

Urban Landscape Effects on Bees and Food Production

by

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Dedication

To all environmentalists who work to understand, preserve, and highlight the importance of our natural world.

Acknowledgements

I recently spoke to a friend—fresh from defending his own dissertation—and we commiserated on how surprisingly lonely the doctoral experience could feel. And yet, as the conversation deepened, we realized we each had a long list of people keeping us company along the way. Numerous people supported me in diverse ways throughout this doctoral journey, and without their support, the journey would've been impossible. I am extremely grateful to the following people for their company and support:

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Abstract

Bees are a critically important functional group, contributing to the pollination of many of the world's leading food crops and flowering plants, but concern is growing over signals of bee declines. Habitat loss associated with urbanization is thought to contribute to bee decline, but studies show that bees have variable and complex responses to urbanization. This variability has challenged our ability to understand the patterns, function, and management of wild bees in urban landscapes. This dissertation aims to address these challenges by using the patch-corridor matrix model and urbanization gradient analyses to investigate 1) whether bees show variable response patterns to urbanization due to an issue of scale, 2) how urbanization affects the function of pollination in urban agriculture, and 3) the effect of small flower plantings on bee management in urban landscapes.

First, I propose that bees show variable response patterns to urbanization due to an issue of scale, more specifically the resolution at which land cover data is measured. To test this, I first review prior studies of urban landscape impacts on bees, and then use remote sensing technology to test whether a shift from coarse- to fine-resolution land cover data reveals new patterns. In the literature review, I find studies continue to show variable results, with most studies finding no significant effects in how urban landscapes impact wild bees. I also find most studies use coarse-resolution land cover data to test landscape effects. When comparing bee response patterns between coarse- and fine-resolution land cover data, I find fine-resolution land cover data reveals patterns that are obscured by coarse-resolution land cover data.

Second, I conduct a field experiment to test how urbanization in south-eastern Michigan impacts pollinators and the ecosystem service of food production in urban agriculture. I find that the urban heat island effect affects food production quantity and quality, while the presence of pollinators in gardens affects food production stability.

Third, I conduct a final field experiment to test how floral additions of one to ten pots of flowers impact wild bee populations in urban landscapes. I find that small flower plantings can positively impact pollinators in urban areas, although a nonlinear and saturating relationship between flower quantity and bees means that smaller floral additions have higher impacts than large floral additions.

At a time when urbanization is projected to continue expanding at rapid rates, and the status of wild bee health is uncertain, this research deepens our understandings of the links between urbanization, wild bee populations, and effects on their ecosystems services and management. To deconstruct the variability seen across past studies, this dissertation underscores the importance of matching scales of measurements to the scales of the biological species of interest. My results also show that bees can act as a stabilizing force in urban agriculture, and that encouraging citizens to plant flowers can be an effective bee management strategy.

Chapter 1

Introduction

Background

“The last 50 years have without doubt seen the most rapid transformation of the human relationship with the natural world in the history of humankind.”

(Steffen et al. 2004)

The latter half of the twentieth century brought unprecedented global changes, in an era called the Anthropocene. Within this time period, the continued rapid increase of urban populations has been described as “one of the most important trends of all” (p.89, Steffen et al. 2015). The trend of urbanization remains important because it shows no signs of slowing down, yet we understand that it drives complex environmental changes such as altered biogeochemical cycles or impacts on biodiversity (Grimm et al. 2008). This dissertation explores environmental effects of urban landscapes from an ecological perspective, with a focus on broadening our understanding of bee patterns, function, and management in urban landscapes.

Bees are essential as pollinators of many food crops and wild plant species (Klein et al. 2007). Animal-mediated pollination is needed for over 85% of the world’s flowering plants (Ollerton et al. 2011) and 87 of the world’s 115 leading crops (Klein et al. 2007); it also accounts for roughly \$200 billion of the world’s food production (Gallai et al. 2009).

Although honey bees are the most widely recognized and researched bee species, this dissertation focuses on unmanaged bee species, or wild bees. Over 20,000 wild bee species exist around the world, with over 4,000 species in North America (Michener 2007; Wilson and Carril

2016). Yet, our knowledge of the natural history and population statuses of these species remains limited. Like honey bees, wild bee species also depend on flowers for food. Unlike honey bees, however, few wild bees species live in hives, and instead most live in nests dug into bare soil (70%), dead wood, or small cavities such as hollow stems (Wilson and Carril 2016). Recent evidence suggests that wild bee pollinators are more effective pollinators than honey bees, and therefore have a significant impact on global food production (Garibaldi et al. 2013). After collecting data from 600 fields on all continents except Antarctica, for example, Garibaldi *et al.* (2013) found that crops visited by wild pollinators experienced significant increases in yield 100% of the time, while crops visited by honey bees only experienced significant increases 14% of the time.

Despite the key role of wild bees in ecosystems, concern is growing over signals of bee species declines (Winfree 2010; Vanbergen and the Insect Pollinators Initiative 2013; Goulson et al. 2015). Very few long-term monitoring programs exist for the world's wild bee species, leaving many knowledge gaps in our understanding of how global change is affecting bee populations and communities (LeBuhn et al. 2013). Piecemeal data from North America and Europe show that some bee species have experienced severe declines or gone extinct, raising concern that declines in other species and regions are likely (Goulson et al. 2015).

Although multiple drivers have negative effects on bees, there is clear consensus that habitat loss—the destruction of the natural environment—has been a main driver of bee declines for decades (Goulson et al. 2015). Urbanization is associated with moderate to severe habitat loss, where downtown areas can be covered by over 80% pavement and buildings (Glaum et al. 2017), and projections that urban landscapes will increase by 1.2 million km² worldwide by 2030 are assumed to negatively impact biodiversity (Seto et al. 2012). For bee biodiversity, however,

urbanization does not have uniformly negative effects, with studies showing variability in both the magnitude and directionality of bee's responses to urbanization (Cariveau and Winfree 2015; Goulson et al. 2015; Senapathi et al. 2017). Efforts to tease apart the complex response patterns are ongoing (Cane et al. 2006; Cariveau and Winfree 2015). Without a thorough understanding of urbanization effects on bee community patterns, challenges remain in understanding consequences for ecosystem services and bridging gaps between knowledge and practice (McDonnell 2015).

One major motivation for maintaining bee populations in urban areas is their potential contributions to urban agriculture. Urban agriculture shares a long history with urbanized areas, but has experienced a recent resurgence in popularity as communities seek to increase food security, community resilience, and human health within urban areas (Mougeot 2005; Hodgson et al. 2010). Urban agriculture has been associated with various ecological and social benefits centered around sustainability and reconnecting humans and nature, but the difficulty in measuring these benefits means little empirical work has been done to confirm the associations (Lawson 2005; WinklerPrins 2017). It is estimated that urban agriculture contributes 15-20% to the global food system (Hodgson et al. 2010), and The Food and Agriculture Organization (FAO) of the United Nations has recognized that to meet UN Development and World Food Summit goals concerning hunger—especially to minimize hunger within growing low-income urban populations—urban agriculture must be included in city development initiatives (Food and Agriculture Organization of the United Nations 2017). To successfully produce many varieties of fruits and vegetables in cities, however, ecosystem functions such as pollination must be conserved (Klein et al. 2007). Multiple studies have established that pollinator communities change in urban landscapes (Hernandez et al. 2009), but only recently have studies begun to

determine whether these changes trickle down to impact urban food production (Lowenstein et al. 2015; Potter and LeBuhn 2015).

This dissertation therefore advances our understandings of the links between urbanization, wild bee populations, and the ecosystem service of food production in urban landscapes (**Figure 1.1**). The purpose of this dissertation is to deepen understanding of the patterns (Chapter 2), function (Chapter 3), and management (Chapter 4) of wild bees in urban landscapes. I use both gradient analysis and patch-corridor matrix frameworks to ground this research.

Research frameworks

This research is grounded in urban landscape ecology and uses two common frameworks as foundations, the patch-corridor matrix model and urbanization gradient analyses (Francis et al. 2016).

Investigating relationships between urban landscapes and bees requires an awareness of spatial contexts and the interactions between biotic and abiotic elements—both central ideas in urban landscape ecology. Urban landscape ecology emerged as a union of two more recent branches of ecology—urban ecology and landscape ecology—in the 1970’s (Forman 2014; Francis et al. 2016). Coincidentally, these fields emerged as the great acceleration of the Anthropocene was hitting its stride. Although definitions vary (Pickett et al. 2011; Wu 2014), urban ecology generally investigates interactions among organisms, the physical environment, and built structures where people are concentrated (Forman 2014), while landscape ecology ties in the spatial-temporal aspects to understand relationships between spatial patterns and ecological processes at multiple scales (Wu 2013). Urban landscape ecology, therefore, considers how

spatial-temporal contexts affect ecological patterns within urban areas, and provides useful frameworks, such as the patch-corridor matrix and urban gradient models, to approach these complex topics.

The patch-corridor matrix model is a foundational conceptual model in landscape ecology, and patch-matrix dynamics therefore inform how many urban landscape ecologists conceptualize landscapes (Francis et al. 2016). Partly inspired by MacArthur and Wilson's theory of island biogeography (1967), the model was developed by Forman and Godron (Forman and Godron 1986; Forman 1995). Originally focused on agricultural or forested landscapes, it is also widely applied to urban landscapes (Forman 2014; Francis et al. 2016). In the model, landscapes are composed of three spatial elements: the matrix is the common land cover type throughout a landscape, while patches are non-linear and corridors are linear areas embedded within the matrix (Forman and Godron 1986; Francis et al. 2016). Applying this model to bees in urban landscapes, the matrix is often considered the built environment, made of buildings, pavements, and other impenetrable surfaces, while patches are areas where floral or nesting resources suitable for bees are present. Corridors, or linear habitat areas, are less mentioned in the urban bee landscape ecology literature, as there is no evidence that linear habitat patches affect bees differently than non-linear patches in urban areas. Each chapter of this dissertation is permeated by the patch-matrix model framework, in which the distribution of resource patches (flower and nesting resource patches) throughout a landscape is assumed to be the core of what impacts bee population patterns.

Gradient analyses are also widely used in the assessment of urban landscape impacts on ecological patterns and processes (McDonnell and Hahs 2008; Francis et al. 2016). Drawing on earlier ecological work of vegetation gradients (Whittaker 1967), McDonnell & Pickett (1990)

saw the potential of using spatially ordered environmental variation—e.g. in cities that could mean denser built environments at the core, with decreasing density as one travels from the core to the city fringes—to reveal insights of urbanization impacts on ecological patterns and processes. While gradient analyses have been critiqued for failing to incorporate the non-linear and complex nature of cities (Ramalho and Hobbs 2012), they provide a systematic tool enabling “researchers to order an ecological response along an axis of environmental conditions” (McDonnell et al. 2012). Within this dissertation I use gradient analyses as a valuable tool to establish initial patterns, but also make efforts to consider non-linearity and complexity. I remove assumptions of linearity by using quantitative landscape metrics to define the gradient, and address parts of the complexity by exploring more precise quantifications of urbanization (in relation to bees) and considering additional variables that may influence bee population patterns.

Study Area

The remote sensing work and field experiments conducted in this dissertation are situated in southeastern Michigan, USA. This region is part of the Great Lakes Plains, an area where a history of ice ages and glaciers left sandy lake-beds, wetlands, prairies, and fertile topsoil (Vachon 2017). Around the turn of the twentieth century, southeast Michigan began to transform from a largely agricultural area to an increasingly urban one due to the rise of automobile manufacturing in Detroit (Dunbar 1980). After several decades of urban growth, Detroit manufacturing jobs began to disappear as companies went elsewhere, and the area entered a phase of post-industrial urban decline (Thomas 1990). Recently, in this climate of decline, an urban agriculture movement has grown and regained prominence in Detroit (Colasanti et al. 2013), creating a fitting opportunity to understand the environmental context within which these

gardens are situated, and how the level of urbanity might influence key species that operate in these gardens, such as bees.

Dissertation Overview

This dissertation is divided into three separate studies, each dedicated to advancing our understanding of urbanization impacts on the patterns, function or management of bees in urban areas. Chapter 2 examines patterns through the treatment of scale in the urban bee ecology literature, and tests whether a change in scale reveals new insights that may reduce the variability seen in bee response patterns to urbanization. Chapter 3 examines function by documenting urbanization's effect on food production in urban agriculture, viewed as an ecosystem service provided by pollinators. Chapter 4 examines management by testing whether small flower additions help increase bee abundance or species density in urban settings. The final chapter, Chapter 5, summarizes findings and reflects on future directions.

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Figure

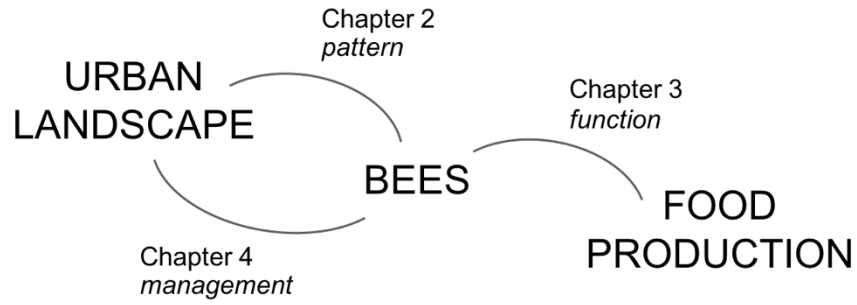


Figure 1.1 Dissertation overview. Three main concepts are explored throughout this dissertation: urban landscapes, bees, and food production. Chapter 2 explores how to improve pattern-detection of urban landscape impacts on bees. Chapter 3 explores function by testing how food production is impacted by changes in bee communities across urban landscapes. Chapter 4 explores management by testing how bee communities respond to resource manipulations in urban landscapes.

Chapter 2

The case for moving towards finer landscape resolutions in urban bee ecology: a mini-review and test case

2.1 Abstract

Context. Anticipated urban expansion and signals of bee decline have increased interest in how bees respond to urbanization. Trends have been difficult to ascertain, however, as bee response to urbanization appears to be highly variable. We suggest a change in scale, from using coarse- to more fine-resolution land cover data, may help resolve this variability and improve pattern-detection in bee response to urbanization.

Objectives. Our first objective was to review past studies of urbanization effects on bee response and determine whether consistent trends have emerged. Our second objective was to test whether comparisons of bee response between coarse- and fine-resolution land cover data revealed new insights into urbanization effects on bees.

Methods. To complete our first objective, we conducted a brief literature review of 28 studies examining urban landscapes' effects on bees in the USA, and documented the scales used in each study. To complete our second objective, we sampled bees in four gardens across an urbanization gradient, created a new fine-resolution (5 m) land cover data set for the surrounding area, and compared bee response patterns between coarse- and fine- resolution land cover data sets.

Results. Our literature review showed that studies reported variable but mostly non-significant results, and used a wide range of spatial scales that made comparisons difficult. Our comparison

between coarse- and fine-resolution land cover data showed that fine-resolution land cover data revealed important potential floral and nesting resources that were left undetected by coarse-resolution land cover data.

Conclusions. Our results show that the use of fine-resolution land cover data decodes the variability seen across urban bee studies. Urban landscapes should therefore be quantified at scales more aligned with the scales at which bees resources are found in urban areas.

2.2 Introduction

To manage for the sustainable use of natural resources it is important that we understand how ecosystems change under human influence. Urban landscapes are the epitome of an area under heavy human influence, but efforts to understand how ecosystem functions and services change within them are still relatively new (Wu 2014; Francis et al. 2016; Pickett and Cadenasso 2017). Here we focus on advancing our understanding of wild bee dynamics in urban landscapes, because although wild bees provide essential ecosystem functions and services, our ability to predict how projected urban expansion will affect these communities is still lacking (Seto et al. 2012; Viana et al. 2012; Senapathi et al. 2017).

