, V. A., G. W. Frankie, R. W. Thorp, & J. L. Hernandez. 2008. Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *J. of the Kansas Ent. Soc.* 81: 15-28.

Wojcik, V. A. & J. R. McBride. 2012. Common factors influence bee foraging in urban and wildland landscapes. *Urban Eco.* 15(3): 581-598.

Xiao, R., Z. Ouyang, H. Zheng, W. Li, E. W. Schienke, & X. Wang. 2007. Spatial pattern of impervious surface and their impacts on land surface temperature in Beijing, China. *J. of Env. Sc.* 19(2): 250-256.

Youngsteadt, E., A. G. Dale, A. J. Terando, R. R. Dunn, & S. D. Frank. 2015. Do cities stimulate climate change? A comparison of herbivore response to urban and global warming. *Global Change Bio.* 21: 97-105.

Youngsteadt, E., R. C. Henderson, A. M. Savage, A. F. Ernst, R. R. Dunn, & S. D. Frank. 2015. Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods. *Global Change Bio.* 21(3): 1103-1115.

Yuan, F. & M. E. Bauer. 2007. Comparison of impervious surface area and normalized difference vegetation index as indicators of surface urban heat islands effects in landsat imagery. *Remote Sensing of Env.* 106(3): 375-386.

Zanette, L. R. S., R. P. Martins, & S. P. Ribeiro. 2005. Effects of urbanization in neotropical wasp and bee assemblages in Brazilian metropolis. *Landscape and Urban Planning.* 71(2): 105-121.

FIGURES

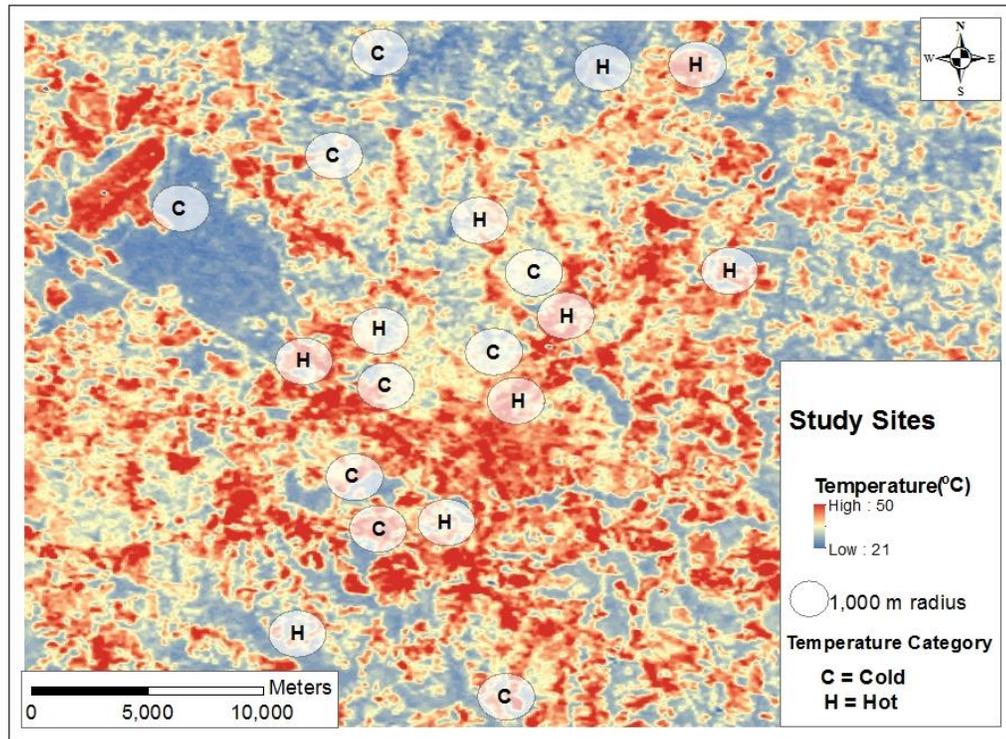


Figure 1.1. Thermal map of Raleigh, NC on August 18, 2007. Blue represents cooler areas and red represents warmer areas. White circles with C or H are the 19 study sites with C indicating the 9 coolest sites and H indicating the 10 hottest sites. Data source Meineke et al. 2013.

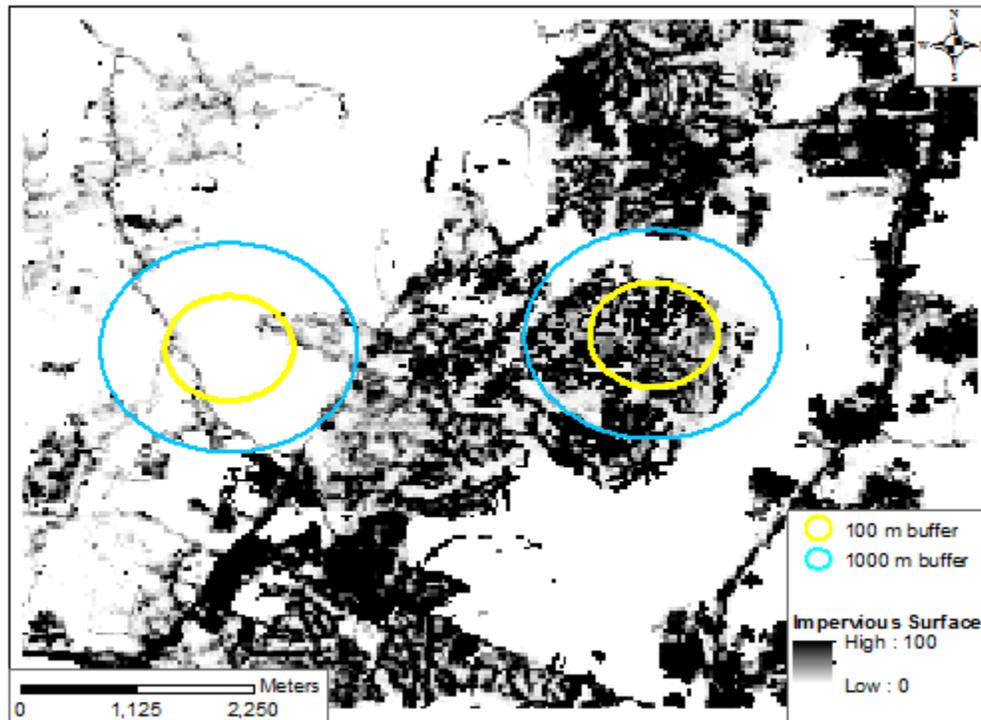


Figure 1.2. A natural preserve (left) compared to an urban area (right). The natural preserve has 0% impervious surface cover at the 100m radius (yellow buffer) and 1.58% impervious surface cover at the 1,000 m radius (cyan buffer). The urban residential area has 48.11% impervious surface cover at the 100 m radius and 19.46% impervious surface cover at the 1,000 m radius. Impervious surface is pixel percentage. Data source 2011 National Land Cover Database.

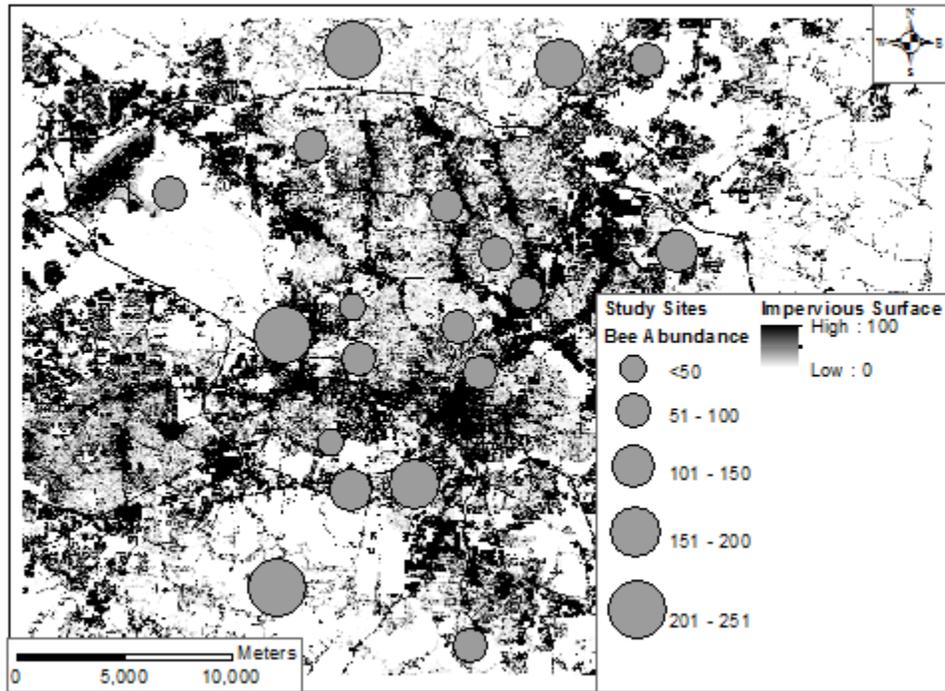


Figure 1.3. Wild bee abundance decreases as percent impervious surface increases at the 100 m and 1,000 m radii. Impervious surface is in pixel percentages. The inner city, with the most impervious surface cover, has lowest bee abundances. Data source 2011 National Land Cover Database.

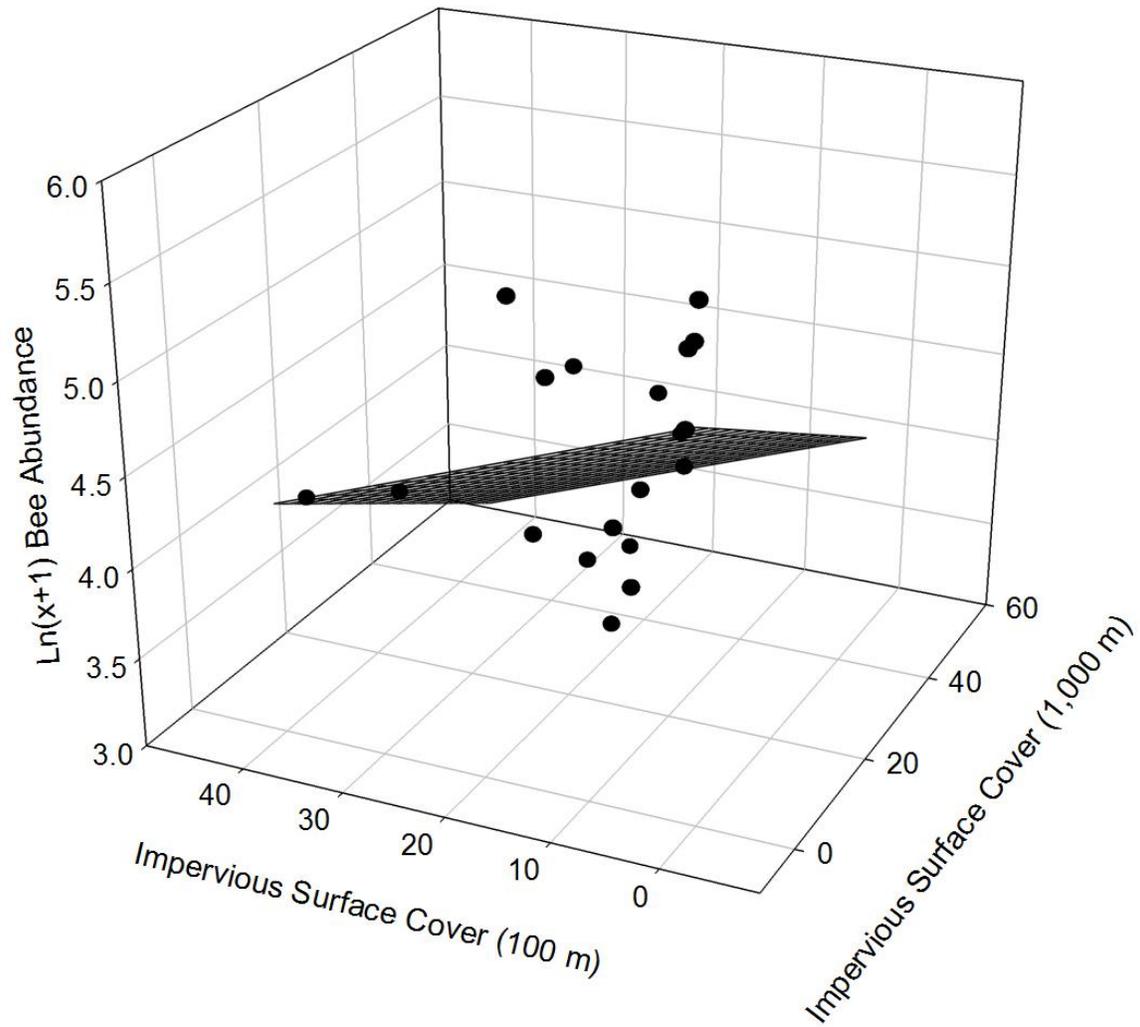


Figure 1.4. I used AIC_C to select this general linear model with impervious surface ground cover predicting bee abundance per study site. Bee abundance decreases with increasing impervious surface covers at the 100 m and 1,000 m radius buffers around study sites.