Across studies, clear trends in how urbanity affects bees at the landscape scale remain elusive. In 2009, the only review of urban bee ecology literature to date reported a lack of urban landscape-scale assessments, and noted that this omission limited the ability to identify causal drivers of changes in bee diversity from rural to urban locations (Hernandez et al. 2009). In line with their finding, subsequent reviews of anthropogenic effects on bees were unable to address the effects of urban landscapes adequately because of insufficient studies (Winfrey et al. 2009, 2011; Williams et al. 2010; Viana et al. 2012). In *A meta-analysis on bees' response to*

anthropogenic disturbance (Winfree et al. 2009), for instance, only one out of the 50 papers analyzed dealt explicitly with the anthropogenic disturbance of urbanization; most of the remaining papers dealt with the disturbances of agriculture and fragmentation. Later, a broader review on *Native pollinators in anthropogenic habitats* only found four papers addressing bee response to landscape-scale urbanization, while in contrast, 49 papers addressed bee response to landscape-scale conversion to agriculture (Winfree et al. 2011). Since 2011, however, increasingly more studies have considered how landscape-scale urbanization affects bee communities, and findings vary (Cariveau and Winfree 2015) but have yet to be systematically synthesized.

We suggest that the variation seen across studies is exacerbated by an issue of scale, namely the use of inappropriate scales for understanding urban bee dynamics (McDonnell and Hahs 2008; Senapathi et al. 2017). Here we refer to scale as a spatial measure and focus on resolution (also known as grain), defined for the purposes of this study as “the minimum unit of observation” in landscape land cover data (Wiens 1989; Levin 1992; Schneider 2001). The widely used National Land Cover Database (NLCD) map, for example, has a resolution of 30 m, meaning that the landscape is divided into square 900 m² (30 x 30) areas and each square is categorized by the dominant land cover type within that area (<https://www.mrlc.gov/>).

The important role of scale in understanding patterns and processes has long been recognized in ecology (Levin 1992) and is an area of ongoing research (Higgins et al. 2012). In landscape ecology, for example, extensive work has shown that changes in resolution or the number of land cover classes can alter landscape pattern metrics in either predictable and unpredictable ways (Wu et al. 2002; Wu 2004; Buyantuyev and Wu 2007; Corry and Laforteza 2007). However, fewer studies address how changes in scale impact response variable patterns,

such as species abundance or richness patterns throughout an urban landscape (*but see* Grafius et al. 2016). Different phenomena occur at different scales, and the scales at which we choose to measure phenomena will affect outcomes (Rahbek 2005; Grafius et al. 2016). Take a study of plant richness, for instance. Examining plant richness at the scale of within 50m of a river bank might suggest the community is structured by soil moisture levels, whereas examining plant richness at global scale would suggest the plant community is most structured by climatic conditions. Given that there is no universally correct scale at which to measure ecological processes and that choices of scale are produced by observers, it is important that our choices of scale strive to match the underlying ecology of organisms of interest (Wiens 1989; Levin 1992; Sayre 2005).

Bees need spaces with floral, nesting, and overwintering habitat within flying distance for survival (Westrich 1996). Although bee foraging distances typically range from 0.2-km to 4-km (with a few exceptions, Greenleaf et al. 2007), the resources used by bees are often less than a few centimeters in size. With floral resources, for example, wild bees need flowers with nectar for adults or pollen grains for their young. In our field experience documenting floral communities in southeast Michigan, it was rare to find flower species other than sunflowers with flower-head diameters wider than 10-cm. With nesting or overwintering resources, the majority of wild bees nest or overwinter in soil, wood, or pith (Michener 2007), and the burrows created within these substrates often seem to allow only one individual to enter at time. To give an idea of the potential sizes of these nest-entrances, the average head size of one of the largest bees found in our study area of southeast Michigan, *Xylocopa virginica*, is approximately 0.66 cm (Barthell and Baird 2004). Since the width of *Xylocopa virginica*'s body is wider than its head,

we can deduce that the sizes of some of the largest bees' nest entrances are at most several centimeters.

In the case of wild bees in urban landscapes, many analyses understandably use anthropogenically-centered land cover data, where the resolution is too coarse for proper documentation of potential bee resources in such heterogeneous landscapes (Senapati et al. 2017). Similar to Grafius *et al.*(2016), we propose that a finer resolution, or more organism-centered scale, is more appropriate for bees going forward (Wheatley and Johnson 2009). Urban landscapes are highly heterogeneous, and coarse resolution data (considered for these purposes as land cover data with 30 m or higher resolution) can omit many smaller areas of resources that may impact organisms such as bees. In our own work sampling bees in Detroit, for example, we saw one parking lot with a small, resource-rich garden nearby, while another parking lot area was entirely devoid of vegetation, yet both tracts of land could be equally classified as “high intensity developed” under coarse-resolution classifications. How much detail is obscured can change depending on the spatial patterning of the landscape. Turner *et al.* (1989), for example, showed that rare land covers are increasingly lost with coarse-resolution analysis when landscape patterns are patchy.

We hypothesize that coarse-resolution datasets do not match the scale at which pollinators operate, and can therefore produce unrepresentative results. Grafius *et al.* (2016), for example, compared the influence of scale on estimated pollination services across three cities in the U.K., and found that coarse (25 m)-resolution land cover data generally estimated higher pollination services than fine (5 m)-resolution land cover data when using the same pollinator data. We have not yet developed the ability to test which prediction is more accurate, but since finer-resolution land cover data theoretically reflects details in bee resource availability that

coarse-resolution cannot, we argue that models based on fine-resolution data should be more accurate. Similar critiques of models based on coarse-resolution data have been made (Peterson et al. 2016; Peterson 2017). For example, with endangered bird occurrence maps, Peterson *et al.* argue that coarse-resolution data is more prone to omission errors and therefore less appropriate for fine-scale conservation applications. We fully acknowledge that coarse resolution data is used more broadly due to its wider availability and despite the tradeoff with accuracy (McDonnell and Hahs 2008). However, finer resolution datasets are becoming more widely attainable, and will significantly advance our ability to uncover patterns and mechanisms behind the variability often observed in bees across urban landscapes.

There are two objectives to this study. First, we conduct a brief literature review of studies examining urban landscapes' impact on bees in the USA and ask the following questions: (1a) what are the recent trends of urban landscapes' impact on bees? and (1b) what ranges of scales are used across studies in terms of sampling scale, landscape scale, image resolution, and extent? Second, we create a new, fine-resolution (5 m) land cover data set to determine (2) what new insights does a change from coarse to fine resolution reveal about how urban landscapes impact pollinators?

2.3 Methods

(1) Literature Review

To review current literature on the impact of urban landscapes on any wild bee community metric, we conducted an ISI Web of Science search on May 3, 2016 with the search terms “(pollinator* OR bee OR bees OR Apoidea OR pollinat*) AND (urban OR impervious OR suburban OR urbanity OR city).” The pollinator-related search terms mirror those used by

Winfree *et al.* (2009) in their meta-analysis of bees' responses to anthropogenic disturbances. To maintain a level of consistency in the types of urban landscapes studied and to reduce the impact of regional or cultural differences on a global scale (De Palma *et al.* 2016), the resulting list of 1,622 articles was then narrowed by restricting the Countries/Territories category within ISI's search engine to "USA." Those 288 papers were further narrowed to studies that used statistical tests to analyze the significant of increases or decreases in pollinator outcomes such as abundance, richness, diversity, community composition, disease prevalence, nesting density, etc., between less urbanized and more urbanized locations. We considered studies that used space (e.g. changes in habitat type or surrounding habitat) as a proxy for increasing urbanization. A small "snow-ball" effect was also implemented, whereby additional relevant papers were found from citations or as related content, and therefore included for a final count of 28 papers.

Similar to Winfree *et al.* (2009), we collected data on the less- and more-disturbed habitat types compared in each study (limiting results to habitat types related to urbanization), the outcome variable(s) tested (e.g. bee abundance), and the direction of each relevant statistical test (positive, negative, or if there was no significant difference, neutral). Since each relevant statistical test conducted in a study was included as a separate data point, many studies contributed multiple data points. To quantify the use of scale across studies, data on resolution, sampling, landscape, and extent scales were collected, in addition to data on study location (estimated latitude and longitude).

When land cover data were used, the resolution of data were recorded when available. One study used Google aerial images for land cover data, and in this case we were unable to find official documentation of the images' resolution, and therefore used the upper limit of the range found in Google Earth's wiki page, or 15 m (en.wikipedia.org/wiki/Google_Earth). Sampling

scale was interpreted as the radius of the area where bees were sampled in each site; when transects were used the longest edge of the transect was divided in half to provide the radius. Landscape scale was defined as the radial distance used to assess land cover around each independent site. It should be noted that a variety of papers tested multiple landscape scales, but often chose the scale most highly correlated to response variables for statistical analyses; we only included scales chosen for statistical analysis. Estimated latitude, longitude, and extent were obtained using information or maps provided by each study, and estimated with Google Earth Pro version 7.1.5.1557 when maps were absent. When studies included multiple sites, the center-most point in between all the sites listed was selected as the latitude and longitude coordinate for the overall study, and the rectangle formed by the most north-, south-, east-, and west-facing points was used to estimate area extent. Large bodies of water—i.e. the Great Lakes and the Atlantic or Pacific Oceans—were excluded from extent measurements. Since exact geographic coordinates were rarely reported in studies, these measurements provide rough estimates sufficient for general comparisons of geographic coverage.

(2) Comparison of fine and coarse resolution land-cover data

Sites: The four garden sites selected to compare results from coarse- and fine-resolution land cover were part of a larger study sampling bee abundance and richness across 24 garden sites across southeastern Michigan, U.S.A. (Fitch *et al.*, *forthcoming*) The four gardens in this study were selected to represent the widest range of impervious surface area within 500 m of each garden, calculated by summing area labeled as medium and high intensity developed according to the 2011 National Land Cover Database (NLCD, Multi-Resolution Land Characteristics Consortium, mrlc.gov). The Lafayette Greens garden site in Detroit was the most

urban (72,536 m² medium and high intensity developed area within 500 m of garden, labeled Site A in **Figure 2.1**), Perry Community Garden (34,062 m², Site B) and Clague Elementary Garden (15,432 m², Site C) in Ypsilanti and Ann Arbor, respectively, were considered to be mid-range, and M'Lis' Farm was the least urban garden site (0 m², Site D). Each garden was dominated by vegetable and ornamental flowering plants, often with additional 'weedy' flowers nearby. Only four garden sites were selected for this study because of the time-intensive process required to create fine-resolution land cover data for each site, and because we intended this study to be a first step in determining whether fine resolution data revealed insights worth pursuing (if so, subsequent studies would need to automate the process of fine-resolution data creation).

Bee Sampling: Bee abundance and richness data for each of the four gardens were also obtained as a subset of the larger study (Fitch *et al.*, *forthcoming*). To sample bees, two rows of three pan traps (small 3-oz. plastic bowls filled with water and a small drop of blue unscented Dawn soap) were used, with one yellow, one blue and one white pan trap in each row. These three colors were used to attract as wide a range of bee species as possible, since certain bee species can be more attracted to one color over others. Each pan trap was placed 2 m from the next pan trap, with 2 m in between each row. Traps were placed in each garden every two weeks from mid-May to mid-September in 2014. Additionally, in that four-month period, bees were netted four times, or roughly once a month, for 30 minutes in the morning (9 a.m.-12 p.m.) and afternoon (1 p.m.-4 p.m.). Bees were then washed, dried, and pinned for identification, with most identifications done by Jaime Pawelek or Jason Gibbs. Since land cover analysis would be carried out within a 300-m radius of each site for this study, we subset the bee sample data to include only small species with estimated foraging ranges of 300-m or less. Foraging ranges

were calculated using body size measurements (Greenleaf et al. 2007) obtained from either existing literature or, as done by Greenleaf *et al.*, from the mean of the intertegular span of 5 females per species from our collection. Bee abundance and richness were calculated by averaging four groupings of bee collection events: the first netting date and first two trapping dates formed the first group, the second netting date and following two trapping dates formed the second group, etc.

Coarse-Resolution Land Cover Data (30 m): To tabulate land cover area at a resolution commonly used in national studies, the most recent National Land Cover Database (NLCD) data at the time, from the year 2011, were selected. NLCD data are produced by a consortium of USA's federal agencies who use Landsat images to create freely available, 30-m resolution land cover data sets with categories modified from Anderson *et al.* (1976; **Figure 2.2a**). Given the three-year difference between NLCD data (2011) and bee data collection (2014), we searched for land cover differences between 2011 and 2015 using Google Earth historical images and found only a few, small areas where land cover had changed significantly between years; the changes seemed too few to significantly impact results. The total area of each land cover class was tabulated within a 300-m buffer of each garden site using ArcMap software (**Figure 2.3a**; ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) and analyzed as a proportion of total area.

Fine-Resolution Land Cover Data (5 m): To tabulate land cover area at a finer resolution, a dataset of 5-m resolution was created with 'heads-up' digitizing (manually tracing over features with a mouse) over high-resolution imagery. We chose a 5-m resolution because it appeared to capture smaller areas of potential bee habitat—such as gardens—while remaining feasible to label manually. A grid of sampling points spaced every 5-m was generated in ArcMap

software with the Fishnet tool, generating roughly 11,000 data points per site (**Figure 2.3b**). Land cover was scored manually for each sampling point within 300 m of each garden site. Base layers for data creation were high-resolution (15.24 cm, or 6 in) 4-band (RGB and infrared) aerial images of Washtenaw and Wayne Counties in Michigan taken in the spring of 2010. Both sets of images were obtained from the Washtenaw County GIS Program. The four-year difference between aerial imagery (2010) and the year of bee data collection (2014) meant that a small proportion of the land surrounding gardens had undergone land-cover changes; in these cases, Google Earth historical images as close to 2014 as possible and ArcMap's Imagery Layer were used to define land cover for those small areas. When aerial image interpretation was difficult, a combination of Google Earth (aerial images and street-view scenes) and ground-truthing was used to clarify land cover classifications. After all sampling points were classified, the sum of points per land cover class was calculated and analyzed as a proportion of total sampling points per site.

To document floral or nesting resource potential for bees more directly, a slightly modified classification scheme was created for fine-resolution mapping, that contained the same general categories as NLCD's coarse-resolution land cover classifications (**Figure 2.2b**, general categories indicated by color). In the modified classification scheme, sampling points were labeled in a hierarchical fashion, such that every point was first labeled as either Impervious or Non-Impervious, for example, and then points labeled as Impervious were also labeled as either Pavement, Roof, etc., while points labeled as Non-Impervious were labeled as Vegetation, Non-Vegetation, or Water, and so forth. The full hierarchy of land cover types can be seen in **Figure 2.2b**, with further description of each category in **Table 2.1**.

Quality Control and Consistency Measures for Fine-Resolution Data: Multiple observers (Maria-Carolina M. Simao, Jill Matthijs, and Maggie Mianecke) contributed equally to the scoring of land cover data, with J.M. and M.M. trained by the most experienced scorer (M.C.M.S.). The scoring protocol included several steps aimed at minimizing measurement error. First, points were labeled in three stages: first, points covering pavement and roofs were labeled, then trees, then low-lying vegetation or non-vegetation areas. In each stage of labeling, points found to be incorrect were reclassified, providing multiple opportunities for re-assignment as methods developed. Second, any point found too difficult to classify from aerial imagery (or Google Earth) was flagged, and classified by the most experienced scorer M.C.M.S. either through ground-truthing or heads-up digitizing, depending on the situation (points located in private property for instance, could not be ground-truthed). To ensure that these difficult points did not bias results, data were visualized both with and without flagged points. Third, as a final step, to test measurement consistency of this classification system and method, 5% of the points at each site were randomly selected, re-classified by M.M. (but without ground-truthing), and compared against original classifications in a contingency matrix. Although contingency matrices are traditionally used to assess accuracy between automatic classifications and reference data, in this case both of the data layers being compared are viewed as reference data, and the contingency matrix therefore measures how consistently each point was labeled.

Comparison of Coarse- and Fine-Resolution Land Covers with Bees

To compare coarse- and fine-resolution land covers and their relationship with bee abundance and richness, land cover classifications belonging to the same general category (either built environment, water, woody plants, herbaceous plants, and crops, as seen in the legend of

Figure 2.2a) were aggregated into one measure for each resolution. For example, for coarse-resolution land cover, areas classified as open, low-intensity, medium-intensity, and high-intensity developed were summed into a total area to represent the built environment under coarse-resolution classification (**Figure 2.2**). For fine-resolution land cover, areas classified as pavement, roof, artificial turf, stone walls, city grates, and fences were summed into a total area to represent the build environment under fine-resolution classification. Given each resolution had a different classification scheme, this aggregation allowed for more direct comparisons between the two types.

2.4 Results

(1a) What are the recent trends of urban landscapes' impact on bees?

In our review of studies within the USA, we found studies addressing bees and urban landscapes were published more in recent years, meaning attention on this topic has increased (**Figure 2.4**). Most studies addressed patterns in bee abundance and richness, with few other response variables represented. Of the studies examining bee abundance and richness outcomes, the majority of statistical tests reported neutral results, i.e. no significant impact of urban landscapes on bee abundance or richness.

(1b) What ranges of scales are used across studies in terms of sampling scale, landscape scale, image resolution, and extent?

There is little consistency in the overall use of scale across studies (**Table 2.2**), but certain measures of scales show some consistency. For resolution, most studies used 30-m resolution land cover data, or simply did not quantify their categorizations of site urbanity with

land cover data. Most authors made unique choices in sampling scale and extents, sampling bees in areas that ranged from 0.5 to 600 m in radii, and covering extents ranging from roughly 7 to nearly 235,000 km² (**Figure 2.5**). Landscape scales showed a higher level of consistency, such that the studies that did quantify their categorizations of site urbanity used some selection of the 0.2, 0.5, 1.0, 1.5, and 2.0 km radial distances.

(2) What new insights does a change from coarse- to fine-resolution reveal about how urban landscapes impact pollinators?

Comparing relative areas of land covers classified between coarse- and fine-resolution classifications, we see some similarities overall (**Figure 2.6**) but differences in the details (**Figure 2.7**). Overall, the dominant thematic classes of each resolution are well matched (**Figure 2.6**); for example, when thematic classes representing the built environment dominated in coarse resolution classifications (such as higher proportions of high and medium intensity developed), they also dominated in fine resolution classifications (such as proportions of pavement and roofs). Coarse-resolution classifications categorized three sites (Sites A, B, C) as completely developed but with decreasing levels of intensity (from mostly high-intensity in Site A to mostly low-intensity developed by Site C) and one site (Site D) as mostly agricultural. Fine-resolution classifications also categorized Sites A, B, C, and D with decreasing amounts of development (categorized as pavement or roof), but showed more details in the types and amounts of land covers filling less urban pockets of land—e.g. the proportion of the non-impervious land cover classified as proportion of tree, lawn, etc.

Closer inspection of land covers present in small proportions (<5% of total land area) present more striking differences (**Figure 2.7**, note difference in x-axis). The starkest difference

is the appearance of barren land covers in the fine-resolution classification, a feature completely absent from coarse-resolution classifications. In addition, wild, garden, and water (often man-made ponds) land covers are also visible in fine but absent in coarse resolution data. Lastly, fine-resolution classifications distinguish between number of trees or shrubs and lawns in urban landscapes, whereas coarse resolution only reveals the presence of trees when large tracts of forests are present—a rare occurrence in most urban landscapes.

When data from coarse- and fine-resolution classifications are compared with observed bee abundance and richness data (**Figure 2.8**), the ability of fine-resolution classifications to reveal new patterns emerges. In coarse-resolution classifications, only built environment land covers vary enough to show relationships with bee abundance and richness data. In fine-resolution classifications, however, not only built environment land covers show enough variation to form relationships, but also barren, woody, and herbaceous land covers. Looking at each individual land cover—rather than aggregated land cover categories, as used in **Figure 2.8**—shows the same trend across multiple individual land covers, where variation in bee abundance or richness is observed across most land covers when defined by fine-resolution, but variation in bee abundance or richness is only observed with built environment land covers when defined by coarse-resolution (**Figure 2.9, Figure 2.10, Figure 2.11, Figure 2.12**).

Consistency of fine-resolution land cover data

We found that results were not biased by points flagged as difficult to identify. Our fine-resolution classification system and method showed 91% overall consistency between experienced data scorers (**Figure 2.13**). Pavement, roof, gravel, sand, woody plants, lawn, and crop land covers were scored with high consistency (over 80% consistency, **Figure 2.13**). Wild

and garden land covers showed reasonable consistency between scorers (52-74%), while orchards showed low to moderate consistency (39% and 73%) between scorers. Mulch and soil land covers however showed very poor consistency in scoring (13-33% consistency, **Figure 2.13**). A few land covers were confused with other land cover types more often than others, for example, several points marked as lawn in the original data were marked as trees in the checked data and vice-versa. This likely reflected the occasional difficulty in distinguishing where tree crowns ended and lawns began, especially when portions of aerial images were leaf-off.

2.5 Discussion

In this study, we first reviewed 28 studies on how urban landscapes impact bees in the USA and focused on each study's treatment of scale. We found mostly neutral effects and little consistency in overall treatment of scale. When land cover data were used to quantify urbanity, most studies used coarse-resolution data. Second, we investigated whether a change from coarse- to fine-resolution land cover classification, with slight modifications in land cover classes, revealed new insights into how urban landscapes impact bees. We found that the subtleties of fine-resolution land cover classifications revealed variations in bee response that were obscured by coarse-resolution land cover classifications.

In our literature review, we found that many studies addressed the impact of urban landscapes on bee abundance and richness (**Figure 2.4**). The large number of studies addressing patterns in bee abundance and richness match previous findings (Winfree et al. 2011), and likely reflect a field still in the early stage of urban ecological systems research, i.e. a stage in which faunal patterns are established (Pickett et al. 2011; Francis et al. 2016). Once patterns of bee abundance and richness are better established, the field can progress to increased focus on

ecological processes and resulting functions, e.g. pollen deposition, competition, or interactions between trophic levels (Pickett et al. 2011).

Within this first stage of establishing faunal patterns, however, the majority of studies reported neutral effects (**Figure 2.4**), i.e. no significant impact of urban landscapes on bee abundance or richness. This result matches findings of other reviews of landscape effects on bees, some reporting the variation in response (Roulston and Goodell 2011; Senapathi et al. 2017) and others also finding a dominance of neutral effects when comparing bee response in more anthropogenic to less anthropogenic habitats (Winfree et al. 2011). This dominance of neutral effects raises an interesting question that we cannot answer here, but hope more fine-scale resolution studies can resolve: does the dominance of neutral effects reflect the reality that many bee communities are not affected by urban landscapes, or does it reflect a mismatch of scale, in which an over-simplification of land cover details obscures actual effects?

The scales used across studies in our review varied (**Table 2.2**), making comparisons and the ability to detect patterns less straightforward. Each study employed a unique set of choices across the different scales, and as seen in previous reviews (Hernandez et al. 2009; Wheatley and Johnson 2009), a fair number of studies did not even qualify their categorizations of habitat variation with details or measurements. The lack of consistency in use of scale is a common issue across studies—and is understandable given that the nuances of research questions and situations lead to variations in methodology—but it becomes problematic when looking to compare studies to find patterns. In all cases, however, choices of scale should be tethered to the biological organism or process of interest (Wiens 1989; Levin 1992). Here we make some recommendations on adopting more uniform approaches to sampling, landscape, image

resolution and extent scales in urban bee ecology, but they are starting points and likely require further input and refinement.

For sampling scale, following the standardized method put together by seasoned bee researchers LeBuhn *et al.* (2003) is likely a good starting point; they recommend sampling plots of 1 ha.

For landscape scale, it seems most appropriate to use scales that match the average foraging ranges of the bee species of interest—a distance that can be estimated from species body size, which has been shown to predict bee foraging ranges (Greenleaf *et al.* 2007). For a small *Lasioglossum* spp. bee, for example, an appropriate landscape scale for analysis might be 0.2 km, while for a large *Bombus* spp. bee a landscape scale of 1.5 km may be more appropriate. A recent study of bees in commercial blueberry farms in New Jersey, for instance, found that larger bees were more strongly affected by land cover at larger scales (1,500-m radius), while smaller bees were more strongly affected by land cover at smaller scales (300-m radius, Benjamin *et al.* 2014).

For resolution scales, our review confirms that coarse-resolutions or undefined scales are more widespread in the field of urban bee ecology than fine-resolution scales. Coarse-resolution scales have the advantage of being more accessible and providing insights into a broader picture, since larger amounts of area can be defined and analyzed. Fine-resolution scales, however, can provide insights into important details that may link to mechanisms (Wiens 1989). Consider carpenter bees (*Xylocopa* spp.), for instance, or other species that nest in wood. In our coarse-resolution classification, it is impossible to separate buildings from pavement—both are impervious surfaces, but one is a potential resource patch for carpenter bees since they nest in wood, while pavement does not have resource value for carpenter bees. A shift towards using a

fine-resolution classification could reveal that carpenter-bee response to urbanization is best explained by wood quantity. In remote sensing, resolution scales are recommended to be 2 to 5 times smaller than the spatial feature of interest (O'Neill et al. 1996); for bees this could mean resolutions as small as a fraction of a centimeter, a scale that is not yet technologically feasible. Still, a shift downward from using resolution scales 3,000 times the size of bees (e.g. 30 m resolution for a 1 cm-long bee) to 500 or 100 times the size of bees will move us closer to detecting relevant patterns.

For extent scales, it may be more difficult to standardize across studies, but linking the total distance covered by a study's sites to bee foraging ranges may be a start.

When comparing proportional areas of land cover classes between coarse- and fine-resolution classifications, we found minor differences overall but significant differences in the details (**Figure 2.6, Figure 2.7**). Overall proportions of land cover classes between coarse- and fine-resolution classifications told similar stories: sites classified as highly urban in coarse-resolution would also be classified as such in fine-resolution, and the same was true for less urban sites. This was expected since general urbanization patterns do not appear to be affected by changes in resolution when extent is kept constant (Wu et al. 2011). One important difference, however, is that fine-resolution classifications provided data on relative proportions of trees and lawns, when coarse-resolution classifications simply classified the same areas as “less developed” categories. This distinction is relevant because trees and lawns can provide nectar or pollen resources for certain bee species (Larson et al. 2014; Hausmann et al. 2016; Lerman and Milam 2016; Somme et al. 2016). Therefore, knowing relative proportions of trees and lawns in a landscape provides relevant information on bee-resource quantities that are otherwise obscured by coarse-resolution in urban landscapes.

The significant differences between coarse- and fine-resolution classifications emerged in observations of land cover classes occupying less than 5% of total land area in relation to bee response patterns (**Figure 2.8**). At lower proportions of total land area, patterns with land cover classes absent from coarse-resolution data emerged in fine-resolution data. This is a well-known result of increasing resolution in a heterogeneous landscape (Turner et al. 1989). What makes it significant in the context of urban landscapes and wild bees, is that the thematic classes that emerge in fine-resolution classifications—barren, woody plants, and herbaceous plants—are precisely some of those with highest potential for hosting bee nesting and flowering resources, and therefore those with the greatest potential to directly impact bee abundance, richness, and composition patterns. In our fine-resolution classifications, for example, bee richness shows a trend towards increasing with the proportional area of barren and herbaceous land covers, although with only four sites, the trend is not definitive; future studies including sufficient replicates will provide a rich base for pattern-detection. The contribution of fine-resolution land cover for pattern detection of small animals was observed in a related study, in which landscape-pattern indices were computed from fine-resolution data to test effects on small mammal populations (Corry 2004). By using fine-resolution data, the author was able to capture the smaller and linear landscape features relevant to small mammals that remained obscured by coarse-resolution classifications.

Detecting suggestive patterns with barren land cover in particular may be our most important finding, as barren land cover is often the most direct measure of potential wild bee nesting space—as a majority of bees species nest in soil (Michener 2007). Unfortunately, however, with our fine-resolution classification method only some barren land cover types were consistently classified among scorers (**Figure 2.13**). Mulch and soil were rarely labeled

consistently, while gravel and sand showed high levels of consistency. The lack of consistency in our labeling of mulch and soil land cover types is because these categories remain difficult to distinguish from aerial imagery and rely more heavily on ground-truthing and access to private property in heterogeneous urban landscapes. Our checked data were not ground-truthed, and therefore did not match up well with our original data. Still, with our original, fine-resolution classified land cover data, a visual examination of barren land cover data showed a potentially positive trend with bee species richness that warrants further exploration.

Various studies address links between bees and flowering resources in anthropogenic landscapes (Winfree et al. 2011; Lowenstein et al. 2014), but few have been able to address critical links between bees and nesting resources—especially in urban landscapes (Winfree 2010; Roulston and Goodell 2011; Winfree et al. 2011). A recent study modeling how competition for nest sites affected bumble bee and bird populations emphasized the important role of nesting resources in population dynamics, as early-nesting species out-competed late-nesting species when nest-site availability was reduced (Higginson 2017). In addition, the widely used National Land Cover Data (the coarse-resolution data used here) have been consistently poor in classifying barren land (Hollister et al. 2004), and therefore cannot be used to explore such nesting relationships for urban bees in the USA. A fine-resolution method opens the door to further exploration of how the distribution of landscape nesting resources impact bees. Going forward, we do not recommend a broad application of the fine-resolution classification method we used here, where roughly 11,000 points were labeled manually through heads-up digitization. This method is time-consuming and impractical for studies needing sufficient replicates for statistical analysis. Instead, we suggest using it as a base for improvements, where perhaps the

grid of points is kept at the underlying structure, but the process of labeling point is automated for future use.

In conclusion, we find sufficient evidence to encourage urban bee ecology researchers to work with finer resolution land cover scales that are more appropriate for studying bee dynamics, especially in heterogeneous environments. Our call for a shift towards finer-resolutions matches other calls related to advancing our understanding of ecological responses under urban anthropogenic effects (McDonnell and Hahs 2008; Pickett and Cadenasso 2012; Cariveau and Winfree 2015).

There are several advantages to making this change. First, a move towards finer resolution will enhance our ability to detect the smaller land cover features important to bees. Second, using finer resolutions will allow better tailoring of thematic classes to land covers from a bee's perspective—on the scale of centimeters, where flower and nesting resources are the focus—rather than an anthropogenic one. Lastly, others have suggested that one of the major sources of variation seen in bee response is differential species response to different anthropogenic drivers (Cariveau and Winfree 2015). Using finer resolutions and more appropriate thematic classes permit analyses to better identify differences among species. In our fine-resolution classification, this distinction is possible, making pattern detection more likely.

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Tables

Table 2.1 Description of fine-resolution classifications created by authors, as seen in **Figure 2.2**.