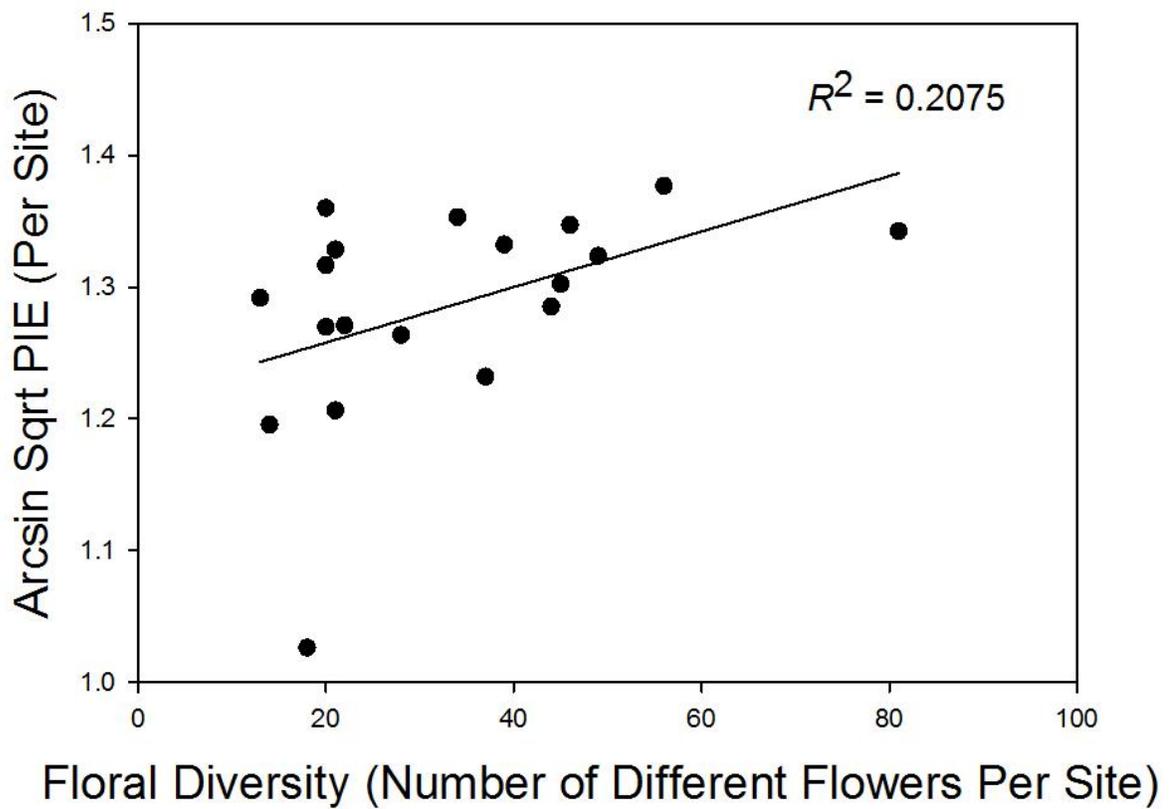


Figure 1.5. I used AIC_C to choose this general linear model with floral diversity predicting PIE (probability of interspecific encounter). Higher PIE means the study site has higher probability of inter specific encounter.

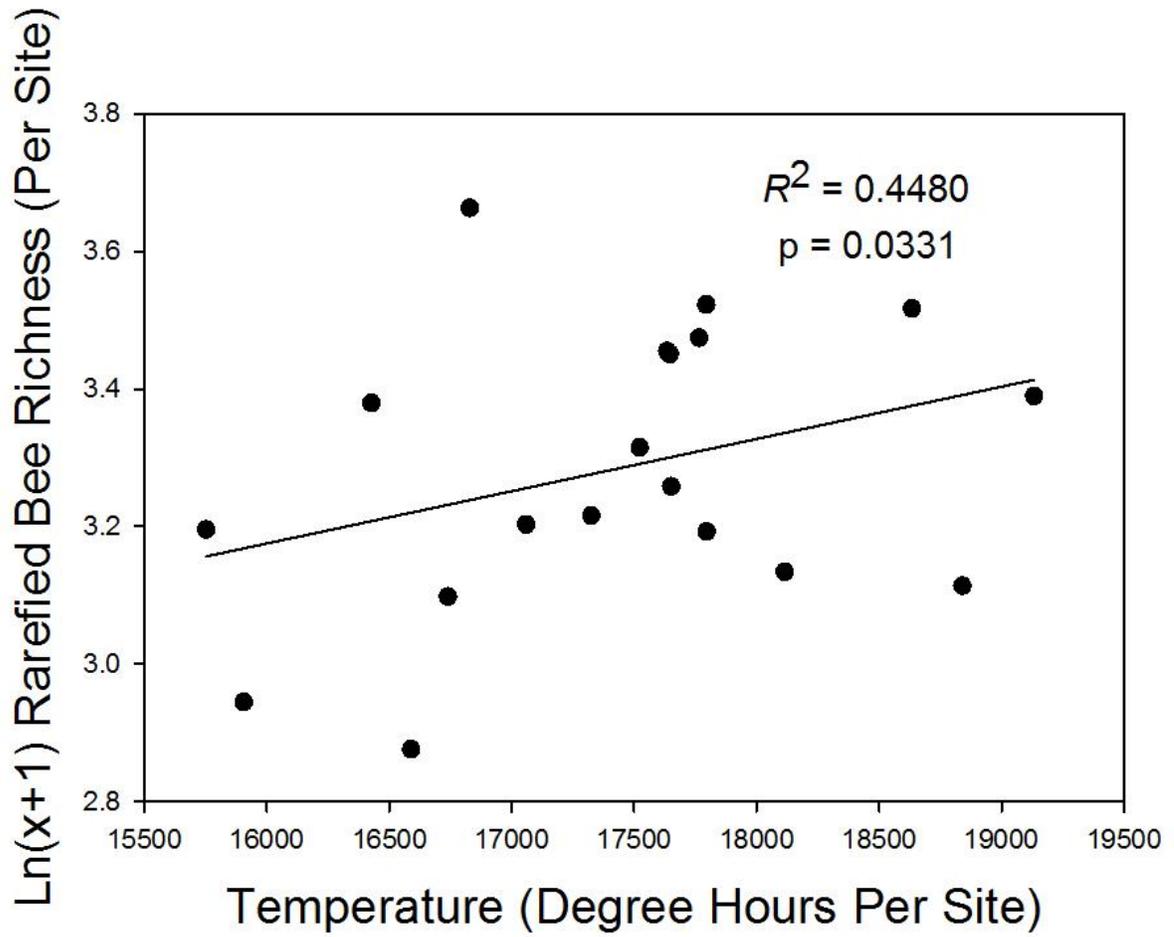


Figure 1.6. General linear model used without AIC_C model selection with temperature predicting rarefied bee richness. Higher rarefied bee richness means the study site has higher species richness.

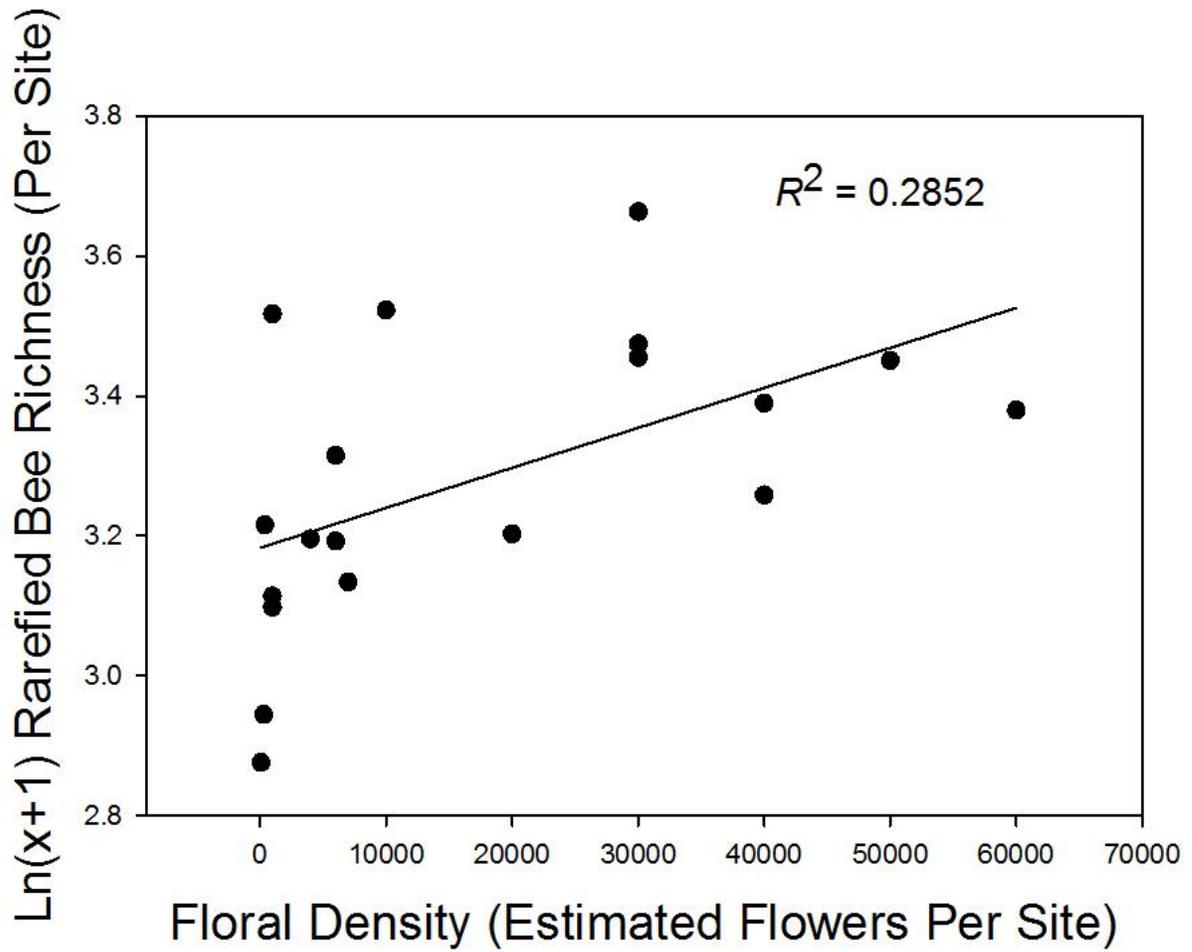


Figure 1.7. I used AIC_C to select this general linear model with floral density predicting rarefied bee richness. Rarefied bee richness increases as floral density increases.

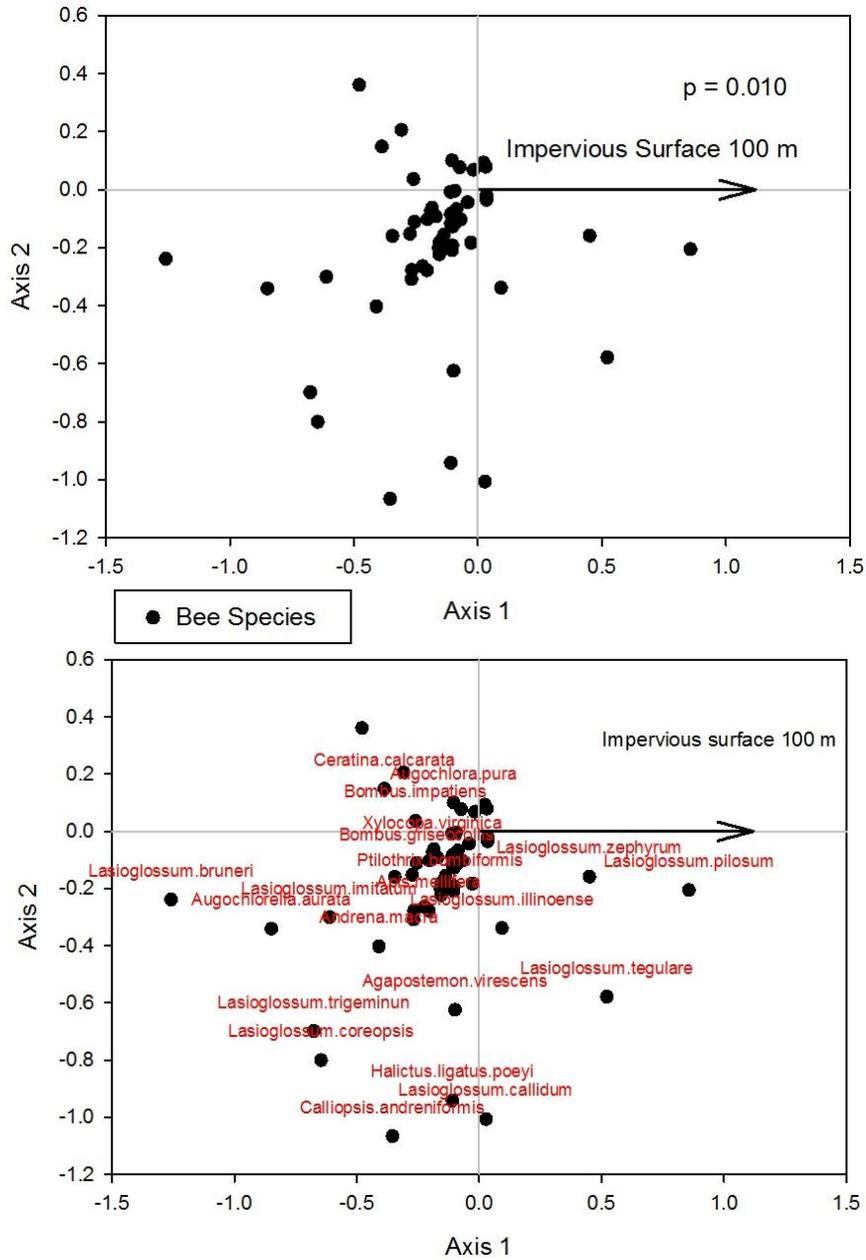


Figure 1.8. Model selection and db-RDA used to show species community composition related to the strongest predictor. Bee species community composition varies with impervious surface cover at the 100 m radius. Axis 1 represents the impervious surface cover, while Axis 2 represents explained variation in species composition.