Land cover	Description
Impervious	Paved or built-up areas, impenetrable to water.
Pavement	Roads, parking lots, sidewalks, etc. made of concrete.
Roof	Top of buildings.
Turf (Artificial)	Artificial grass made of synthetic material or other man-made material.
Stone Wall	Constructions of stone and an adhesive material, built as fences in residential homes in this study.
City Grate	Metal grates covering recessed spaces in cities.
Fence	Fences, often made of wood.
Non-Impervious	Permeable surface, able to absorb water.
Non-Vegetated	Permeable surface without vegetation.
Mulch	Small chips of wood.
Soil	Bare dirt exposed.
Gravel	Small chips of stone, often < 1.5cm.
Sand	Tiny grains, formed from the erosion of rocks.
Wood Planks	Used for backyard decks. Distinguished here because impossible to know if area underneath deck was soil, mulch, etc.
Water	Permanent bodies of water, e.g. ponds, lakes, rivers, fountains.
Vegetated	Plants.
Woody	Trees or shrubs, whether agricultural or not.
Trees/Shrubs	Any woody plant not used for agriculture.
Orchard	Agricultural field of tree crops.
Herbaceous	Forbs or grass.
Lawn	Monoculture of a grass species, mowed.
Wild	Forb cover, unmanaged by humans.
Garden	Forb cover, managed by humans.
Crop	Agricultural field of annual crops.

Table 2.2 Scales used in literature review studies, ordered by resolution scale. Resolution scale refers to minimum pixel size of landscape land cover data or imagery used to calculate site urbanity. Sampling scale refers to the radial distance of the area sampled for bees at each site. Landscape scales refer to the radial distance(s) used to calculate site urbanity; when “Categories” are listed, analyses used categorical variables to distinguish among levels of urbanity, rather than using quantitative measures of urbanity. Extent scales refer to the minimum rectangular area needed to cover all sampling sites, excluding large bodies of water. To place each study’s use of scale in context with its results, the statistical outcomes reported for each study are sorted into negative (–), neutral (±), or positive (+) bee responses to increasing urbanization.

Study	Scales used per study				Number of negative, neutral, and positive effects of urbanization on bee response		
	Resolution (m)	Sampling (m)	Landscape (km)	Extent estimate (km ²)	–	±	+
Kearns & Oliveras (2009)	31.8	35	252.31, Categories	–	1	32	
Carper et al (2014)	30	35	1, Categories	843	1	4	3
Cusser et al (2015)	30	25	0.2, 2	65		4	
Leong et al (2014)	30	25	0.5, Categories	400		16	9
Pardee & Philpott (2014)	30	1	0.5, 1, 2	305		35	1
Quistberg et al (2016)	30	2.5	0.1, 2	5,340	4	31	1
Jha & Kremen (2013a)	30	600	200	10,840			1
Leong et al (2016)	30	32.5	Categories (0.5) ^a	400		3	
Youngsteadt et al (2015)	30	–	1.5	11,625	2	8	2
Larson et al (2014)	15	20	0.2, 0.5, Categories	1,296	3	17	3
Tonietto et al (2011)	15	0	0.5, Categories	2,833	6	9	2
Jha & Kremen (2013b)	5	600	0.25, 2	576	1	3	
Winfree et al (2007)	1	55	1.6, Categories	398	1	5	2
Matteson & Langellotto (2010)	0.9	15.4	0.2, 0.5	9		4	
Lowenstein et al (2014)	0.9	75	0.1	351		10	2
Phillips & Gardiner (2015)	0.3	30	0.5, 1, 1.5	7,568	5	21	16
McIntyre & Hostetler (2001)	–	2.5	0.02, Categories	2,185	19	11	
Appler et al (2015)	–	–	Categories	25,900		6	
Barthell et al (1998)	–	–	Categories	233,099	1		1
Bennett & Lovell (2014)	–	40	Categories	837	1		
Cane et al (2006)	–	43.3	Categories	218		6	2
Hinners et al (2012)	–	6	Categories	1,861		2	1
Irwin et al (2014)	–	–	Categories	–		1	2
Liu & Koptur (2003)	–	–	Categories	7		3	1
McFrederick & LeBuhn (2006)	–	15.8	1	48	2	2	
Molumby & Przybyłowicz (2012)	–	55	Categories	1,481	1	2	
Neil et al (2014)	–	6.1	Categories	2,243	8	10	
Wojcik & McBride (2012)	–	0.5	Categories	49	1	5	4

^aStudy distinguished levels of urbanization with a categorical variable, but categories were first created by measuring urbanity within 0.5 km radius

Figures

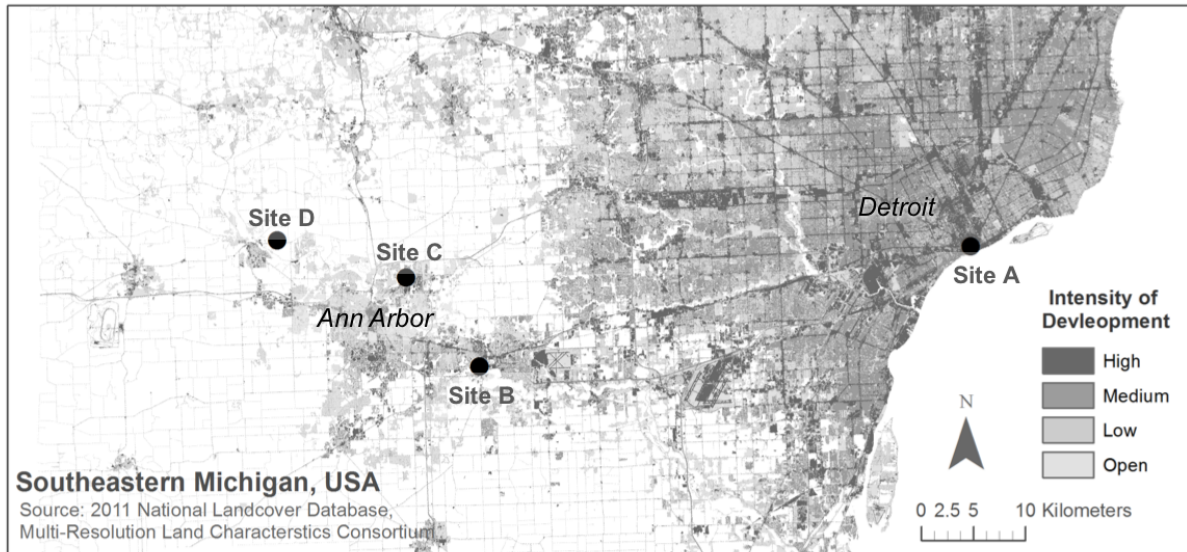
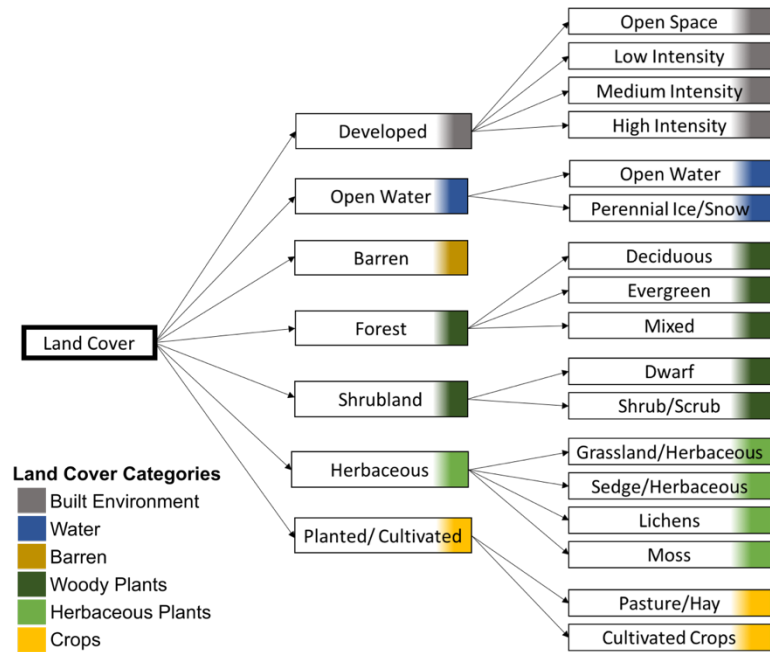


Figure 2.1 Map of garden sites sampled for bee abundance and richness across southeastern Michigan. Sites were selected to span an urban gradient, with Site A as the most urban, Site B as moderately urban, Site C slightly less urban than Site B, and Site D as the most rural site.

(a) **Coarse-Resolution Land Covers**
 derived from National Land Cover Database (NLCD)



(b) **Fine-Resolution Land Covers**
 derived from heads-up digitizing for SE Michigan

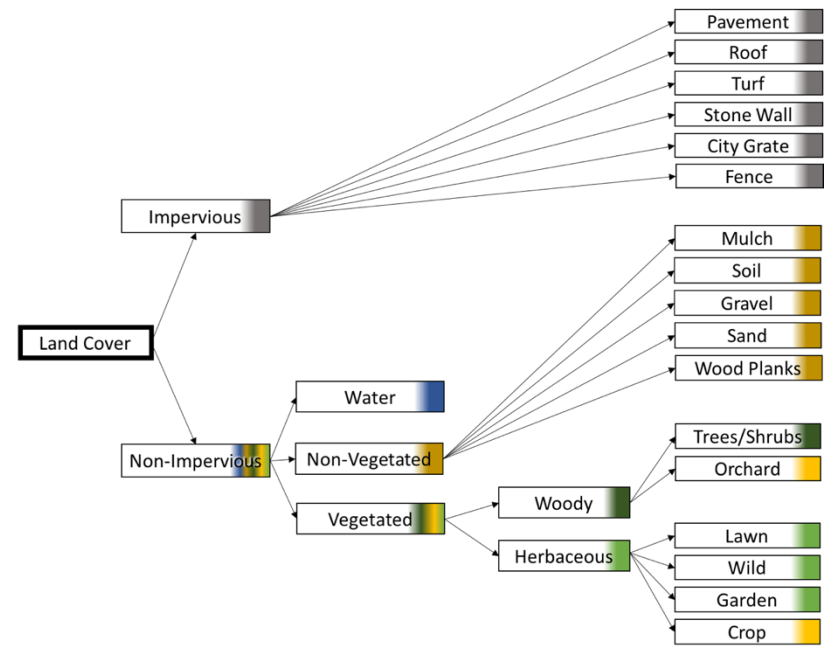


Figure 2.2 Hierarchy of land cover categories used for coarse (a) and fine (b) resolution mapping. (a) The land covers associated with the coarse-resolution map are derived from the National Land Cover Database 2011 land covers. Further descriptions can be found at: https://www.mrlc.gov/nlcd11_leg.php. (b) The land covers associated with fine-resolution map were intended to reflect potential presence or absence of flowering or nesting resources for bees. Figure should be read from left to right, where all sampling points were labeled with a type of ground cover (either Impervious or Non-Impervious), and points labeled as Impervious, for example, were subsequently also labeled as Pavement, Roof, etc.; likewise points labeled as Non-Impervious were subsequently also labeled as either Non-Vegetated, Water, or Vegetated, and so on. As shown in the legend, colors within the figure draw connections between the comparable land covers within the coarse- and fine-resolution classification; this legend applies to all remaining figures with land cover data. Descriptions of each fine-resolution land cover classification can be found in **Table 2.1**. *Design credit:* Maggie Mianecke and M.C.M. Simao.

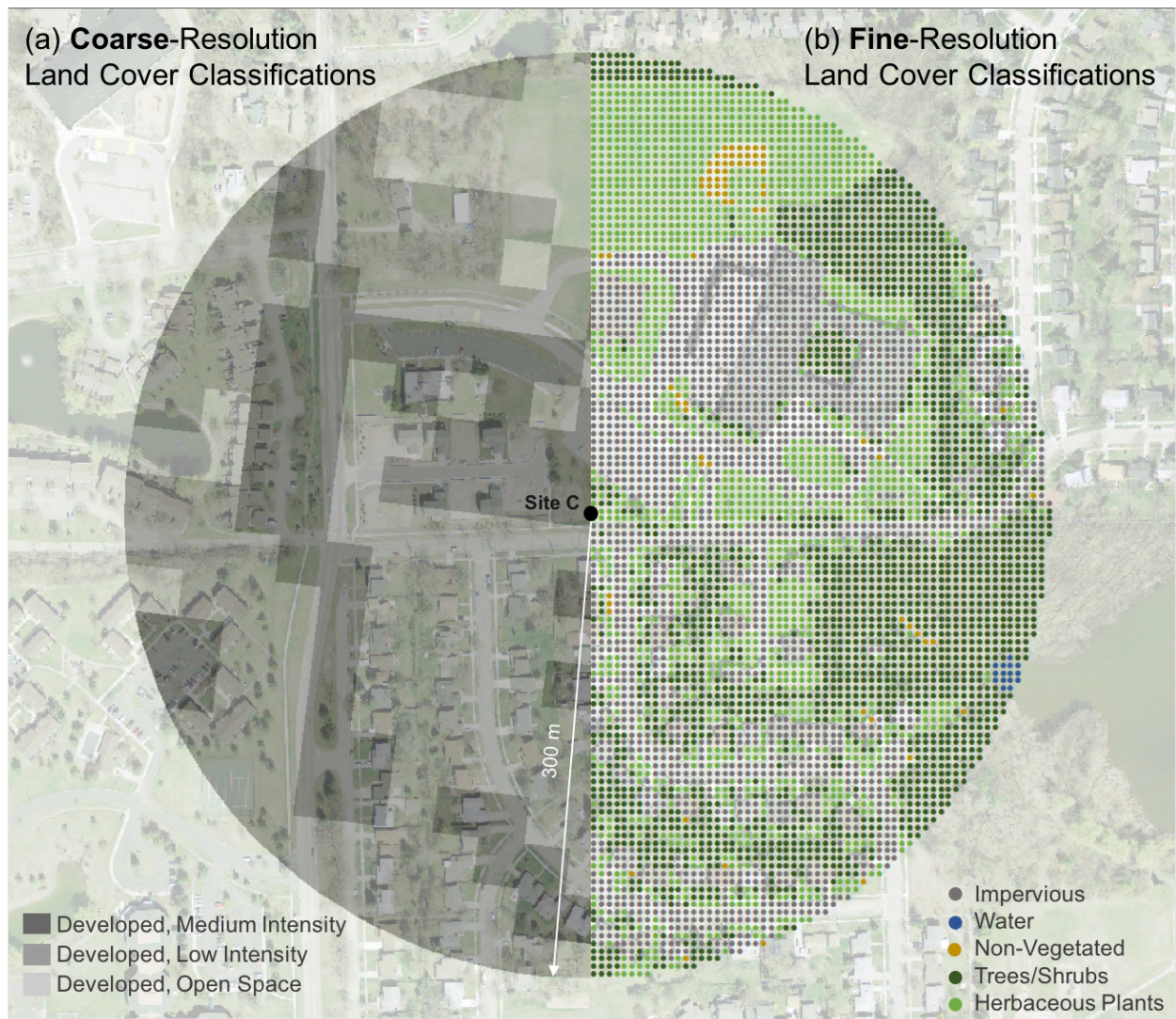


Figure 2.3 Map of coarse-resolution (a) and fine-resolution (b) land cover data obtained for Site C, superimposed on a transparent, high-resolution aerial image. Coarse-resolution land cover data are classified for every 30 m x 30 m area, while fine-resolution land cover data are defined every 5 m. The comparison makes clear the increased level of detail obtained from fine-resolution land cover classification.

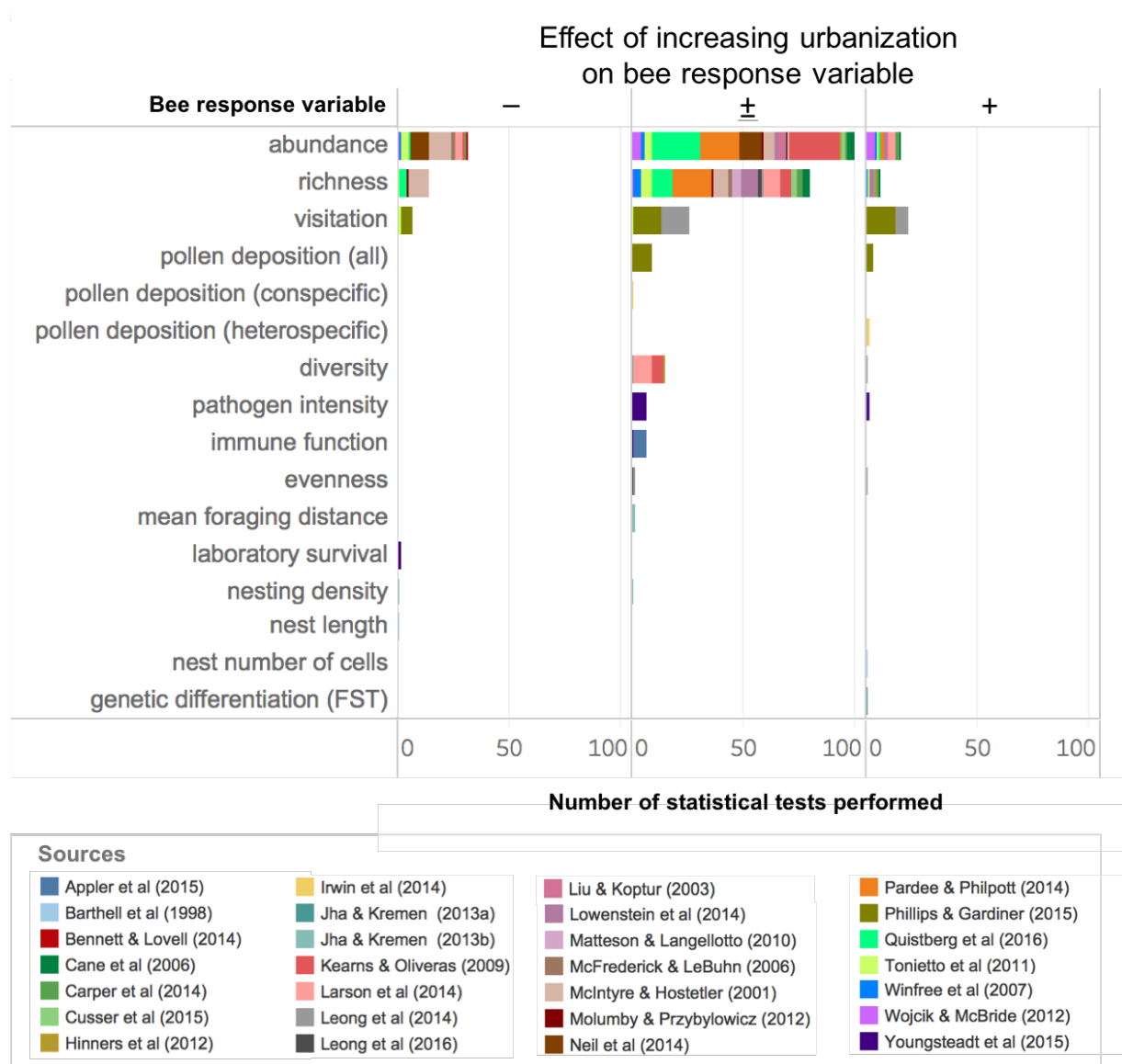


Figure 2.4 Summary of urbanization effects on bees from literature review. The response variables tested across studies are listed in first column, with the number of statistical tests showing significantly negative (–), neutral (\pm), or positive (+) effects of urbanization on each response variable shown in subsequent columns. Certain studies conducted more statistical tests than others, and therefore appear to inflate the magnitude of the result. Most studies found no significant (i.e. neutral) effects of urbanization on bee abundance and richness.

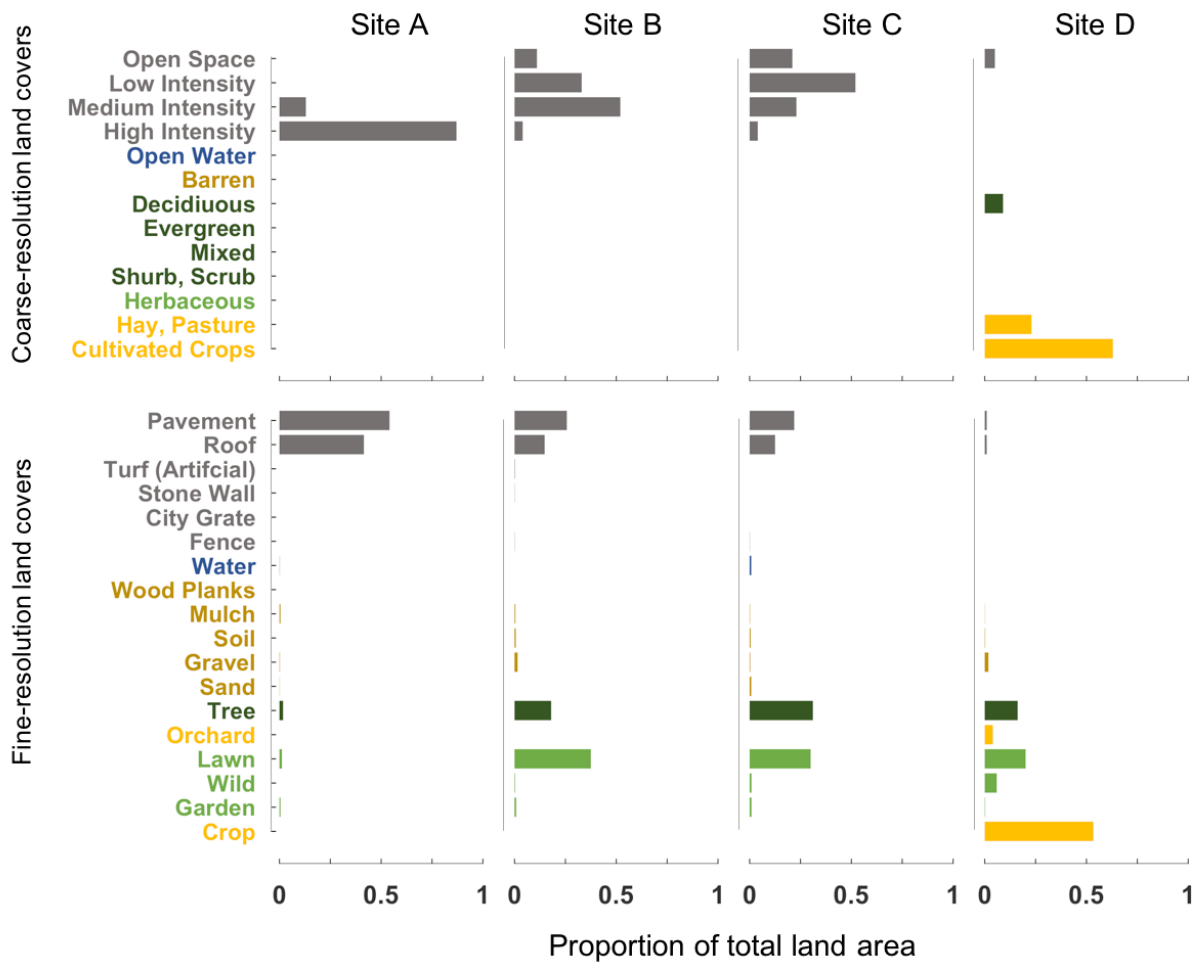


Figure 2.6 Comparison of total land area classified in coarse- and fine-resolution classifications for the four study sites (Sites A, B, C, and D). X-axis is proportion of land area within 300 m of site where bees were sampled. Colors correspond to categories found in legend of **Figure 2.2** and permit comparisons between similar categories in coarse- and fine-resolution.

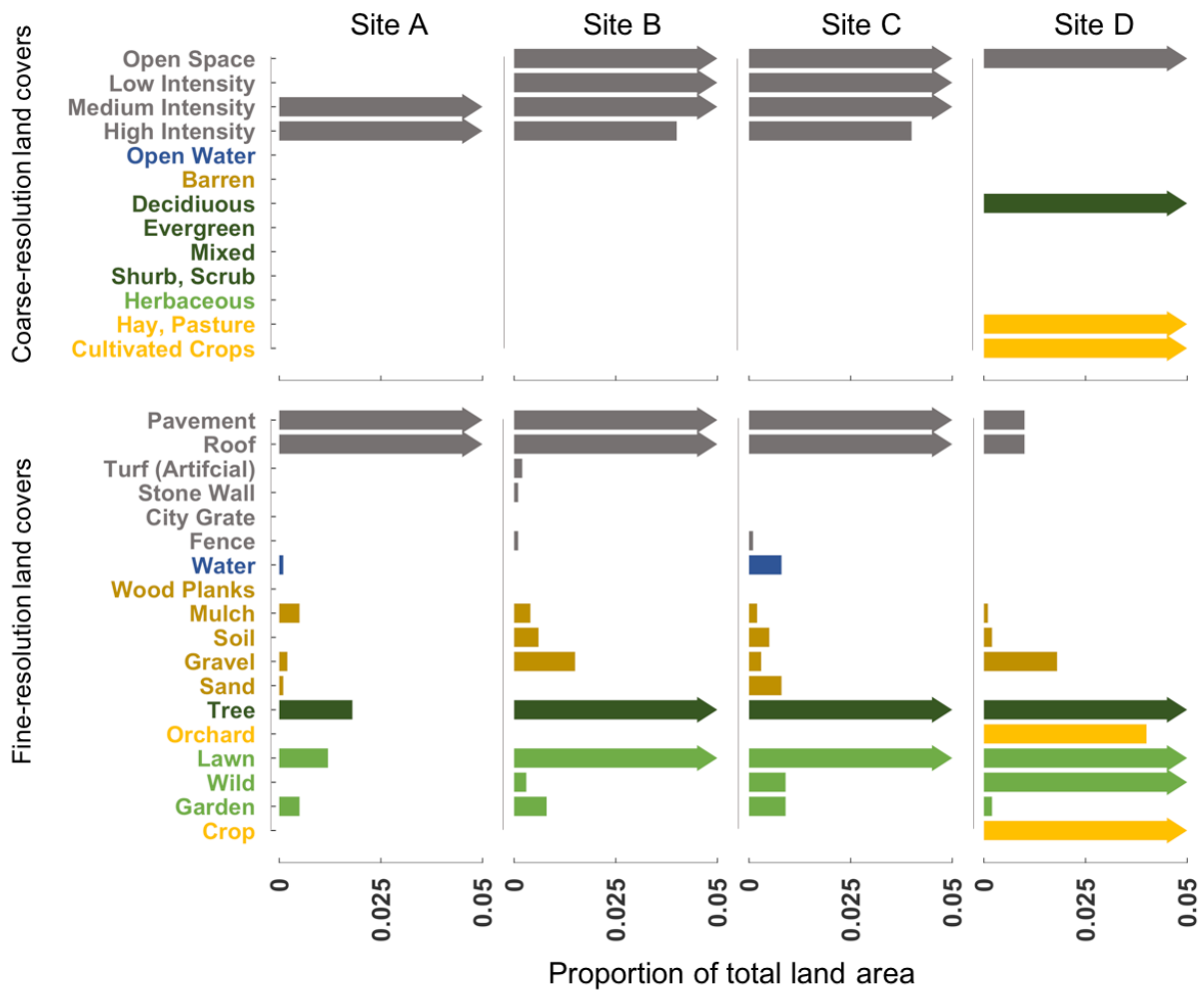


Figure 2.7 Comparison of total land areas in coarse- and fine-resolution classifications for the four test sites (Sites A, B, C, and D), but magnified to show land covers occupying < 5% of total land area (note difference in x-axis from **Figure 2.6**). Land covers occupying more than 5% of total land area are indicated with arrows. X-axis is proportion of land area within 300 m of site where bees were sampled. Colors correspond to categories found in legend of **Figure 2.2**.

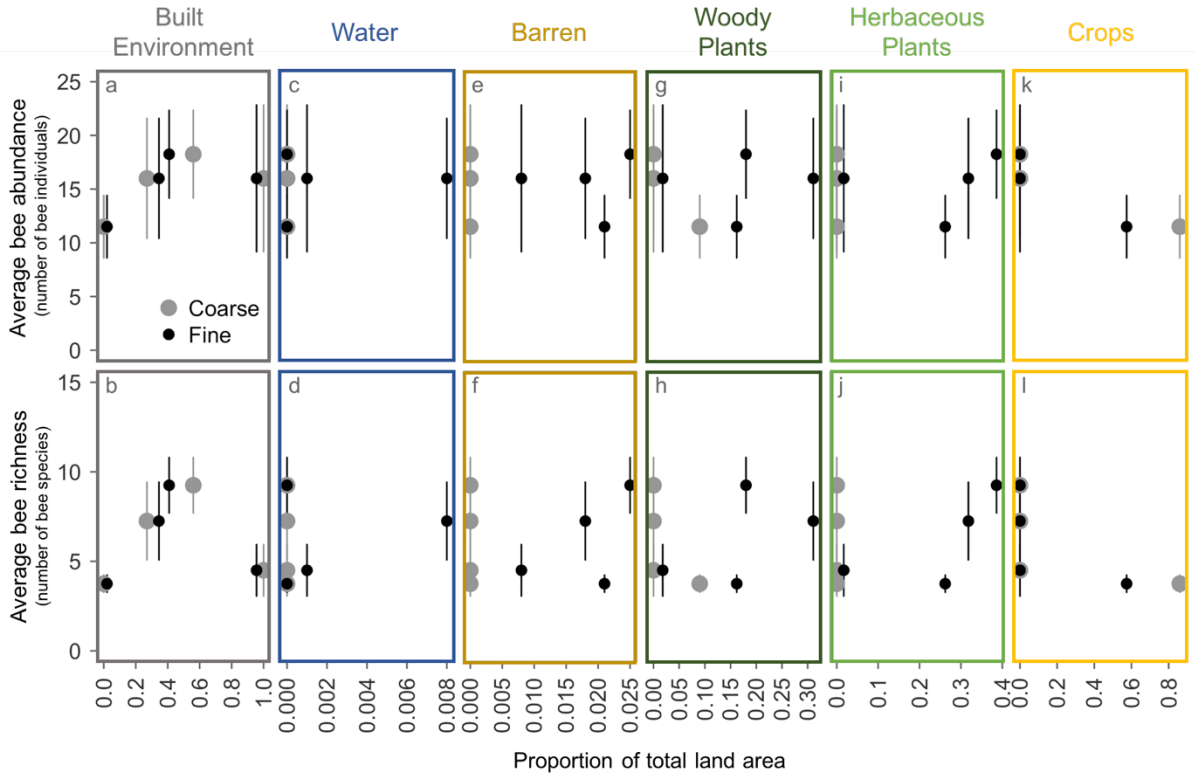


Figure 2.8 Comparison of total land area between coarse- and fine-resolution land cover classifications against bee abundance (a, c, e, g, i, k) and richness (b, d, f, h, j, l) across Sites A, B, C, and D. Proportional areas of land covers were aggregated into categories corresponding to the coloration of each land cover in **Figure 2.2**. For example, for the Barren graphs (e, f), the coarse-resolution data corresponds to areas labeled as barren, while the fine-resolution data correspond to the sum of areas labeled as mulch, soil, gravel, sand, and wood planks. The exception is in the Built Environment (a, b) where the coarse-resolution data is the sum of areas labeled as medium and high intensity land covers, as this aggregation was found to be more representative of urbanization than with the inclusion of low- and open space land covers.