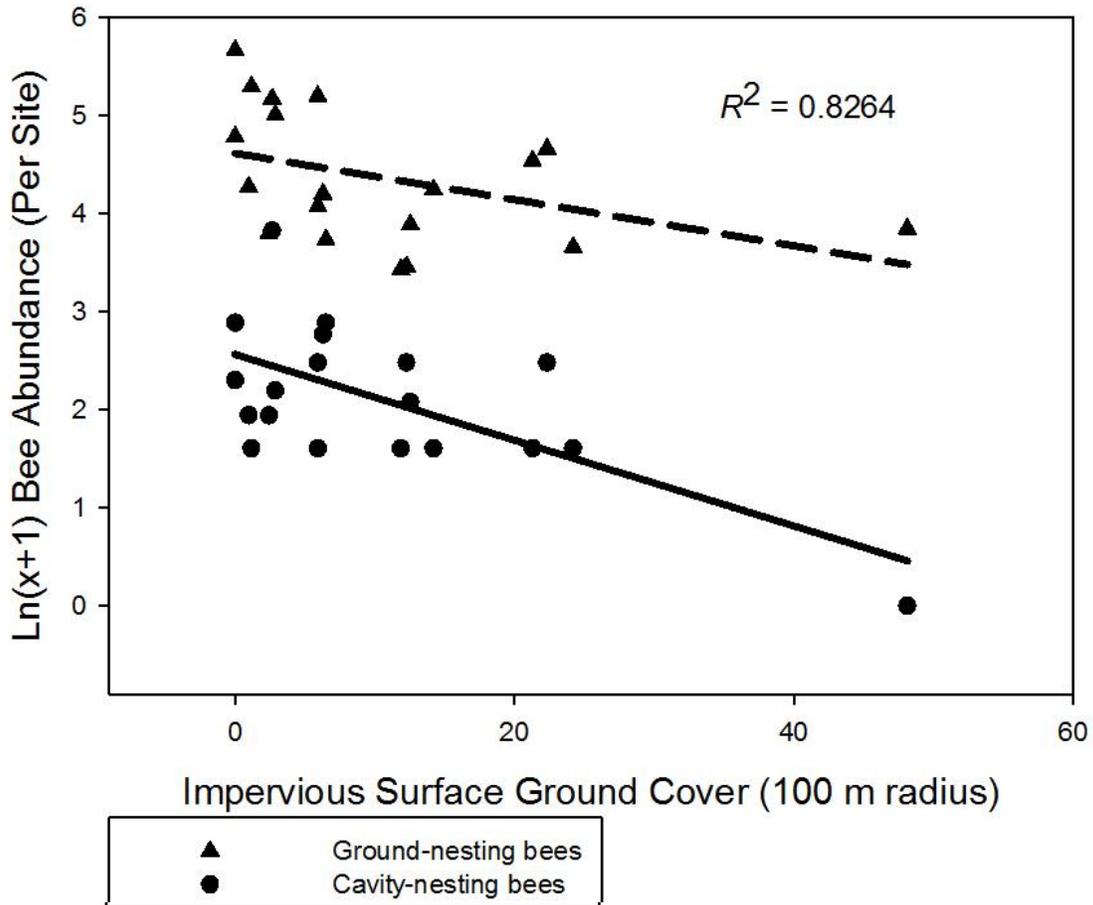


Figure 1.9. Ground-nesting bees (triangles) and cavity-nesting bees (circles). General linear model showing impervious surface cover predicting bee abundance based on nesting. Ground-nesting and cavity-nesting bees are decreasing at the same rate as impervious surface cover at the 100 m radius increases.

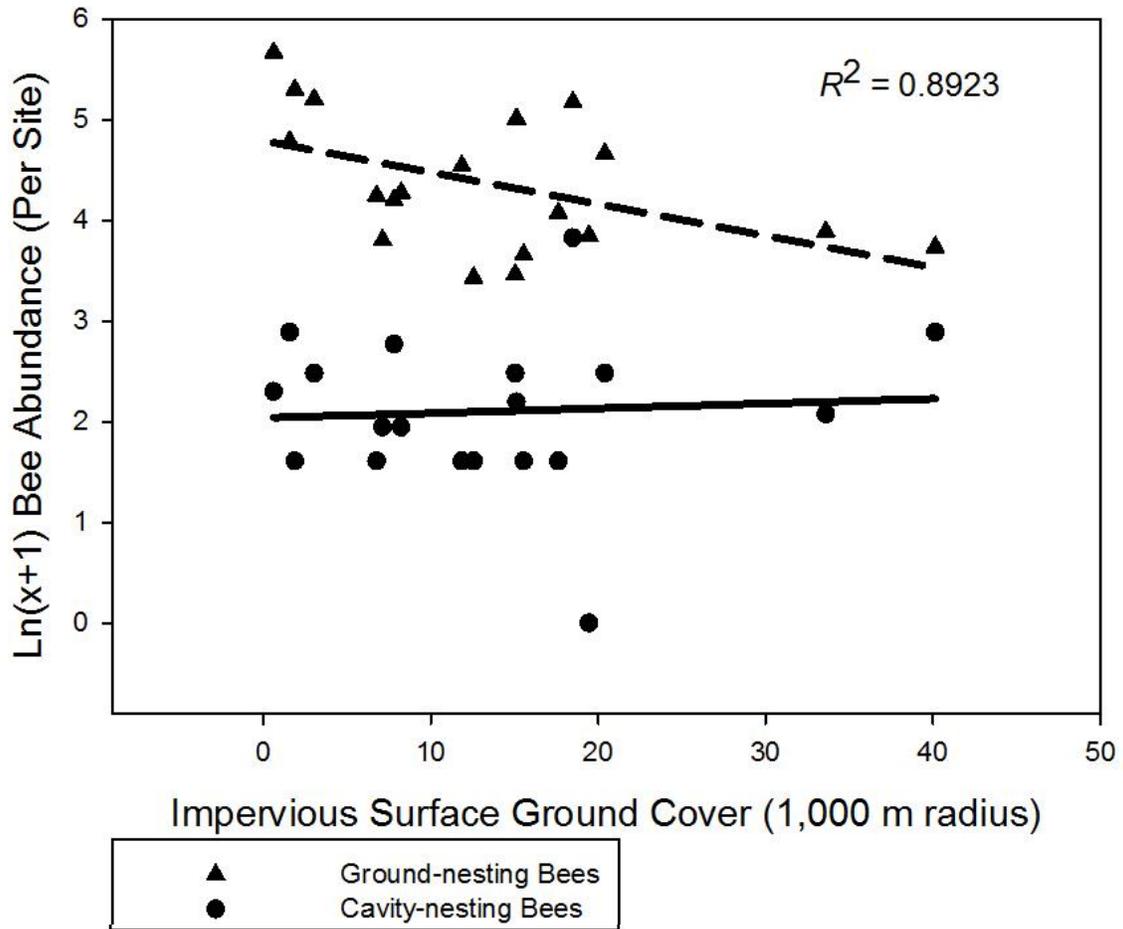


Figure 1.10. Ground-nesting bees (triangles) and cavity-nesting bees (circles). General linear model showing impervious surface cover predicting bee abundance based on nesting. When ground-nesting and cavity-nesting bees were analyzed separately, ground-nesting bees declined significantly with impervious surface cover at 1,000 m radius (p-value = 0.0347) and cavity-nesting bees did not (p-value = 0.7970).

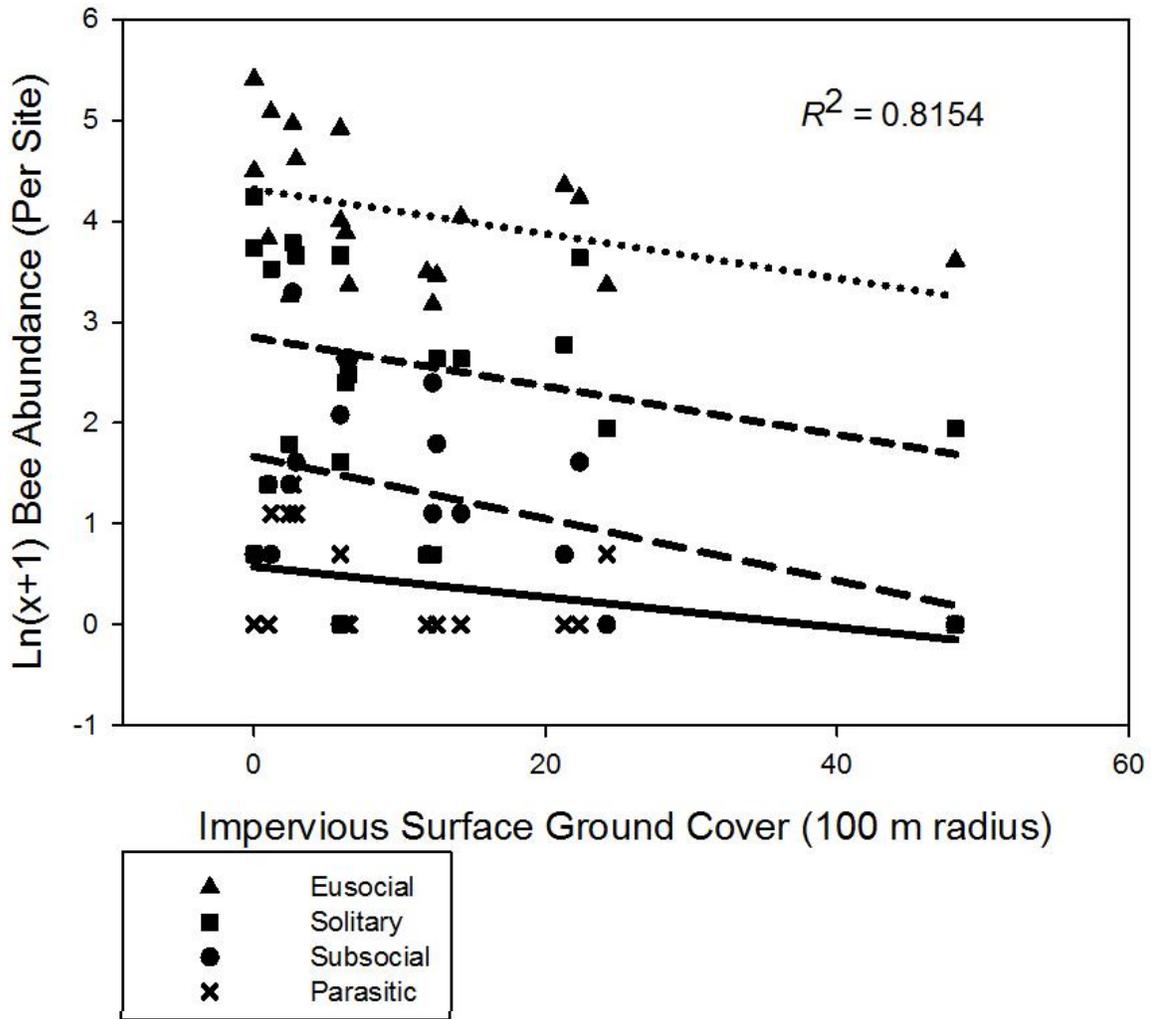


Figure 1.11. Eusocial (triangles), solitary (squares), subsocial (circles), and parasitic bees (Xs). General linear model showing impervious surface cover predicting bee abundance based on life history categories. All life history categories are decreasing at the same rate as impervious surface cover at the 100 m radius increases.

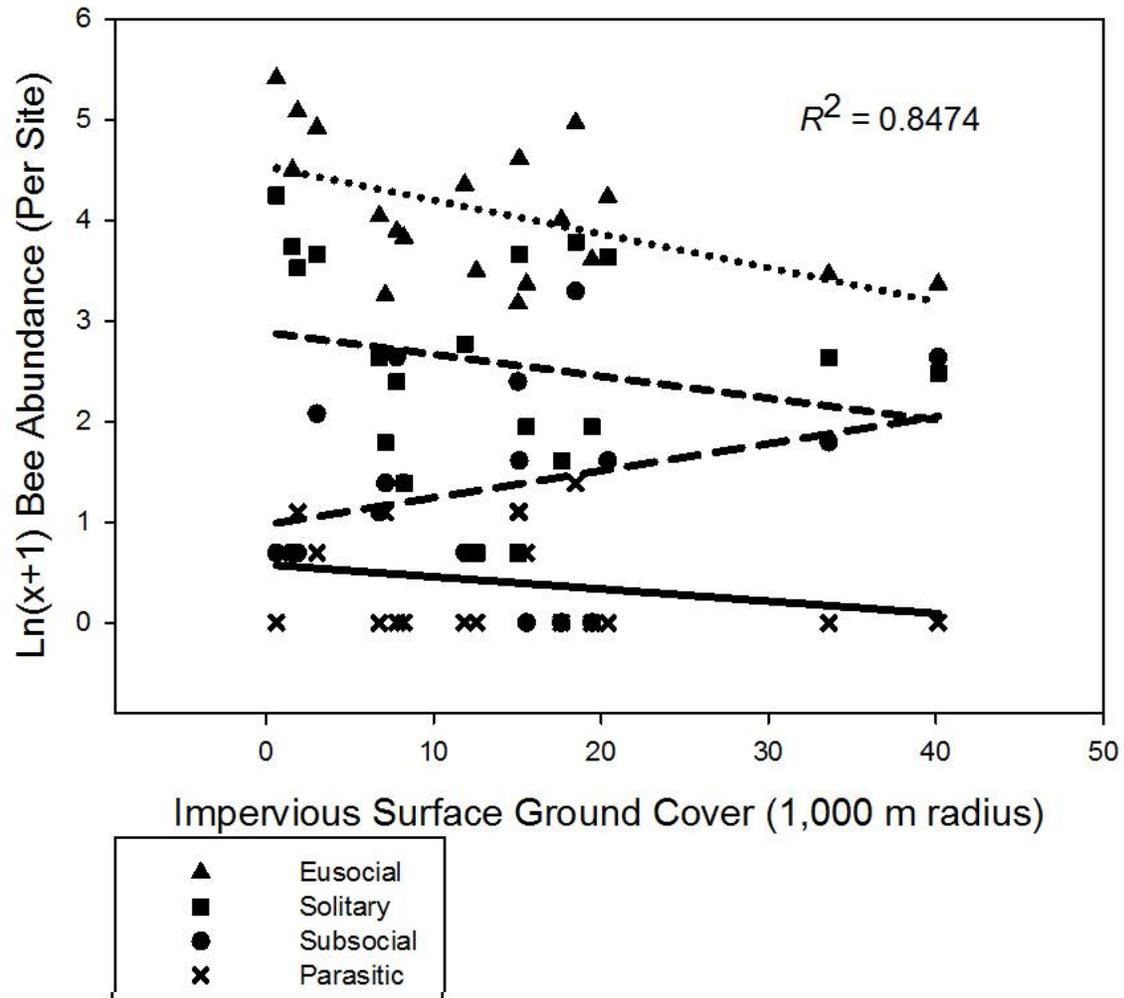


Figure 1.12. Eusocial (triangles), solitary (squares), subsocial (circles), and parasitic bees (Xs). General linear model showing impervious surface cover predicting bee abundance based on life history categories. Because the interaction between life histories and impervious surface cover at the 1,000 m was significant, the life history groups were not changing at the same rate. Because of this, I separated the life history categories and found that eusocial bees declined significantly with impervious surface cover (p-value = 0.0249), yet the other life histories did not (solitary p-value = 0.3874; subsocial p-value = 0.2297; parasitic p-value = 0.3205).

TABLES

Table 1.1. Results of general linear model analyses testing my hypothesis that temperature does not affect bee abundance, floral density increases bee abundance, and impervious surface cover reduces bee abundance. Bee abundance is unaffected by temperature, floral density, impervious surface cover, and their interactions.

Parameter	p-value	R^2
Model	0.7216	0.4593
Temperature (Degree Hours)	0.9764	
Floral Density	0.6316	
Impervious Surface Cover (100 m)	0.9144	
Impervious Surface Cover (1,000 m)	0.7088	
Temperature*Floral Density	0.6305	
Temperature*Impervious Surface Cover (100 m)	0.9899	
Temperature*Impervious Surface Cover (1,000 m)	0.7288	
Floral Density*Impervious Surface Cover (100 m)	0.8089	
Floral Density*Impervious Surface Cover (1,000 m)	0.7876	
Impervious Surface Cover (100 m)*Impervious Surface Cover (1,000 m)	0.4952	

Table 1.2. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting bee abundance with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The final model has an adjusted R^2 of 0.2677.

Predictor	w_i	Estimate
Temperature (Degree Hours)	0.191799	0.000007
Floral Diversity	0.258049	-0.00158
Floral Density	0.222802	9E-07
Impervious Surface Cover (100 m)	0.694329	-0.01671
Impervious Surface Cover (1,000 m)	0.573525	-0.01424

Table 1.3. Results of general linear model analyses testing my hypothesis that temperature does not affect bee diversity but floral diversity increases bee diversity. PIE is unaffected by temperature, floral diversity, and their interaction.

Parameter	p-value	R^2
Model	0.1537	0.2882
Temperature (Degree Hours)	0.1431	
Floral Diversity	0.1600	
Temperature*Floral Diversity	0.1886	

Table 1.4. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting PIE with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The final model has an adjusted R^2 of 0.1748.

Predictor	w_i	Estimate
Temperature (Degree Hours)	0.240051	0.000002
Floral Diversity	0.505124	0.00058
Floral Density	0.369281	3E-07
Impervious Surface Cover (100 m)	0.230845	0.00011
Impervious Surface Cover (1,000 m)	0.393662	0.00062

Table 1.5. Results of general linear model analyses testing my hypothesis that temperature does not affect bee richness but floral diversity increases bee richness. Rarefied bee richness is significantly affected by temperature. Rarefied bee richness has a positive relationship with temperature; as temperature increases rarefied bee richness also increases.

Parameter	p-value	R^2
Model	0.0269	0.448
Temperature (Degree Hours)	0.0331	
Floral Diversity	0.0618	
Temperature*Floral Diversity	0.0786	

Table 1.6. Akaike weights (w_i , larger values have greater support) and model-averaged parameter estimates (values near 0 have the least influence) for predicting rarefied bee richness with a general linear model. Bolded predictor variables were selected to be a part of the strongest model. The model has an adjusted R^2 of 0.2852.

Predictor	w_i	Estimate
Temperature (Degree Hours)	0.418911	0.00003
Floral Diversity	0.446126	0.00197
Floral Density	0.692937	0.000004
Impervious Surface Cover (100 m)	0.213006	-0.00046
Impervious Surface Cover (1,000 m)	0.21991	0.00059

Table 1.7. Results of general linear model analyses of the effects of impervious surface (100 m radius) and nesting strategy on bee abundance. Impervious surface cover and nesting affected bee abundances in nesting categories, but they were changing at the same rate because the interaction is not significant.

Parameter	p-value
Impervious Surface Cover (100 m)	0.0017
Nesting	<0.0001
Impervious Surface Cover*Nesting	0.2384

Table 1.8. Results of general linear model analyses of the effects of impervious surface (1,000 m radius) and nesting strategy on bee abundance. Nesting affected bee abundances in nesting categories, but they were changing at the same rate because the interaction is not significant. When cavity and ground nesting bees were analyzed separately, they were changing at a different rate. Cavity-nesting bees were unaffected by impervious surface cover at 1,000 m radius (p-value = 0.7970), yet ground-nesting bees declined as impervious surface cover increased at the 1,000 m radius (**p-value = 0.0347**).

Parameter	p-value
Impervious Surface	
Cover (1,000 m)	0.3377
Nesting	<0.0001
Impervious Surface	
Cover*Nesting	0.0555

Table 1.9. Results of general linear model analyses of the effects of impervious surface cover (100 m radius) and life history categories on bee abundance. Impervious surface cover and life histories affected bee abundances in life history categories, but they were changing at the same rate because the interaction is not significant.

Parameter	p-value
Impervious Surface	
Cover (100 m)	0.0355
Life Histories	<0.0001
Impervious Surface	
Cover*Life Histories	0.9000

Table 1.10. Results of general linear model analyses of the effects of impervious surface cover (1,000 m radius) and life history categories on bee abundance. Life histories and the interaction between life histories and impervious surface cover at 1,000 m affected bee abundances in nesting categories. This means the different life history categories were changing at different rates because the interaction is significant. Particularly, eusocial bees declined with increased impervious surface cover at 1,000 m radius (**p-value = 0.0249**).

Parameter	p-value
Impervious Surface Cover (1,000 m)	0.4412
Life Histories	<0.0001
Impervious Surface Cover*Life Histories	0.0479

CHAPTER 2 – Do Thermal Limits Predict Wild Bee Community

Responses to Urbanization?

Introduction

Global temperatures are predicted to increase 1-2°C by the end of this century (Pachauri et al. 2014). Wild animals will increasingly experience temperatures that are higher than those in which they evolved, and ectotherms may be particularly affected by higher temperatures since the environment regulates their body temperatures. The physiological and behavioral responses of insects—the most diverse group of ectotherms—to warming can affect species distributions, community structure, and ecosystem processes like pest control and pollination (Kudos & Ida 2013; Meineke et al. 2014).

Urban areas contain diverse animal communities but can be ~10°C hotter than surrounding natural areas (Gago et al. 2013). Insects in urban areas can experience particularly intense and acute warming. In some cases, environmental temperatures can exceed an insect's physiological tolerance with negative fitness consequences (Amarasekare & Sifuentes 2012). For example, in semidesert habitat, on particularly hot days when male bees looking for females fly too low and hit the layer of hot air they quickly overheat, lose control of their flight muscles, and die (Chappell 1984). The temperature at which insects become unable to function and cannot escape a lethal habitat is called the Critical Thermal Maximum (CTmax) (Diamond et al. 2012b; Lutterschmidt & Hutchison 1997). Rader et al. (2013) found that many bee species have optimal thermal ranges and times of the day when they can and will fly. When warming increases temperatures during these timeframes, bee

activity may become restricted and could result in sensitive species relocating and being replaced with more tolerant species.

A long term increase in temperature can cause species' ranges to shift poleward and become extinct in the warmest parts of their previous range (Bennie et al. 2013; Diamond et al. 2012a; Hill et al. 2011; Kerr et al. 2015; Wilby & Perry 2006). Kerr et al. (2015) spatially analyzed bumble bee records from the last century and found that many species are now absent from historical localities because of hotter temperatures. If insect species are heat tolerant, their ranges would be expected to follow such patterns of warming. Some southern-ranged bees expand and disperse north to urban areas taking advantage of their hot environments (Banaszak-Cibicka 2014). Less tolerant species, like some species of bumble bees (Kerr et al., 2015), may become rare or locally extinct. Because CTmax predicts the physiological limits of an insect, it has been used to predict range shifts and behavior patterns of urban ants. Cities often have ant communities composed of more southern and western species, with higher CTmax, in higher densities than species from surrounding natural areas (Angilletta et al. 2007; Diamond et al. 2012a; Menke et al. 2011).

Wild bee communities change in urban areas but the mechanisms are not well known (Winfree et al. 2011). Community composition can be related to the thermal environments (Nooten et al. 2014). I predicted that the occurrence of bee species in urban habitats will be related to their thermal tolerance. I hypothesized that CTmax will predict bee distribution throughout the environment based on local measurements of temperature and large-scale measurements of impervious surface cover. Diamond et al. (2012a) found that ants with higher CTmax occurred in greater densities in warmer locations. I also predicted bees with

higher CT_{max} will be more common in hotter sites and bees with lower CT_{max} will be more common in cooler sites.

Animals that live in thermally insulated environments such as soil or water often have lower CT_{max} than those in exposed habitats (Nyamukondiwa & Terblanche 2009). In Chapter 1, I found that ground-nesting and cavity-nesting bees declined at the same rate with percent impervious surface cover within the 100 m radius of the site. However, only ground-nesting bees declined with percent impervious surface cover within the 1,000 m radius of the site. Since impervious surfaces absorb and radiate heat, surface temperature increases linearly with percent impervious surface (Dale & Frank 2014; Yuan & Bauer 2007). This suggests that ground-nesting bees are less tolerance of urbanization and potentially high temperatures. I predicted ground-nesting bees will have lower CT_{max} and decline at sites with more impervious surface cover since soil nesting provides them a thermal buffer. This likely means that the bees would have lower CT_{max} and be unable to forage at hot urban temperatures.

Factors other than nesting strategy such as size and phylogenetic origin can also affect thermal tolerance (Rader et al. 2013; Stone & Willmer 1989; Willmer & Stone 2004). Larger ant species have lower CT_{max} than smaller ant species CT_{max} (Verble-Pearson et al. 2015). Larger bees warm up faster than smaller bees so they can fly at lower temperatures, but also take longer to cool down once heated (Stone 1993). I predicted that larger bees will have lower CT_{max} than smaller bees.

In Chapter 1, I collected bee community data for 19 study sites along an urban-temperature gradient. In Chapter 2, I identified the CT_{max} of bee species in laboratory assays

to test my hypotheses. I then assessed if CTmax could predict the distribution of bee species across the 19 previously sampled urban sites.

Methods

To test bees' CTmax, I collected bees at the J. C. Raulston Arboretum, on campus at North Carolina State University (NCSU), or a residential yard which had floral resources located within 2 miles away from the lab so that I could return to the lab within 10 minutes. During each trial, I collected bees for 15-35 minutes, placed each bee in a 50 ml plastic tube, and returned them to the laboratory in a cooler to prevent overheating. From May to August, 2014 and 2015, I collected, tested, and analyzed data from 283 individual bees (not including controls) in 15 native bee species and 1 non-native bee species—*Megachile rotundata* (Table 2.1).

I measured CTmax using a circulating water bath (Overgaard et al. 2011; Overgaard et al. 2012; Verble-Pearson et al. 2015; Wepprich, unpublished data). The heating apparatus used was the JLD612 Dual Display PID Temperature Controller measuring temperature with a Premium Stainless Steel Waterproof PT100 Temperature Sensor Probe (LIGHTOBJECT, Sacramento, CA). With these two components, the water temperature was measured to 0.1°C resolution with 0.2% accuracy (LIGHTOBJECT, Sacramento, CA). To conduct the CTmax trials I placed each bee into a 45ml glass vial. Vials were weighted with a mix of plaster and metal masses at the bottom to keep them from floating and sealed with cotton at the top, leaving 25ml space open for the bee. I put 7 vials with a bee in each in the water bath for 20 minutes to let the bees acclimate to room temperature (25°C) before heating them. I left the other one to seven bees in tubes in a tub of water at room temperature to test if bees died

during the trial for a reason other than heat stress. Only control *Apis mellifera* died, so *Apis mellifera* were removed from analyses. An iButton thermochron temperature logger (Maim Integrated, San Jose, CA) recorded temperature and humidity every minute within a glass vial in the control tub and water bath to measure temperatures the bees were experiencing during heating.