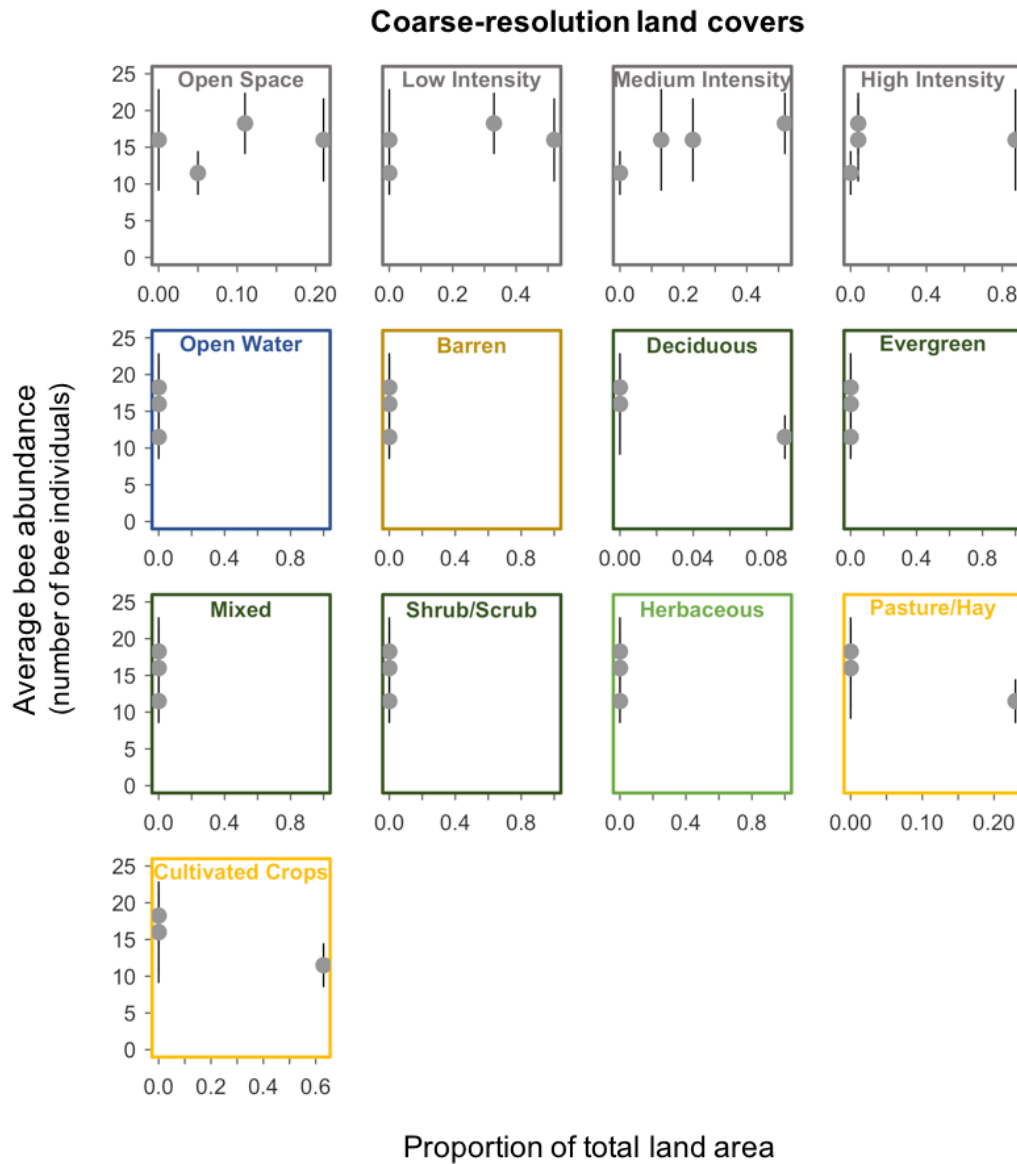


Figure 2.9 Relationship between each individual coarse-resolution land cover classification and bee abundance for Sites A, B, C, and D. Some charts only appear to have three points because Sites A and C had equal average bee abundance values, and when these sites also have equal land cover areas the points overlap and obscure each other.

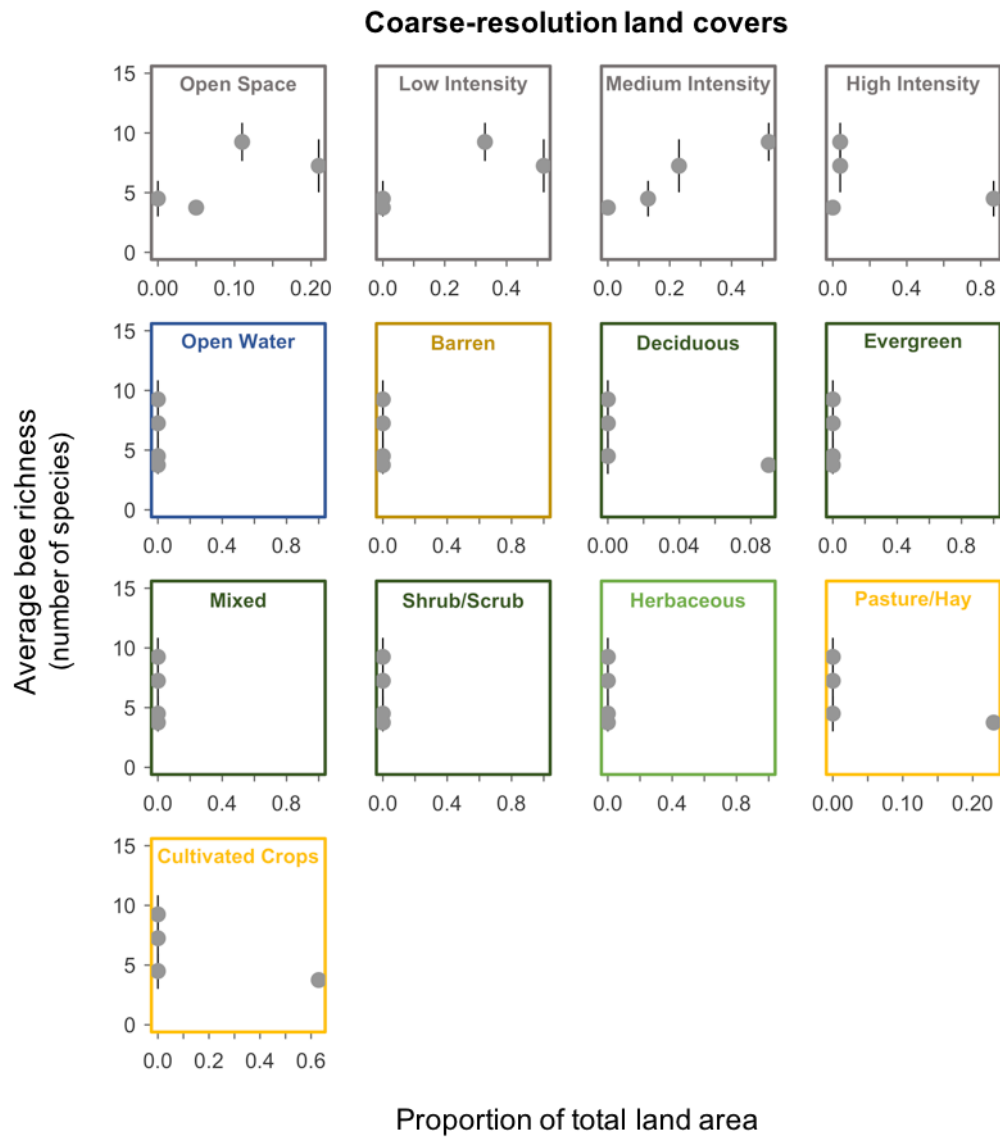


Figure 2.10 Relationship between each individual coarse-resolution land cover classification and bee richness for Sites A, B, C, and D.

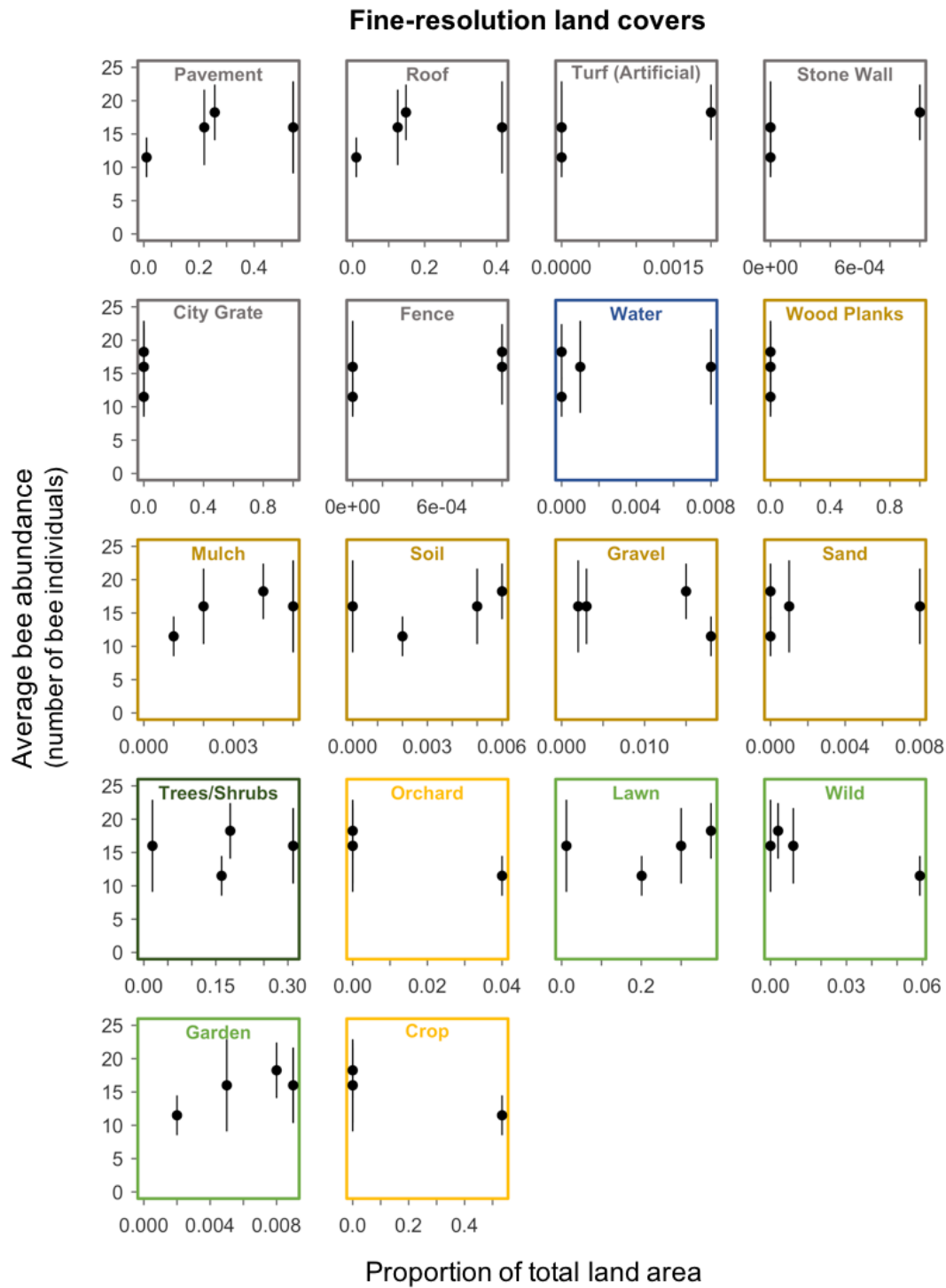


Figure 2.11 Relationship between individual fine-resolution land cover classifications and bee abundance for Sites A, B, C, and D. Some charts only appear to have three points because Sites A and C had equal average bee abundance values, and when these sites also have equal land cover areas the points overlap and obscure each other.

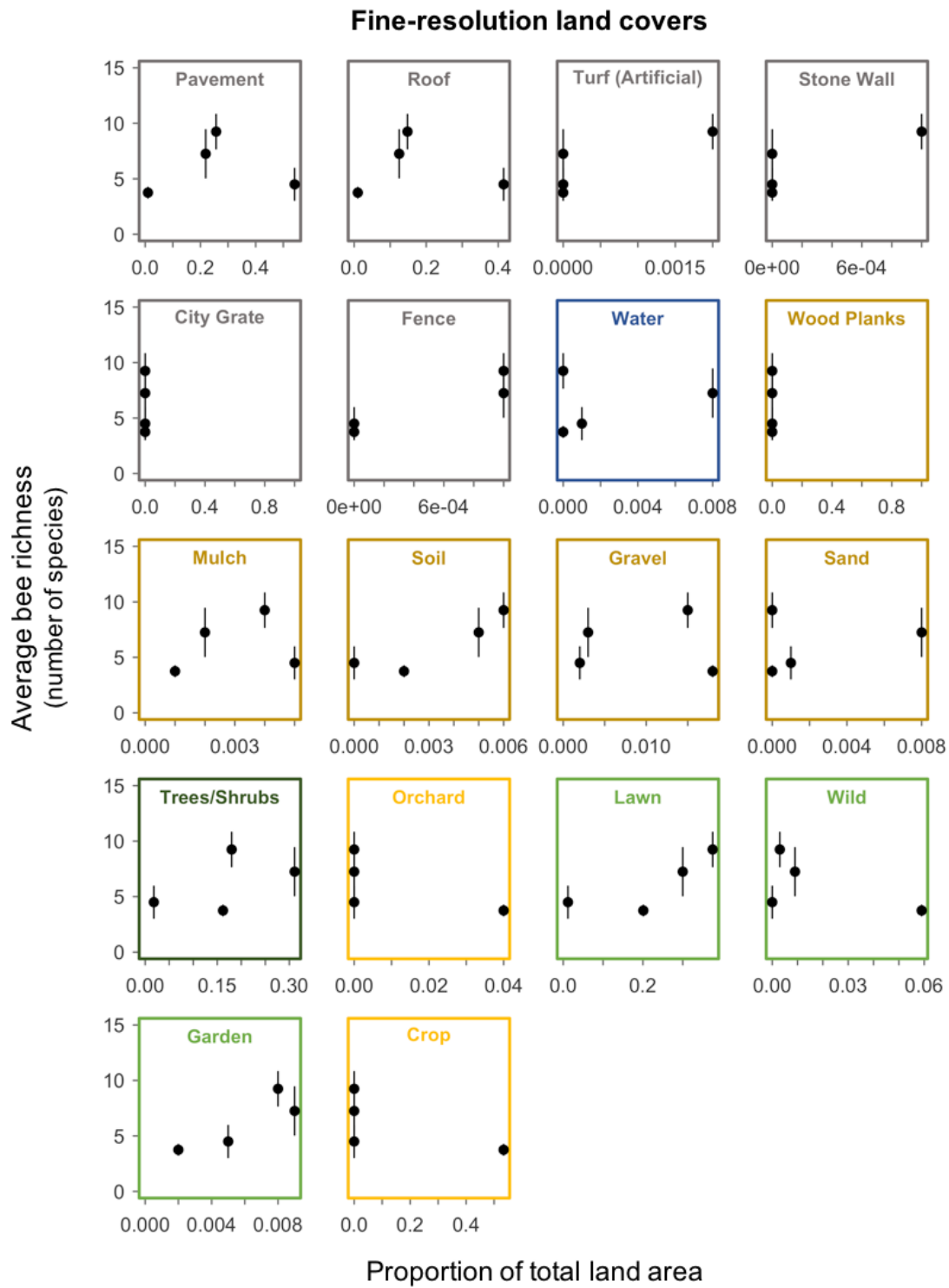


Figure 2.12 Relationship between individual fine-resolution land cover classifications and bee richness for Sites A, B, C, and D.