After 20 minutes at room temperature, I started increasing the water bath temperature by 0.5°C/minute (Lutterschmidt & Hutchison 1997). I used this rate to detect differences in thermal tolerance and to avoid lag effect where the animal's temperature lags behind that of its environment (Lighton & Turner 2004; Lutterschmidt & Hutchison 1997; Mitchell & Hoffmann 2010; Vorhees & Bradley 2012). I recorded bee behavior every minute for heated bees and every ten minutes for control bees. I recorded the CTmax temperature for a bee when it lost its righting response (Lutterschmidt & Hutchison 1997). This was when a bee on its back could no longer right itself after 30 seconds. Loss of muscular function is very close to the lethal thermal limit of insects (Le Lann et al. 2011; Overgaard et al. 2012; Sørensen et al. 2001). Although bees could still be moving at this temperature, they could not control their muscles. This means that they would not be able to escape from a lethal environment (Diamond et al. 2012a).

After pinning and labeling the bees, I measured each bee's intertegular distance as an indicator of bee size (Greenleaf et al. 2007). I identified bees to species using the online Discover Life key (<http://www.discoverlife.org/>) and by comparing specimens to reference collections in the North Carolina State University Insect Museum. I separated *Lasioglossum* into morphospecies. In 2014, I consulted experts to verify bee identification

and identify *Lasioglossum*. Based on species, I was able to categorize bees as cavity or ground nesting. Specimens will be deposited in the North Carolina State University Insect Museum.

I used an ANOVA and Tukey's Honestly Significant Difference test in JMP (JMP Pro 11.2.0; SAS Instituted, Cary, NC, USA) to separate different species thermal tolerances. All other models were analyzed in R (R 2.15.0; R Foundation for Statistical Computing, Vienna, Austria). I used general linear modeling with ordinary least squares (ols) to analyze these data. I first analyzed if nesting behavior or size influenced bee CTmax. I then used regression to analyze CTmax as the predictor variable and average temperature or impervious surface cover of the sites where each bee species occurred as the response variables showing bee distribution. The next models tested if CTmax predicted species response to warming. The response for each species was the regression coefficient of a model that related that species' abundance or incidence to temperature or impervious surface cover across sites.

To test for phylogenetic signaling in CTmax, I first made a phylogenetic tree. I downloaded a dataset generated by Hedtke et al. (2013) and only selected the lineages of interest for the study. To improve phylogenetic resolution among species from the family Megachilidae, I retrieved nucleotide sequences for the mitochondrial gene cytochrome oxidase I (COI) from the National Center for Biotechnology Information (NCBI). When DNA sequences for the species of interest were not available, I used sequences from the phylogenetically closest species. The final alignment comprised a total of 18,748 nucleotides. Alignments were visually inspected in Mesquite v.1. Maximum likelihood trees were

searched under the GTR-GAMMA model of sequence evolution in RAx-ML using 1,000 bootstrap replicates (Hedtke et al. 2013).

After testing for and finding phylogenetic signaling in R (Table 2.3) I then re-fit all linear models using phylogenetic generalized least squares (pgls) in R (R Core Team 2013) with Caper Version 0.5.2, Phytools Version 0.4-60, and Ape packages Version 3.3 (Orme et al. 2013; Revell 2012; Paradis et al. 2004). I used the lambda transformation to scale model covariance within each model. Data used for species CTmax in all models was collected in this study. Data used for study sites and species distribution was collected in Chapter 1.

Results

Xylocopa virginica, *Ceratina calcarata*, *Ceratina strenua*, *Megachile rotundata*, and *Ptilothrix bombiformis* had the highest CTmax. *Agapostemon virescens*, *Bombus bimaculatus*, and *Bombus griseocollis* had the lowest CTmax (Figure 2.1). Although different bee species had different thermal tolerances, cavity-nesting and ground-nesting bees CTmax did not differ (Figure 2.2). Most cavity-nesting bees nest above ground, yet bumble bees (*Bombus* spp.) can nest below or above ground. Bumble bees also have low CTmax. Because of this, bumble bees may be hiding a relationship between obligate ground-nesting bees and above-ground cavity-nesting bees. To check this, I eliminated bumble bees (*Bombus* spp.) from the dataset and analyzed the data again. Cavity and ground nesters' CTmax do not differ regardless of bumble bees being included in the analyses or not (ols p-value = 0.1090; pgls p-value = 0.5503). CTmax was also independent of bee size (Figure 2.3).

CTmax did not predict species distribution based on the measurement of temperature in degree hours, but did predict species distribution based on the measurement of mean

maximum temperature (Figure 2.4 and Figure 2.5). This relationship was only revealed once the data was phylogenetically corrected. As CTmax increased, the maximum temperatures at the study sites where the bees occurred decreased.

CTmax did not predict species distribution based on impervious surface cover at the 100 m radius but CTmax did predict species distribution based on impervious surface cover at the 1,000 m radius. This relationship was evident with or without correcting for phylogeny. As CTmax of species increased, the impervious surface cover at the 1,000 m radius from the study sites increased where the species occurred (Figure 2.6, Figure 2.7, and Figure 2.8).

CTmax did not predict responses to warming based on the regression coefficients of any variable for any species (Table 2.2 and Table 2.4).

Discussion

Temperature could be an important factor regulating the distribution and abundance of arthropods in urban areas and as the global climate warms. My goal was to determine if CTmax differed among urban bee species and if CTmax could predict species nesting strategy and distribution in an urban environment. I expected cavity-nesting bees to have higher CTmax than ground-nesting bees, yet this was not the case. Insect eggs and larvae are often the most vulnerable stages of insects to environmental stress. Larvae may be more vulnerable to warming because they cannot leave to escape high temperatures and often have lower CTmax than adults (Brooks & Sassaman 1965; Scherber et al. 2013; Vorhees & Bradley 2012). Thus, more research is needed to determine how temperature affects bees throughout their life cycles. However, based on my results from Chapters 1 and 2, cavity-

nesting and ground-nesting bees probably presently decline with increasing impervious surface cover because it limits nesting resources, not necessarily because it is too hot. This could happen with future hotter temperatures, though, so it should be monitored regularly.

I tested for the effect of temperature on bee abundance or incidence in a habitat. However, the effects of temperature on bees may also appear in more subtle ways by changing phenotype or fitness. For example, mosquito larvae exposed to high temperatures have lower mass, but adults exposed to warmer temperatures have higher mass (Gray 2013). Although scale insects are more abundant in warmer urban temperatures, they also increase in size, survival, and fecundity (Dale & Frank 2014; Meineke et al. 2013; Youngsteadt et al. 2015). Other insects have the opposite effect with urban warming and urbanization. For example, parasitoid wasps have reduced fitness with increasing temperatures because a phenological mismatch can cause parasitoids to emerge at a different time than their hosts, resulting in the inability to find hosts (Meineke et al. 2014). Increasing temperatures also cause reduced fecundity with parasitoids because more of their energy goes into maintaining themselves than laying eggs (Denis et al. 2013). Honey bees have increased rates of black queen cell virus in areas with higher percentages of impervious surface cover, thus reducing fitness (Appler 2014). Studying CTmax during bees' entire life cycles would help identify the subtle effects such as these that abundance and incidence data may miss.

Although I did not find a significant relationship with size and CTmax, other studies have related size to body temperature and thermal tolerance. Larger bees are thought to be good thermoregulators, while smaller bees are considered poor thermoregulators (Willmer & Stone 2004). Larger bees warm up faster and reach higher body temperatures than smaller

bees, but take longer to cool down (Stone & Willmer 1989; Stone 1994; Willmer & Stone 2004). Because of this, larger bees have higher risk of overheating. To mitigate these risks, larger bees forage at the beginning and the end of the day in cooler temperatures generally earlier in the season, while smaller bees forage in the middle, hotter part of the day in the hotter months of the season (Stone & Willmer 1989; Willmer & Stone 2004). Verble-Pearson et al. (2015) also found this relationship in ants as larger ants had lower CT_{max} and smaller ants had higher CT_{max}. Along with my research, other research has also failed to find relationships between body size and CT_{max} (Nyamukondiwa & Terblanche 2009).

CT_{max} predicted species distribution based on maximum temperature of the study sites where the bees were collected in Chapter 1. I predicted higher CT_{max} bee species would occur in hotter temperatures in higher densities. Perhaps surprisingly, I found CT_{max} predicted the opposite pattern. Bees with high CT_{max} occurred in locations that were, on average, cooler than those occupied by closely related bees with lower CT_{max}. Since the relationship was not significant without phylogenetic correction, yet was significant with phylogenetic correction, the relationship was only shown among closely related individuals (Figure 2.5). This means that the relationship is not shown if every species is treated the same, but the relationship is shown when species are phylogenetically corrected. IButton data loggers were also placed in shady tree canopies or shrubs to avoid overheating, but did not measure the open air temperature where bees would be foraging. Thus, my measurements of temperature could be underestimating the true temperature spectrum at the study sites. All mean maximum temperatures were also under 32°C—no bee was even close to reaching its CT_{max} (the lowest CT_{max} was 44.3°C). Max hourly temperature recorded per study site

were all between 35.5°C and 41°C, close to some species CT_{max} but not over. Diamond et al. (2012a) found that ants with high and low CT_{max} were able to persist in warmer temperatures far from their CT_{max} as well. Bees with lower CT_{max} at my study sites could also occur at hotter study sites but behaviorally avoid these hotter temperatures by foraging at cooler times of the day (Willmer & Stone 2004). I am also looking into seasonal temperature variation instead of only measuring temperature with means or cumulative degree hours. Greater seasonal variation in temperature should lead to bees with higher thermal tolerances. Sheldon & Tewksbury (2014) found that beetles had greater thermal tolerance when they were exposed to greater season variation of temperatures, but the best predictor of thermal tolerance was the temperature variation when the species was active. Because of this, I am looking into further analyses with temperature calculations of when bee species were active.

I found CT_{max} to predict species distribution based on impervious surface cover at a 1,000 m radius around study sites. Bees with higher CT_{max} were more abundant in locations with more impervious surface cover. I expected this result because percent impervious surface cover has a positive linear relationship with temperature (Dale & Frank 2014; Yuan & Bauer 2007). The impervious surface cover measured in Chapter 1 was within a 1,000 m radius around the study site to encompass the maximum foraging range for most wild, native bees (Greenleaf et al. 2007). This gives the temperature over a larger habitat in which the bees forage so even if a study site was classified as cold from the iButton temperature measurements, the larger area may be hot and thus induce stress. Impervious surface cover also encompasses things like habitat fragmentation that require longer foraging bouts from bees. By looking at the larger-scale measurement of temperature impervious surface cover,

and other variables, I begin to see relationships bees have with their environment. Urban temperatures are not at the CTmax of many bee species most of the time, but as urban areas expand and climate change causes global temperatures to rise bees will be facing their CTmax in the near future.

It is unknown whether some bees will be able to adapt to these environments based on development of larvae in hotter temperatures, but it is probable that some species will die because of warming. As a society we would have to consider using less impervious surface cover as urban areas expand, or perhaps as a homeowner installing areas of bare ground could help. To help mitigate the influence of warming on wild bees, though, we would likely have to change our views of urban areas only being for humans and utilize them for conserving biodiversity in nature as well.

References

- Amarasekare, P & R. Sifuentes. 2012. Elucidating the temperature response of survivorship in insects. *Funct. Ec.* 26(4): 959-968.
- Angilletta, M. J. Jr., R. S. Wilson, A. C. Niehaus, M. W. Sears, C. A. Navas, and P. L. Ribeiro. 2007. Urban physiology: City ants possess high heat tolerance. *PLoS One*. e258. doi:10.1371/journal.pone.0000258.
- Appler, R. H. 2014. The effect of urbanization on the immunocompetence and pathogen pressure of managed and feral honey bees (*Apis mellifera* Linnaeus). North Carolina State University Thesis.
- Banaszak-Cibicka, W. 2014. Are urban areas suitable for thermophilic and xerothermic bee species (Hymenoptera: Apoidea: Apiformes)? *Apidologie*. 45: 145-155.
- Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth A. N. Lakso, & R. Winfree. 2013b. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Eco. Letters*. 16: 1331-1338.
- Bennie, J., J. A. Hodgson, C. R. Lawson, C. T. Holloway, D. B. Roy, T. Brereton, ... R. J. Wilson. 2013. Range expansion through fragmented landscapes under a variable climate. *Eco. Letters*. 16(7): 921-929.
- Brooks, G. & J. F. Sasser. 1965. Critical thermal maxima of larval and adult *Eurycea bislineata*. *Copeia*. 251-252.
- Chappell, M. A. 1984. Temperature regulation and energetics of the solitary bee *Centris pallida* during foraging and intermale mate competition. *Phys. Zoo*. 215-225.
- Dale, A. G. & S. D. Frank. 2014. Urban warming trumps natural enemy regulations of herbivorous pests. *Eco. Appl.* 24(7): 1596-1607.
- Denis, D., J. Baaren, J. Pierre, & E. Wajnberg. 2013. Evolution of a physiological trade-off in a parasitoid wasp: How best to manage lipid reserves in a warming environment. *Entomologia Experimentalis Et Applicata*. 148: 27-38.
- Diamond, S. E., L. M. Nichols, N. McCoy, C. Hirsch, S. L. Pelini, N. J. Sanders... R. R. Dunn. 2012a. A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology*. 93(11): 2305-2312.

Diamond, S. E., M. D. Sorger, J. Hulcr, S. L. Pelini, I. D. Toro, C. Hirsch, ... R. R. Dunn. 2012b. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Bio.* 18(2): 448-456.

Gago, E. J., J. Roland, R. Pacheco-Torres, & J. Ordóñez. 2013. The city and urban heat islands: A review of strategies to mitigate adverse effects. *Renewable and Sustainable Energy Rev.* 25: 749-758.

Gray, E. M. 2013. Thermal acclimation in a complex life cycle: The effects of larval and adult thermal conditions on metabolic rate and heat resistance in *Culex pipiens* (Diptera: Culicidae). *J. of Insect Phys.* 59(10): 1001-1007.

Greenleaf, S. S., N. M. Williams, R. Winfree, & C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia.* 153(3): 589-596.

Hedtke, S. M., S. Patiny, & B. N. Danforth. 2013. The bee tree of life: A supermatrix approach to apoid phylogeny and biogeography. *BMC Evo. Bio.* 13: 138.

Hill, J. K., H. M. Griffiths, & C. D. Thomas. 2011. Climate change and evolutionary adaptations at species' range margins. *Ann. Rev. of Ent.* 56: 143-159.

Kerr, J. T., S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, ... S. G. Potts. 2015. Climate change impacts on bumblebees converge across continents. *Sc.* 349(624): 177-180.

Kudo, G & T. Y. Ida. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Eco.* 94(10): 2311-2320.

Le Lann, C., O Roux, N. Serain, J. M. Jacques Van Alphen, P. Vernon, & J. Van Baaren. 2011. Thermal tolerance of sympatric hymenopteran parasitoid species: Does it match seasonal activity? *Phys. Ent.* 36: 21-28.

Lighton, J. R., & R. J. Turner. 2004. Thermolimit respirometry: An objective assessment of critical thermal maxima in two sympatric desert harvester ants, *Pogonomyrmex rugosus* and *P. californicus*. *The J. of Exper. Bio.* 207(11): 1903-1913.

Lutterschmidt, W. I. & V. H. Hutchison. 1997. The critical thermal maximum; History and critique. *Canadian J. of Zoo.* 75(10): 1561-1574.

Meineke, E. K., R. R. Dunn, & S. D. Frank. 2014. Early pest development and loss of biological control are associated with urban warming. *Bio. Letters.* 10(11): 1-4.

Meineke, E. K., R. R. Dunn, J. O. Sexton, & S. D. Frank. 2013. Urban warming drives insect pest abundance on street trees. *PLoS One*. 8(3): e59687. doi: 10.1371/journal.pone.0059687.

Menke, S. B., B. Guénard, J. O. Sexton, M. D. Weiser, R. R. Dunn, & J. Silverman. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerance species; an example from ants. *Urban Eco*. 14(2): 135-163.

Mitchell, K. A. & A. A. Hoffmann. 2010. Thermal ramping rate influences evolutionary potential and species differences for upper thermal limits in *Drosophila*. *Funct. Eco*. 24(3): 694-700.

Nooten, S. S., N. R. Andrew, & L. Hughes. 2014. Potential impacts of climate change on insect communities: A transplant experiment. *PLoS One*. 9(1): e85987. doi: 10.1371/journal.pone.0085987.

Nymukondiwa, C. & J. S. Terblanche. 2009. Thermal tolerance in adult Mediterranean and natal fruit flies (*Ceratitis capitata* and *Ceratitis rosa*): Effects of age, gender and feeding status. *J. of Thermal Bio*. 34(8): 406-414.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, & W. Pearse. 2013. caper: Comparative Analyses of Phylogenetics and Evolution in T. T package version 0.5.2. <http://CRAN.R-project.org/package=caper>.

Overgaard, J., A. A. Horrmann, & T. N. Kristensen. 2011. Assessing population and environmental effects on thermal resistance in *Drosophila melanogaster* using ecologically relevant assays. *Jo. of Therm. Bio*. 36: 409-416.

Overgaard, J., T. N. Kristensen, & J. G. Sørensen. 2012. Validity of thermal ramping assays used to assess thermal tolerance in arthropods. *PLoS One*. 7(3): e32758. doi: 10.1371/journal.pone.0032758.

Pachauri, P. K., M. Allen, V. Barros, J. Broome, W. Cramer, R. Christ, ...P. Dasgupta. 2014. Climate change 2014: Synthesis report. Contribution of working groups I, II, and III to the fifth assessment report of the intergovernmental panel on climate change.

Paradis, E., L. Claude, & K. Strimmer. 2004. APE: analysese of phylogenetics and evolution in R language. *Bioinformatics*, 20: 289-290.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rader, R. K. Reilly, I. Bartomeus, & R. Winfree. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Bio.* 19(10): 3130-3110.

Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3: 217-223.
doi: 10.1111/j.2041-210X.2011.00169.X.

Scherber, C., D. J. Gladbach, K. Stevnbak, R. J. Karsten, I. K. Schmidt, A. Michelsen,... C. Beier. 2013. Multi-factor climate change effects on insects herbivore performance. *Eco. and Evo.* 3(6): 1449-1460.

Sheldon, K. S. & J. J. Tewksbury. 2014. The impact of seasonality in temperature on thermal tolerance and elevational range size. *Eco.* 95: 2134-2143.

Sørensen, J. G., J. Dahlgaard, & V. Loeschcke. 2001. Genetic variation in thermal tolerance among natural populations of *Drosophila buzzatii*: Down regulation of Hsp70 expression and variation in heat stress resistance traits. *Funct. Eco.* 15(3): 289-296.

Stone, G & P. Willmer. 1989. Warm-up rates and body temperature in bees: The importance of body size, thermal regime and phylogeny. *J. of Exper. Bio.* 147: 303-328.

Stone, G. N. 1993. Endothermy in the solitary bee *Anthophora plumipes*: Independent measures of thermoregulatory ability, costs of warm-up and the role of body size. *The J. of Exper. Bio.* 174: 299-320.

Stone, G. N. 1994. Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body size. *Eco. Ent.* 19(2): 177-189.

Verble-Pearson, R. M., M. E. Grifford, & S. P. Yanoviak. 2015. Variation in thermal tolerance of North American ants. *J. of Thermal Bio.* 48: 65-68.

Vorhees, A. S. & T. J. Bradley. 2012. Differences in critical thermal maxima and mortality across life stages of the mealworm beetle *Tenebrio molitor*. *The J. of Exper. Bio.* 215(13): 2319-2326.

Wepprich, T. Unpublished data.

Wilby, R. L. & G. L. Perry. 2006. Climate change, biodiversity and the urban environment: A critical review based on London, UK. *Progress in Physical Geo.* 30: 73-98.

Willmer, P. & G. Stone. 2004. Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Advances in the Study of Behavior.* 3(34): 347-466.

Winfree, R., I. Bartomeus, & D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Ann. Rev. of Eco., Evo. and Sys.* 42: 1.

Youngsteadt, E., A. G. Dale, A. J. Terando, R. R. Dunn, & S. D. Frank. 2015. Do cities stimulate climate change? A comparison of herbivore response to urban and global warming. *Global Change Bio.* 21: 97-105.

Yuan, F. & M. E. Bauer. 2007. Comparison of impervious surface area and normalized difference vegetation index as indicators of surface urban heat islands effects in landsat imagery. *Remote Sensing of Env.* 106(3): 375-386.

FIGURES

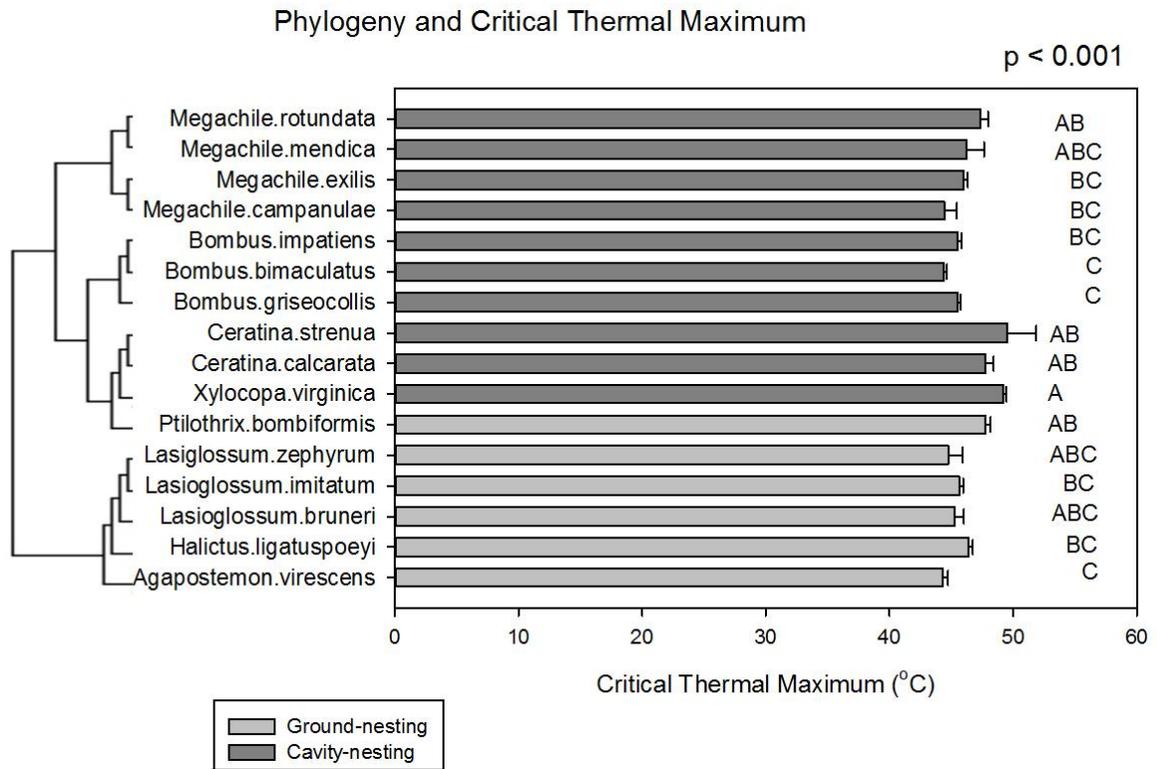


Figure 2.1. Species in phylogenetic tree and their CTmax. If a species on the CTmax graph y-axis did not have a phylogeny available, the next closest related species was used for the phylogeny. Species differ based on ANOVA ($p < 0.001$). Species with the same letter have CTmax that do not differ based on Tukey's Honest Significant Difference test.

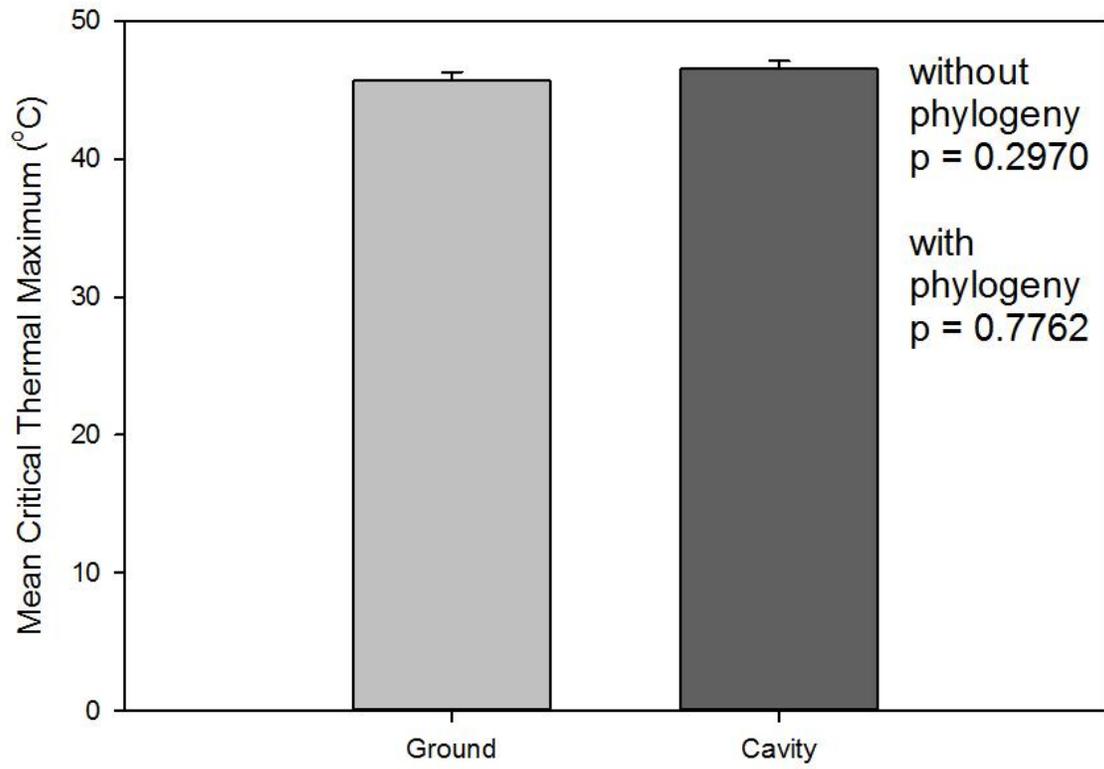


Figure 2.2. Ground-nesting bees and cavity-nesting bees CT_{max} do not differ general linear models with or without phylogenetic correction.