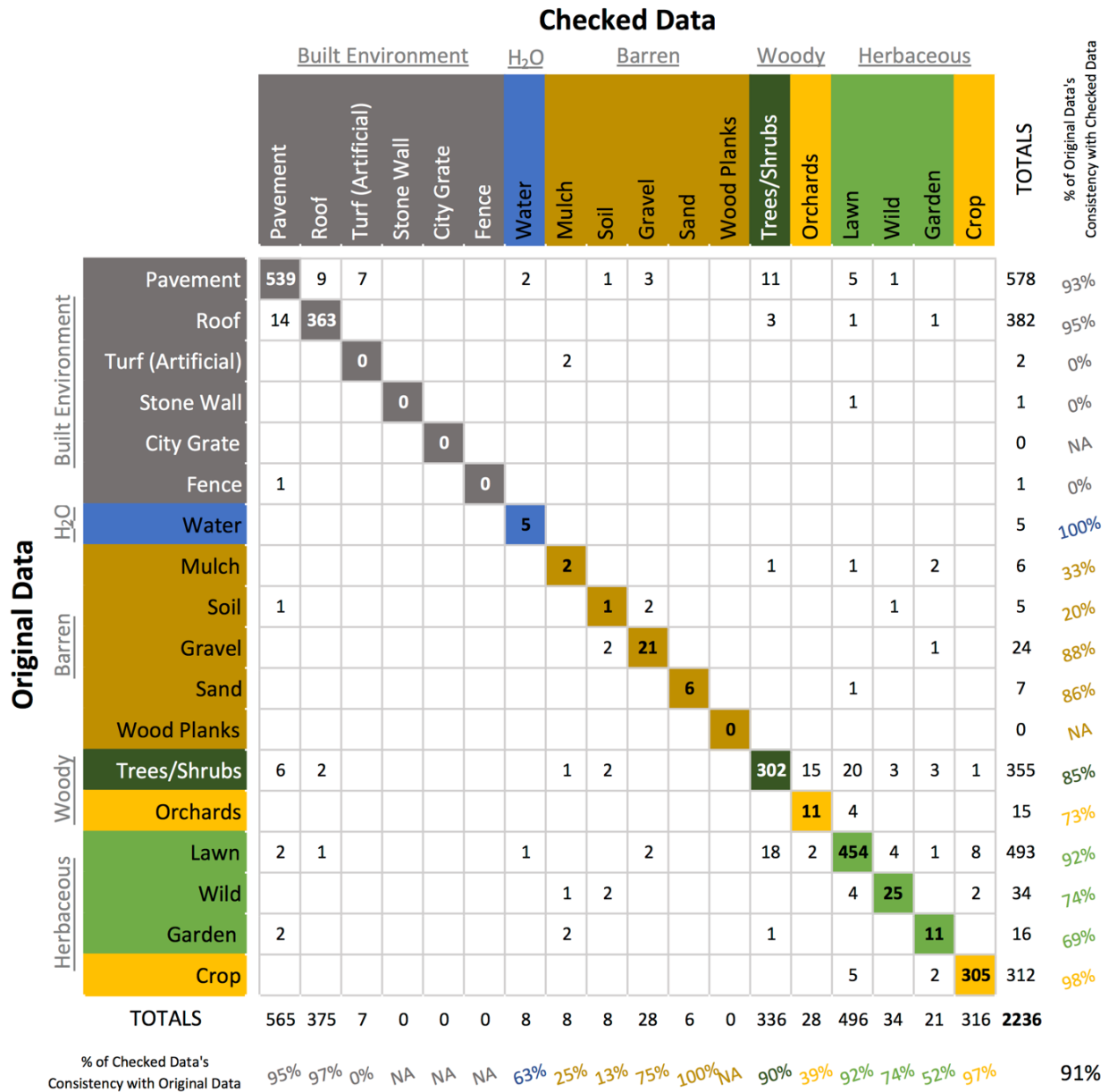


Figure 2.13 Contingency matrix to measure labeling consistency in fine-resolution classification system. Original Data was classified using a combination of heads-up digitizing and ground-truthing. To check consistency in how each point was classified, 5% of the data points from each site were selected and re-classified by another experienced scorer, as seen in the Checked Data. This contingency matrix shows how many points were labeled consistently between scorers for each land cover class (numbers in the diagonal), and which points were labeled differently (numbers outside of the diagonal). The overall consistency measure (91%) was calculated as the sum of all points labeled consistently, divided by the total number of points labeled.

Chapter 3

Urban heat island effect increases food production while pollinator presence increases yield stability in urban agriculture

3.1 Abstract

Urban agriculture can impart a variety of economic, social, and environmental benefits to urban dwellers, but successful food production still depends on ecological functions that may be impacted by urban landscapes. This study tested whether urban landscapes change wild pollinator communities and temperature profiles to the point of affecting food production in terms of quantity, quality, or stability in urban gardens. Lima bean (*Phaseolus lunatus*) plants were used to assess food production in 22 gardens across an urbanization gradient in Michigan, and each garden's pollinator community and daily minimum temperature were tracked. A clear urban heat island effect occurred across the gradient, and urban food production quantity and quality were positively affected by temperature, while food production stability was positively affected by pollinator presence. These results suggest that maintaining a presence of wild pollinator in urban agriculture may be essential in buffering potential yield fluctuations of pollinator-dependent crops. These results also document how climate change may impact agriculture in temperate regions.

3.2 Introduction

Urban agriculture has been regaining popularity as a way to increase food production and access within urban landscapes and is increasingly promoted as a food-security strategy in U.S. cities (e.g. Detroit, Seattle, Philadelphia, Cleveland, Chicago, San Francisco; Hodgson *et al.* 2010). An estimated 15-20% of the global food supply come from urban agriculture, and 40% of global irrigated cropland being within 20 km of urban landscapes (Hodgson *et al.* 2010; Thebo *et al.* 2014), yet most studies addressing factors that influence food production are concentrated in rural agricultural settings.

Urban agriculture gardens may be situated in urban, “unnatural” landscapes, but they are not immune to dependence on natural systems. Successful food production in cities still relies heavily on natural processes and environmental conditions—such as pollination and local weather patterns—that may be altered in urban landscapes. Bee communities are known to change in complex ways across urban landscapes (Cane *et al.* 2006), but whether these changes affect food production—an ecosystem service heavily influenced by pollinators—in urban agriculture is not well documented. For example, although recent studies within Chicago and San Francisco, U.S.A. showed that urban agriculture yields benefit from pollinator visitation (*with eggplant and cucumbers*, Lowenstein *et al.* 2015; *with tomatoes*, Potter and Lebuhn 2015), we have yet to understand how this benefit changes within and beyond city limits, especially given that urbanization can change pollinator visitation rates and pollination success (Geslin *et al.* 2013; Harrison and Winfree 2015). Abiotic elements are also subject to change across urban landscapes, as evidenced by the urban heat island effect, wherein more-developed areas are warmer than less-developed areas (Coseo and Larsen 2014). There is concern that warmer temperatures will cause mismatches in plant-pollinator interactions (Hegland *et al.* 2009), such

that flowers may bloom before or after their pollinators emerge, but it has been suggested that the presence of a diversity of pollinators can buffer a community of plants and pollinators from experiencing these mismatches (Bartomeus et al. 2013; Harrison and Winfree 2015).

This study explores whether the natural process of pollination and local temperature differ across an urbanization gradient, and tests whether any observed changes in these processes impact urban food production. To test this, we placed potted lima bean plants in urban agriculture plots across an urbanization gradient, monitored changes in pollinator and temperature profiles within the plots, and determined the resulting quantity (number of lima beans), quality (overall weight of lima beans), and stability (consistency in number of lima beans produced per pod) of food production.

3.3 Methods

Study sites

We sampled 22 sites across an urbanization gradient in southeastern Michigan, U.S.A. spanning 68 km from the towns of Dexter, Ann Arbor and Ypsilanti to the city of Detroit (**Figure 3.1**). On average, sites were spaced 2.15 ± 2.83 s.d. km from each other. Mantel tests showed no spatial autocorrelation among them for food production measures of quantity, quality, and stability (all $p > 0.36$, **Table 3.1**). This important check confirmed we did not violate any assumptions of independent samples in our subsequent statistical tests. After the last Ice Age this region hosted a range of ecosystems (forests, open oak savannas, prairies, and wetlands), but in the mid-nineteenth century began to transform into its current state of land dominated by agriculture, urban, and suburban development (Dunbar 1980). Sites were selected based on the

presence of vegetable garden plots, and the majority of sites (N=19) were located within community gardens.

Bee measurements

To document pollinators, bees were sampled every two weeks during the time focal lima bean plants were placed in gardens (end of July–early September 2014). To sample bees, two yellow, two blue and two white pan traps (3.25 oz. plastic bowls painted with ultraviolet-reflective paint and filled with soapy water; New Horizons Supported Services, Inc., Upper Marlboro, Maryland, U.S.A.) were placed in two rows of three within a few meters of lima bean plants at each site for 24-hour periods. Rows and traps were spaced 2-m apart. In addition, bees were netted for two 30-minute sessions at each site; the first netting session occurred between 09:00-12:00 and the second between 13:00-16:00 local time. Netting occurred within the 5m-by-5m area containing the highest flower abundance and amount of sunlight within a 20-m radius of pan traps on the observation date. In an effort to have consistent sampling during periods with higher likelihood of pollinator activity, all trapping and netting occurred on sunny to partly sunny days with wind speeds less than 15-km per hour, with the exception of one trapping date when all sites experienced light rain showers due to inaccurate weather predictions.

The majority (64%) of the resulting bee samples was identified by Jason Gibbs and Jaime Pawelek. The remaining specimens (36%) were identified by Ben Iuliano, Chatura Vaidya, Gordon Fitch, Paul Glaum, and the author at the University of Michigan; these identifications were later spot-checked by Jason Gibbs. Voucher specimens are located in the Perfecto Lab at the University of Michigan, and will eventually be stored in the University of Michigan Museum of Zoology Insect Collection. A species list of specimens used for this study can be found in

Table 3.2; the full data set will eventually be stored in University of Michigan's Deep Blue repository (<https://deepblue.lib.umich.edu/data>).

Temperature measurements

One temperature data logger (Onset HOBO Pendant Temperature Data Loggers 8K, Bourne, MA) was placed 0.3-m off the ground at each study site throughout the sampling season. Each logger recorded temperature every hour. Average minimum daily (nighttime) temperature was used for this analysis because nighttime temperatures reflect urban heat island effect better than daytime temperatures (Coseo and Larsen 2014); nighttime temperatures are best reflected by minimum daily temperature in our data. Temperature data were not retrieved for four sites because of missing or corrupted data loggers.

Urbanization estimates

Each site's urbanization level was estimated by quantifying the amount of impervious surface area around each garden using 2011 National Land Cover Database data (Multi-Resolution Land Characteristics Consortium, mrlc.gov). Impervious surface refers to impenetrable surfaces, such as asphalt, roofs, bricks, concrete, etc. In keeping with McKinney's (2008) suggestion of defining urban landscapes as areas with >50% impervious surface, and as described in Glaum *et al.* (2017), areas categorized as high (80-100% impervious) or medium (50-79% impervious) intensity developed were summed to obtain the total area of impervious surface within a 500.0-m, 1.0-km, 1.5-km and 2.0-km radius of sampling sites. These distances were chosen because they encompass average foraging distances for different groups of bees and mirror the scales used across similar studies (Bates *et al.* 2011; Fortel *et al.* 2014).

Food production (quantity, quality, and stability) measurements

Lima bean (*Phaseolus lunatus*) plants were used to standardize measurements of urban food production across the urbanization gradient in southeastern Michigan. Lima beans were selected because their yields are not entirely dependent on pollinators but have been shown to improve in the presence of pollinators (McGregor 1976) and studies document multiple bee species that pollinate lima beans (Magruder and Wester 1939; McGregor 1976). In mid-June 2014, lima bean plants were started from seed (Fordhook No. 242 from W. Atlee Burpee & Co., Warminster, PA) in a greenhouse and individually planted in 10" green plastic pots filled with a 50-50 mix of compost (85% from Matthaei Botanical Gardens daily operations compost, Ann Arbor, MI and 15% from Tuthill Farms & Composting Inc., South Lyon, MI) and gardening soil (Sunshine Natural and Organic Planting Mix, SunGro Horticulture, Agawam, MA). As soon as plants began to flower (fourth week of July 2014) three potted lima bean plants were placed at each garden site (**Figure 3.2a**). Once in the field, all lima bean plants were watered every other day, with an average of three watering visits per week. Constant moisture is important for lima bean plant health (Lambeth 1950), and plants were therefore constantly monitored to ensure that they were not dry.

To isolate the effect of pollinators on lima bean production, buds on each plant were subjected to one of two treatments: blocked from pollinator access, or allowed pollinator access. To block pollinator access, prior to flowering, buds were covered with a fine white mesh (1 mm, Foiled Tulle, JoAnn Fabrics, Ann Arbor, MI) secured by a zip tie (**Figure 3.2b**). A prior study comparing microclimatic conditions inside and outside similar mesh bags found minor differences in temperature and humidity, and concluded the differences were unlikely to affect

“flower phenology, dehiscence, or stigma receptivity” (p.115, Willmer and Stone 1989). Each mesh bag was removed as soon as each flower senesced. To mark whether pods belonged to the blocked or allowed treatment, the petiole of each senesced flower was tagged with a white or green twist tie, respectively (**Figure 3.2b and c**). The two treatments (of blocked and allowed pollinator access) were applied continuously as new buds appeared.

At the end of the flowering period (mid-September 2014), all potted lima bean plants were placed back in the greenhouse, where pods were allowed to dry before harvesting (**Figure 3.2d**). Only pods that reached full development (i.e. were not completely shriveled and empty) were harvested. Once harvested, the number and weight of beans produced per pod were quantified to assess lima bean production quantity and quality, respectively. To assess food production stability, the inverse of the coefficient of variation (i.e. mean divided by the standard deviation) for number of beans produced per pod was calculated for each treatment at each site (as seen in previous studies, see Garibaldi et al. 2011). Yields were assessed on per pod—rather than per plant—basis because we could not control random herbivore activity on the lima bean plants across sites.

Statistical Analysis

EstimateS software (Colwell, R.K. Version9, purl.oclc.org/estimates) was used to run individual-based rarefactions and calculate bee species richness (Chao1 estimator, based on the number of rare species in a sample) and bee diversity (Shannon estimator, based on the species richness and evenness in a sample). Bivariate relationships between bees, temperature, and impervious surfaces were analyzed with ordinary least squares linear regressions using the stats package in R v. 3.1.2 (R 2014).

Food production quantity (number of lima beans produced per pod) was regressed on multiple predictors (temperature, impervious surface, and either bee abundance or estimated-richness or estimated-diversity) using forward selection in ordinal regression models, a multivariate linear regression known as cumulative link mixed models with the ordinal package in R. All model variations included pollinator treatment (blocked/allowed) as a predictor variable and individual plants and garden sites as random effects. Comparison of food production quantity between the two pollinator treatments (blocked/allowed) was also analyzed with a t-test in R. Food production quality (average weight of beans produced per pod) was regressed on the same predictor variables as food production quantity, but using forward selection with linear mixed models from the lme4 and lmerTest packages in R. Each model used restricted maximum likelihood estimation, and as with food production quantity, individual plants and garden sites were included as random effects.