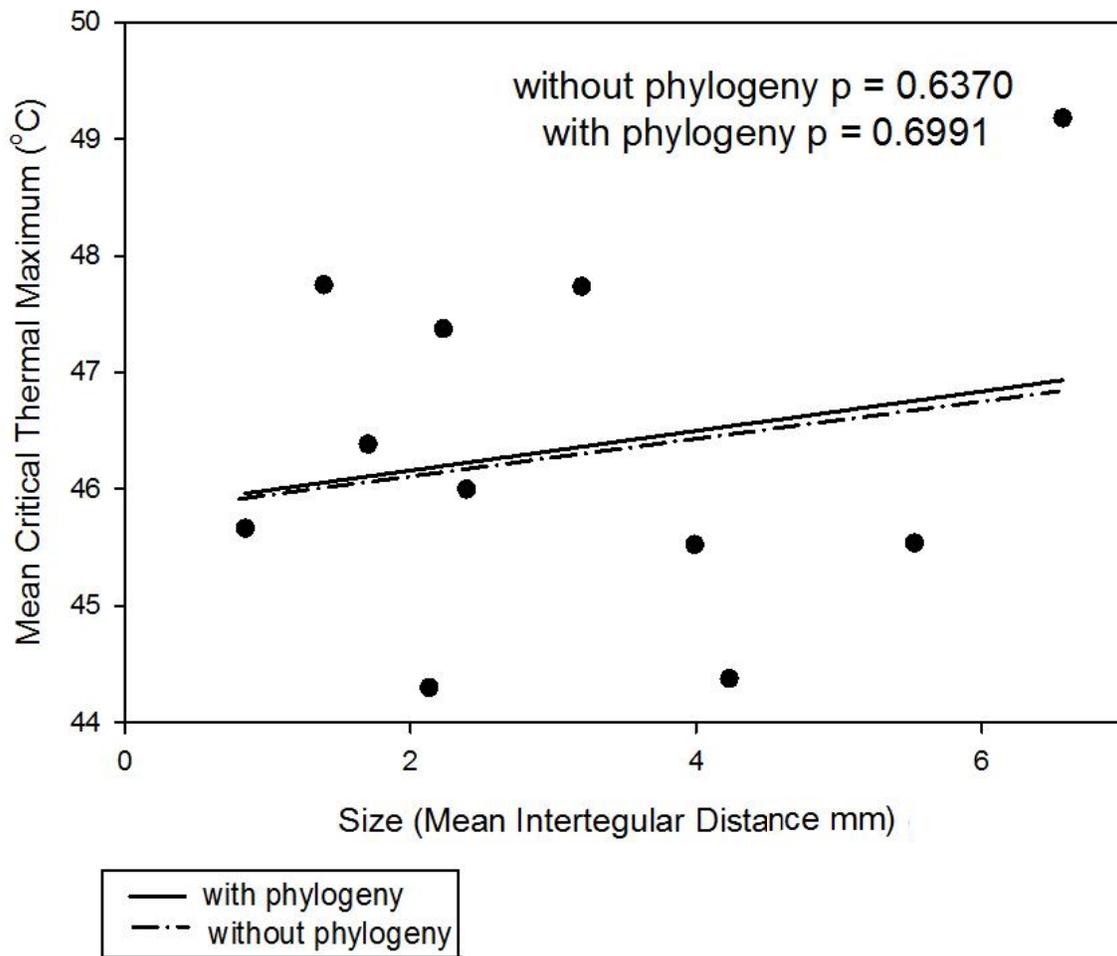


Figure 2.3. Each point on the graph is a species. Size is the mean intertegular distance of each species. Mean critical thermal maximum is the mean CTmax of each species. Bee size was not able to predict bee CTmax with or without phylogenetic correction.

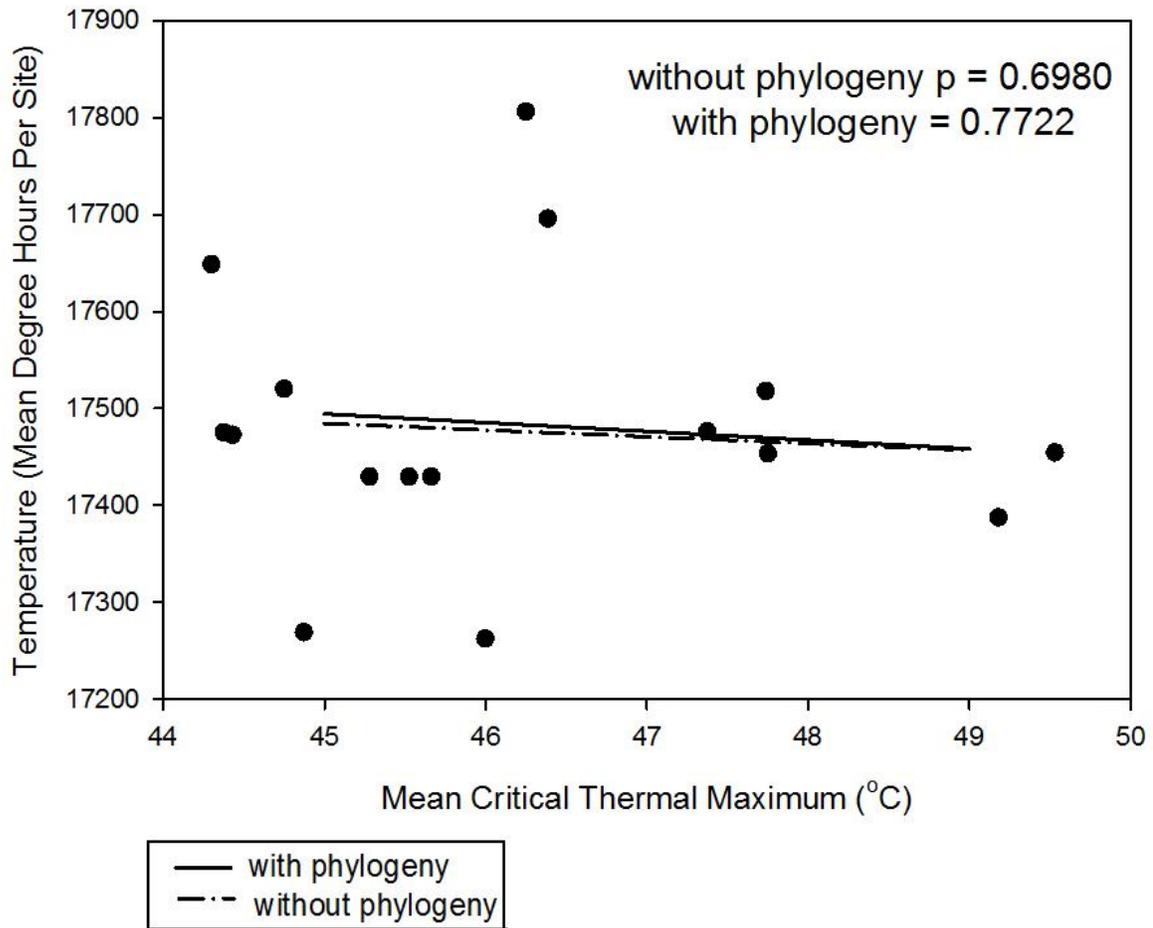


Figure 2.4. Each point on the graph is a species. Mean critical thermal maximum is the mean CTmax of each bee tested averaged by species. Temperature is the mean of the degree hours averaged across all study sites where the species occurred. CTmax did not predict bee species distribution based on temperature with or without phylogenetic signaling.

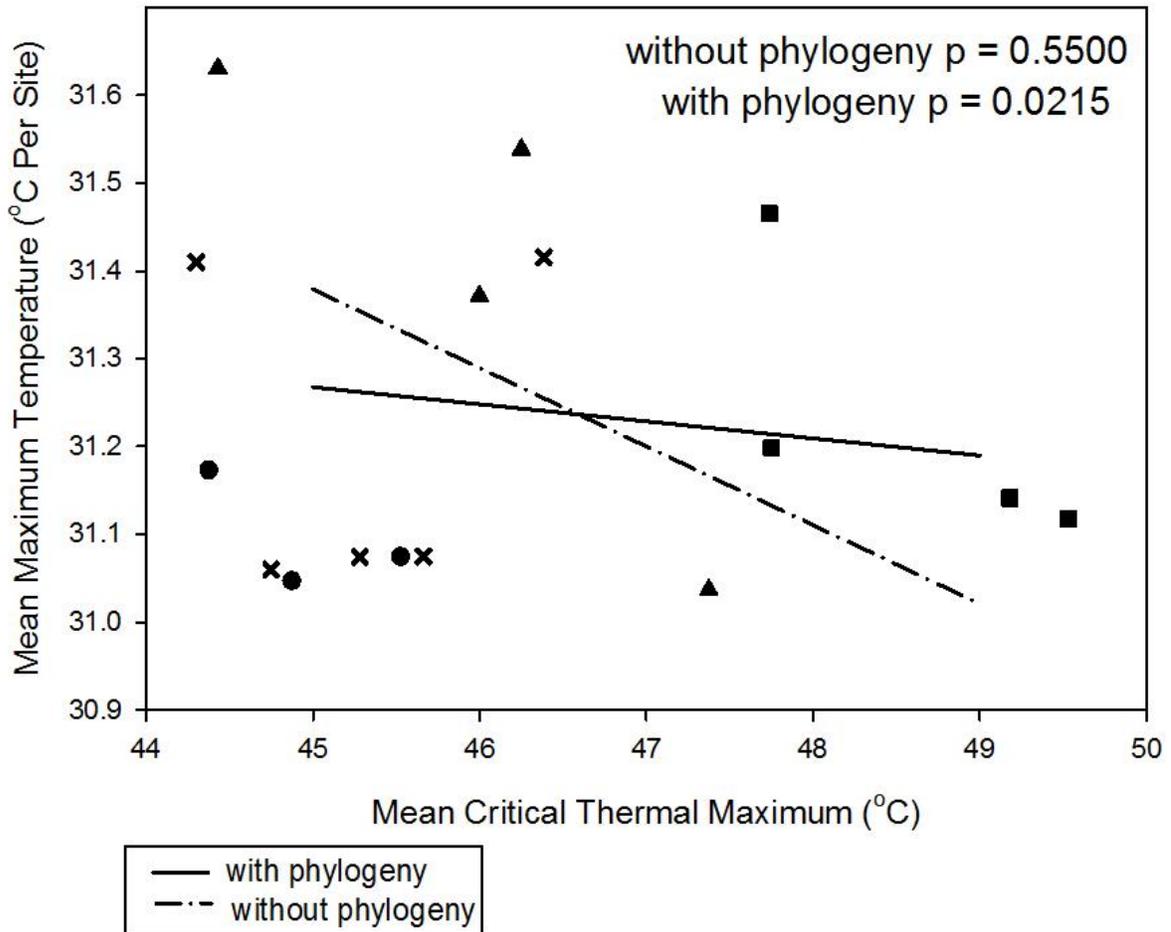


Figure 2.5. Each point on the graph is a species. Corresponding symbols in the graph represent more related species. Mean critical thermal maximum is the mean CTmax of each bee species. Temperature is the mean of the maximum temperature average across all study sites where the species occurred. Without phylogenetic correction, CTmax did not predict species distribution based on mean maximum temperature. Once the data is phylogenetically corrected, CTmax then predicted species distribution based on mean maximum temperature. Lambda is 0.975, meaning that related species diverged more than expected under the Brownian motion model of evolution. The CTmax parameter estimate is -0.101775. As species CTmax increased, the mean maximum temperatures of the study sites where more related species were found decreased.

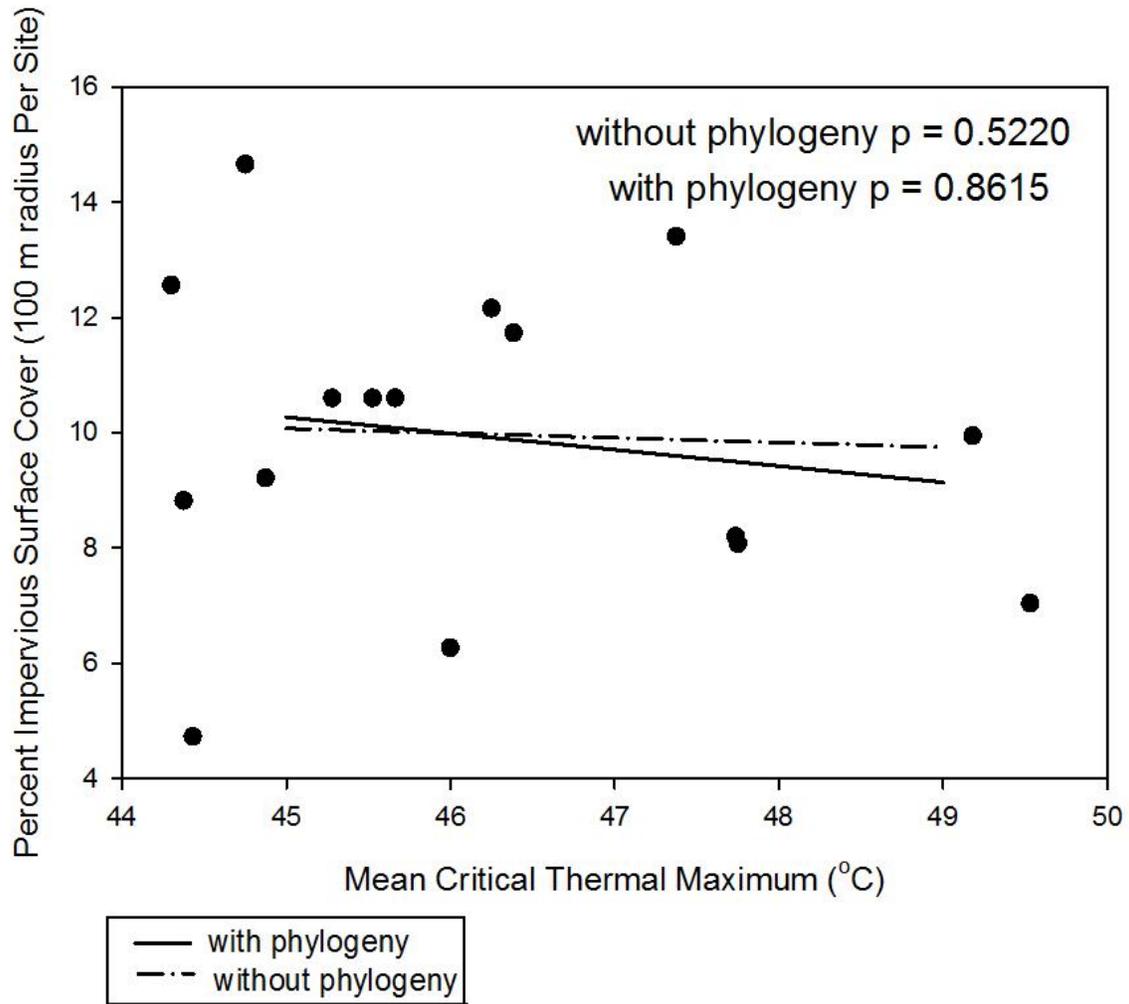


Figure 2.6. Each point on the graph is a species. Mean critical thermal maxima is the CTmax of each bee tested averaged by species. Percent impervious surface cover is the mean of the percent impervious surface cover (100 m radius) averaged across all study sites where the species occurred. CTmax did not predict bee species distribution based on impervious surface cover (100 m radius) of the study sites with or without phylogenetic correction.

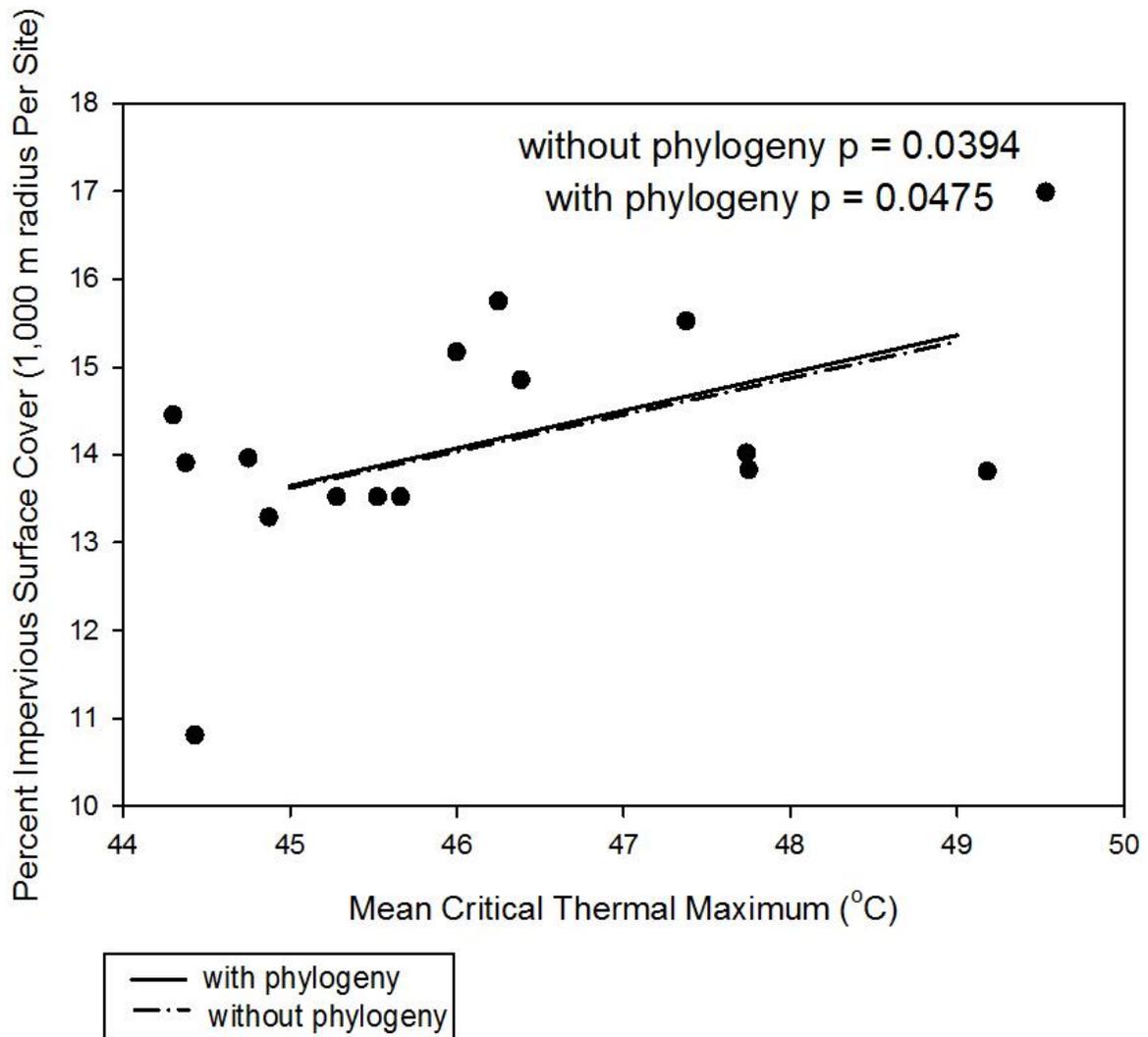


Figure 2.7. Each point on the graph is a species. Mean critical thermal maxima is the mean CTmax of each species. Percent impervious surface cover is the mean of the percent impervious surface cover (1,000 m radius) averaged across all study sites where the species occurred. Without phylogenetic correction, CTmax predicted species distribution based on impervious surface cover (1,000 m radius). When I transformed the data with lambda, lambda was then 0, or independent of phylogeny. With phylogenetic correction, CTmax also predicted species distribution. The CTmax estimate is 1.37696. As species CTmax increased, the impervious surface cover (1,000 m radius) of the study sites where the species were found increased also.

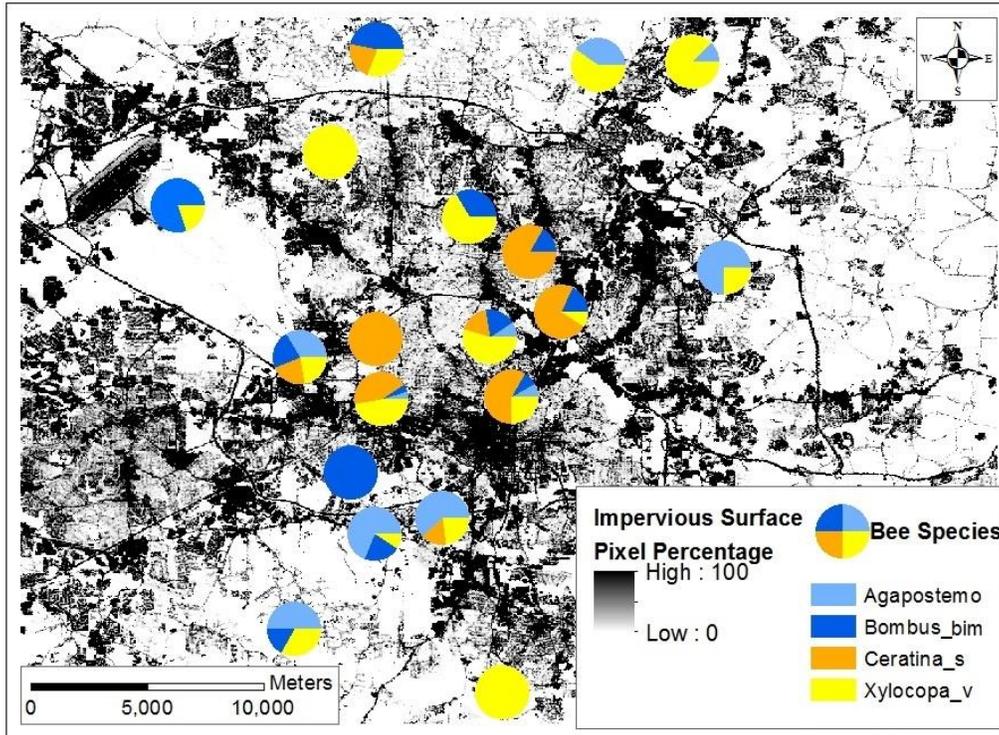


Figure 2.8. Bee CTmax predicted species distribution based on impervious surface cover (1,000 m radius). Bees with higher CTmax were present in areas with higher impervious surface cover. Data above are relative abundances shown for two species with the highest CTmax (*Xylocopa Virginia* and *Ceratina strenua*) and two species with the lowest CTmax (*Bombus bumaculatus* and *Agapostemon virescens*). Data source 2011 National Land Cover Database.

TABLES

Table 2.1. Species with their life history, nesting, mean CTmax, mean CTmax standard error, mean size, and mean size standard error.

Species	N (Sample Size)	Life History	Nesting	Mean CTmax (°C)	CTmax SE	Mean Size (Intertegular Distance mm)	Size SE
<i>Agapostemon virescens</i> (Fabricius, 1775)	22	Solitary	Ground	44.30	0.44	2.13	0.05
<i>Bombus bimaculatus</i> (Cresson, 1863)	24	Eusocial	Cavity	44.38	0.26	4.23	0.08
<i>Bombus griseocollis</i> (DeGeer, 1773)	30	Eusocial	Cavity	45.54	0.20	5.51	0.20
<i>Bombus impatiens</i> (Cresson, 1863)	20	Eusocial	Cavity	45.53	0.29	3.99	0.10
<i>Ceratina calcarata</i> (Robertson, 1900)	10	Subsocial	Cavity	47.75	0.68	1.392	0.03
<i>Ceratina strenua</i> (Smith, 1907)	4	Subsocial	Cavity	49.53	2.34	1.05	0.10
<i>Halictus ligatus/poeyi</i> (Say, 1837)	23	Eusocial	Ground	46.38	0.37	1.70	0.02
<i>Lasioglossum bruneri</i> (Crawford, 1902)	4	Eusocial	Ground	45.28	0.75	1.04	0.15

Table 2.1 Continued

Species	N (Sample Size)	Life History	Nesting	Mean CTmax (°C)	CTmax SE	Mean Size (Intertegular Distance mm)	Size SE
<i>Lasioglossum imitatum</i> (Smith, 1853)	23	Eusocial	Ground	45.66	0.30	0.84	0.03
<i>Lasioglossum zephyrum</i> (Smith, 1853)	3	Eusocial	Ground	44.75	1.14	0.96	0.14
<i>Megachile campanulae</i> (Robertson, 1903)	3	Solitary	Cavity	44.43	1.00	2.40	0
<i>Megachile exilis</i> (Cresson, 1872)	15	Solitary	Cavity	46.00	0.32	2.39	0.04
<i>Megachile mendica</i> (Cresson, 1878)	6	Solitary	Cavity	46.25	1.38	3.14	0.09
<i>Megachile rotundata</i> (Fabricius, 1787)	14	Solitary	Cavity	47.38	0.59	2.23	0.05
<i>Ptilothrix bombiformis</i> (Cresson, 1878)	14	Solitary	Ground	47.74	0.43	3.20	0.09
<i>Xylocopa virginica</i> (Linnaeus, 1771)	32	Solitary	Cavity	49.18	0.26	6.57	0.15

Table 2.2. CTmax did not predict bee abundance or incidence based on temperature or impervious surface cover of study sites where the species was located. This table shows p-values for such models. CTmax is close to being able to predict incidence of bees based on impervious surface cover at the 1,000 m radius, although it is not significant. These results do not consider phylogeny.

Model	Temperature (Degree Hours)	Mean Maximum Temperature (°C)	Impervious Surface Cover (100 m)	Impervious Surface Cover (1,000 m)
Abundance	0.7751	0.7593	0.6476	0.4151
Incidence	0.5555	0.8021	0.3905	0.0591

Table 2.3. CTmax and some other variables showed phylogenetic signaling.

	CTmax	Size	Temperature (Degree Hours)	Mean Maximum Temperature (°C)
p-value	0.002	0.001	0.231	0.315
K	0.951	1.119	0.412	0.164
Phylogenetic Signal	Yes	Yes	No	No

Table 2.3 Continued

	Impervious Surface Cover (100 m)	Impervious Surface Cover (1,000 m)	Temperature (Degree Hours)_ Bee Abundance	Mean Maximum Temperature (°C)_Bee Abundance
p-value	0.340	0.098	0.001	0.114
K	0.099	0.947	2.227	0.482
Phylogenetic				
Signal	No	No	Yes	No
	Impervious Surface Cover (100 m)_Bee Abundance	Impervious Surface Cover (1,000 m)_Bee Abundance	Temperature (Degree Hours)_ Bee Incidence	Mean Maximum Temperature (°C)_Bee Incidence
p-value	0.001	0.001	0.408	0.016
K	2.683	2.638	0.758	0.996
Phylogenetic				
Signal	Yes	Yes	No	Yes

Table 2.3 Continued

	Impervious Surface Cover (100 m)_Bee Incidence	Impervious Surface Cover (1,000 m)_Bee Incidence
p-value	0.005	0.001
K	1.087	1.069
Phylogenetic Signal	Yes	Yes

Table 2.4. CTmax did not predict species’ response to warming, when response was measured as the change in bee abundance or incidence relative to temperature or impervious surface cover of study sites. Response to warming was the slope of the line for a graph of each species where the x-axis was one of the environmental variables listed in the table below and the y-axis was bee abundance or incidence. CTmax was then analyzed to see if it would predict these slopes. This table shows p-values for such models.

Model	Temperature (Degree Hours)	Mean Maximum Temperature (°C)	Impervious Surface Cover (100 m)	Impervious Surface Cover (1,000 m)
Abundance	0.7571	0.3667	0.6319	0.4481
Incidence	0.6373	0.8829	0.9155	0.0743