In both models, impervious surface was treated as a categorical variable after k-means clustering analysis, which grouped sites into five distinct clusters based on impervious surface data at all scales (500.0-m, 1.0-km, 1.5-km, 2.0-km). Bee abundance, richness and diversity measures were recorded as zero for pods from the pollinator-blocked treatment. Model selection was based on the Akaike information criterion (AIC).

Food production stability across sites was also analyzed using linear mixed models in R— one model for food production quantity and another for food production quality—and regressed in a bivariate model on either bee abundance, estimated richness, estimated diversity, or pollinator treatment (blocked/allowed) as a predictor variable with individual garden sites as a random effect. As defined in previous studies (Garibaldi et al. 2011b), food production stability was measured as the inverse of the coefficient of variation in food production, i.e., the mean of food

production quantity (or quality) per site divided by the standard deviation of food production quantity (or quality) per site.

3.4 Results

Bee measurements

In the 6 weeks that lima bean plants were placed in gardens, 1,117 bees were collected across all 22 sites (50.77 ± 25.6 s.d. bees per site). A total of 79 different species were collected, the most common of which were *Mellisodes bimaculatus* (12% of individuals caught), *Bombus impatiens* (9%), *Halictus confusus* (8%), and *Lasioglossum hitchensi* (7%). None of the bee community metrics (abundance, estimated richness, or estimated diversity) varied significantly with either proportion of impervious surface or mean minimum temperature (**Table 3.3, Figure 3.3**).

Temperature and urbanization measurements

Average minimum temperature ranged from 12.4-18.2°C and had a positive, significant relationship with impervious surface at every scale (**Figure 3.4, Table 3.3**).

Urban food production measurements

A total of 352 lima bean pods were collected over the six weeks lima bean plants were situated in gardens, with 138 pods collected from the pollinator-blocked treatment (1.83 ± 0.87 s.e. beans per pod) and 214 pods from the pollinator-allowed treatment (1.98 ± 0.85 s.e. beans per pod) ($t=1.51$, $p=0.13$). In the pollinator-blocked treatment, fewer pods reached full development due to the fragility of flowers post-senescence, as many petioles were accidentally disconnected from

their stems during mesh-bag removal. An average of 2.60 ± 0.20 s.e. pods were produced per plant in the pollinator blocked treatment, while an average of 3.57 ± 0.26 s.e. pods were produced per plant in the pollinator allowed treatment. Field experience and a small follow-up greenhouse experiment confirmed that regardless of human manipulation, the vast majority of lima bean flower petioles disconnect naturally after senescence, a fact also confirmed in experiments by Lambeth (1950). The small follow-up greenhouse experiment also confirmed that the petioles that disconnected during mesh-bag removal were indeed random and not biased towards ‘weaker’ flowers.

Food production quantity

Neither impervious surface, bee abundance, estimated richness or diversity had a significant effect on food production quantity (**Figure 3.5a–c**). Instead, the ordinal regression model using mean minimum daily temperature as a fixed explanatory variable with individual plants as a random effect was the best fit for changes in lima bean production quantity. Mean minimum daily temperature was found to have a small but significantly positive effect on lima bean production (coefficient for temperature: 0.19 ± 0.08 s.e., $p=0.01$, **Figure 3.6a**).

Food production quality

Impervious surface, bee abundance, richness, and diversity did not have a significant effect on food production quality (**Figure 3.5d–f**). The linear mixed model using mean minimum daily temperature as a predictor was the best fit to explain changes in lima bean quality. Mean daily minimum temperature was found to have a minor but significantly positive effect on lima bean production quality (coefficient for temperature: 0.03 ± 0.009 s.e., $p<0.01$, **Figure 3.6b**).

Food production stability

Bee abundance, richness, and diversity did not have a significant effect on food production stability (**Figure 3.5g–i**), but pollinator treatment (blocked/allowed) did. For food production quantity, lima bean pods blocked from pollinators showed significantly less stability (i.e. more variation) in the number of lima beans produced per pod than lima bean pods allowed access to pollinators (coefficient for pollinator treatment: -2.11 ± 0.81 s.e., $p=0.02$, **Figure 3.6c**). For food production quality, however, stability in lima bean weight did not differ between treatments (coefficient for pollinator treatment: 0.30 ± 1.02 s.e., $p=0.77$).

3.5 Discussion

This study tested whether changes in bee communities and temperature across an urbanization gradient altered food production quantity, quality, and stability. Results showed that it was not bee abundance, richness, or diversity that affected urban food production quantity or quality, but rather temperature changes associated with the urban landscape. Bee presence did, however, influence the stability of food production.

Previous work on urban heat islands supports our findings of a positive relationship between impervious surface and temperature (Coseo and Larsen 2014), but the result of temperature—rather than pollinators—having the most influence on lima bean yields was unexpected. In contrast, other studies in urban areas have found significant relationships between pollinator richness (or visitation) and pollination services (Lowenstein et al. 2014, 2015; Potter and LeBuhn 2015), albeit modeling work has shown that the level of pollination service provided can vary widely even within a city (Davis et al. 2017). For lima beans more specifically, our

finding of a lack of pollinators' effect on lima bean quantity and quality adds to the suggestive, but inconclusive, literature on the topic. In a short review on the extent to which pollinators influence lima bean yields, Free (1993) found no experiments that adequately answered the question. The most relevant experiments used cages to block honey bees and found that uncaged lima beans had higher yields and therefore benefitted from pollinators; but, Free points out both experimental designs failed to eliminate the possibility that the cages themselves caused the decline in caged lima bean yields, rather than the lack of pollinators. Our result, in contrast, showed no significant change in lima bean quantity or quality when pollinators were blocked, but our methods faced a similar limitation in lacking methodology to test whether bags used to cover lima bean flowers affected yields. When a bag is used to cover flowers, there is concern that it creates a microclimate that may affect yields. We did not feel this was of large concern in our case, because a previous study using similar mesh material to cover flowers found no significant microclimatic effects of their bags (*but see* Willmer and Stone 1989).

Lima bean pods from sites that reached lower minimum temperatures over the season produced fewer beans per pod and lighter beans, i.e. lower quantity and quality of lima beans. Lima beans are warm-season crops known to be negatively affected by extreme heat, lack of humidity, and lack of soil moisture (Lambeth 1950; Kee and Wootten 1994), but different varieties are known to show variable responses to cooler temperatures (Lambeth 1950; Rappaport and Carolus 1956). One study, for example, compared the effect of night temperatures on the number of pods set by Henderson Bush and Fordhook 242 lima bean varieties and found that nightly temperatures affected Henderson Bush but Fordhook pod set remained relatively unaffected (Rappaport and Carolus 1956). Another study used greenhouse experiments to monitor lima bean pod set at three different temperatures and also found that Fordhook 242 lima

bean plants more tolerant of low temperatures than other lima bean varieties (Lambeth 1950). However, the minimum temperature tested in Lambeth's study was 16.7°C, whereas average minimum temperatures recorded in this study ranged from 12.4-18.2°C. Reduced lima bean pod sets can be attributed to receptive microgametes not reaching an egg in time (Lambeth 1950), and it may be that the minimum temperatures reached at our sites were low enough to interfere with fertilization success, therefore causing reductions in food production quantity and quality.

The emergence of temperature as an influential factor in yield raises potential implications of this study for the future of food production in the face of climate change. Urban landscapes may be an ideal place to study the effects of climate change because the urban heat island effect causes them to be several degrees (°C) warmer than surrounding areas (Oke 1982; Harrison and Winfree 2015). Our study suggests that, at least in temperate climates such as that of Michigan, the warmer temperatures expected with climate change may benefit productivity of some crops (Zavalloni et al. 2008). However, the erratic weather events predicted with climate change may negate this potential positive effect of increased temperature, as any increase in the incidences of severe weather—prolonged cold fronts, draughts, natural disasters, etc.—could also influence food production.

Given the predicted variability of our future climate, our results on pollinators and yield stability suggest that simply maintaining pollinator presence may be essential in buffering potential yield fluctuations of pollinator-dependent crops. Although pollinator presence was not related to the quantity and quality of lima bean production, it was positively related to the stability of lima bean food production, i.e. when bees were allowed access to lima bean flowers, the resulting pods showed less variability in the number of lima beans produced. This result has precedent in ecology given the long history of the diversity-stability literature, in which a higher

diversity of species with different properties and sensibilities to environmental conditions are generally expected to lead to greater stability in ecosystem properties such as productivity (Lehman and Tilman 2000). There is less direct experimental research on whether this relationship holds between pollinator diversity and yield stability in particular, but theoretical work supports the relationship for crops dependent on pollinators (Garibaldi et al. 2011b) and a recent theoretical study suggests that trait-mediated indirect interactions leads to a positive relationship between species diversity and the stability of the ecological community (Bairey et al. 2016). Although our study found that pollinator presence—and not pollinator abundance or richness—affected yield stability, other field observation studies have found that wild bee diversity stabilized pollinator visitation in variable climatic conditions (Rogers et al. 2014), and that yield stability increased in sites closer to natural habitats, presumably due to increased pollinator richness and visitation (Garibaldi et al. 2011a). The former study focused on temporal stability of pollinators and its effect on yield, and the latter study focused on the stability of overall yield as a product of proximity to natural habitat. Our study focused on the stability of food production per reproductive unit (lima bean pod) as a result of the presence of pollinators, and to our knowledge, our study provides the first direct experimental evidence that pollinator presence caused increased stability in lima bean yields.

In summary, we found a clear urban heat island effect across urban agriculture sites, a positive effect of temperature on lima bean yields, and a positive effect of pollinator presence on yield stability. These results suggest that maintaining bee populations in the face of climate change may act as an important insurance mechanism for agriculture, since potential yield decreases from erratic weather events may be recuperated by pollinators ensuring enough pollen grains make contact with receptive flower stigmas. Resource managers should therefore continue

efforts to protect pollinator populations, and within the context of urban green infrastructure, floral and nesting resources (e.g. bare ground) should be promoted. Future work is needed on how urban landscapes affect pollinators and food production of other crops, to determine whether the results of this study reflect larger trends and can inform pollinator conservation efforts as they relate to ecosystem services.

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Tables

Table 3.1 Results of Mantel tests to test for spatial autocorrelation between sites for food production measures. Mantel tests were run in R with the ade4 package using 9,999 permutations. The food production quantity measure was calculated as the average number of beans per pod (regardless of pollinator treatment) per site. The food production quality measure was calculated as the average weight of lima beans (regardless of pollinator treatment) per site. Food production stability measures were calculated as the inverse of the coefficient of variation for the food production quantity and quality measures.

Measured Outcome	Observed Spatial Autocorrelation Between Sites for Measured Outcome	Variance Between Sites for Measured Outcome	p-value
Food production quantity	-0.166	0.013	0.983
Food production quality	0.031	0.019	0.358
Food production stability of quantity	-0.140	0.016	0.882
Food production stability of quality	-0.140	0.026	0.769

Table 3.2 List of bee species, total number of individuals caught throughout sampling period, and natural history information of each species. Natural history data were compiled from records kept and generously shared by J. Gibbs, and from a species list for New York state compiled by The Pollinator Network at Cornell (<https://pollinator.cals.cornell.edu/wild-bees-new-york/species-list-bees-new-york>).

Species	Total Captured	Nesting Substrate	Sociality	Native Status
<i>Agapostemon sericeus</i>	8	ground	solitary	native
<i>Agapostemon splendens</i>	3	ground	solitary	native
<i>Agapostemon virescens</i>	30	ground	communal	native
<i>Anthidium manicatum</i>	9	cavity	solitary	exotic
<i>Anthidium oblongatum</i>	1	cavity	solitary	exotic
<i>Anthophora bomboides</i>	4	ground	solitary	native
<i>Anthophora terminalis</i>	1	wood cavity	solitary	native
<i>Apis mellifera</i>	36	hive	advanced eusocial	exotic
<i>Augochlora pura</i>	34	rotten wood	solitary	native
<i>Augochlorella aurata</i>	12	ground	solitary social	native
<i>Bombus bimaculatus</i>	34	cavity	eusocial	native
<i>Bombus citrinus</i>	1	\N	socially parasitic	native
<i>Bombus fervidus</i>	2	cavity	eusocial	native
<i>Bombus griseocollis</i>	19	cavity	eusocial	native
<i>Bombus impatiens</i>	100	cavity	eusocial	native
<i>Bombus vagans</i>	2	cavity	eusocial	native
<i>Calliopsis andreniformis</i>	3	ground	solitary	native
<i>Ceratina calcarata</i>	38	stem	solitary	native
<i>Ceratina dupla</i>	3	stem	solitary	native
<i>Ceratina mikmaqi</i>	4	stem	solitary	native
<i>Ceratina strenua</i>	1	stem	solitary	native
<i>Colletes latitarsis</i>	2	ground	solitary	native
<i>Dufourea novaeangliae</i>	1	ground	solitary	native
<i>Halictus confusus</i>	91	ground	solitary social	native
<i>Halictus ligatus</i>	36	ground	eusocial	native
<i>Halictus rubicundus</i>	12	ground	solitary social	native
<i>Heriades carinata</i>	1	stem	solitary	native
<i>Hoplitis producta</i>	1	stem	solitary	native
<i>Hylaeus affinis</i>	9	stem	solitary	native
<i>Hylaeus hyalinatus</i>	42	stem	solitary	exotic
<i>Hylaeus leptocephalus</i>	12	stem	solitary	exotic
<i>Hylaeus mesillae</i>	8	stem	solitary	native
<i>Hylaeus modestus</i>	9	stem	solitary	native
<i>Lasioglossum admirandum</i>	38	ground	eusocial	native
<i>Lasioglossum anomalum</i>	1	ground	eusocial	native
<i>Lasioglossum bruneri</i>	4	ground	eusocial	native
<i>Lasioglossum cattellae</i>	2	ground	eusocial	native
<i>Lasioglossum cinctipes</i>	2	ground	eusocial	native
<i>Lasioglossum coriaceum</i>	2	ground	solitary	native

<i>Lasioglossum cressonii</i>	4	rotten wood	eusocial	native
<i>Lasioglossum ephialtum</i>	9	ground	eusocial	native
<i>Lasioglossum foveolatum</i>	12	ground	eusocial	native
<i>Lasioglossum foxii</i>	1	ground	solitary	native
<i>Lasioglossum gotham</i>	2	ground	eusocial	native
<i>Lasioglossum hitchensi</i>	82	ground	eusocial	native
<i>Lasioglossum illinoense</i>	18	ground	eusocial	native
<i>Lasioglossum imitatum</i>	50	ground	eusocial	native
<i>Lasioglossum leucocomum</i>	8	ground	eusocial	native
<i>Lasioglossum lineatum</i>	1	ground	eusocial	native
<i>Lasioglossum oblongum</i>	1	rotten wood	eusocial	native
<i>Lasioglossum paradmirationum</i>	2	ground	eusocial	native
<i>Lasioglossum pectorale</i>	1	ground	solitary	native
<i>Lasioglossum pilosum</i>	8	ground	eusocial	native
<i>Lasioglossum platyparium</i>	1	\N	socially parasitic	native
<i>Lasioglossum smilacinae</i>	2	ground	eusocial	native
<i>Lasioglossum sp.</i>	7	-	-	-
<i>Lasioglossum tegulare</i>	29	ground	eusocial	native
<i>Lasioglossum versatum</i>	15	ground	eusocial	native
<i>Lasioglossum weemsi</i>	1	ground	eusocial	native
<i>Megachile brevis</i>	1	cavity	solitary	native
<i>Megachile campanulae</i>	2	stem	solitary	native
<i>Megachile centuncularis</i>	4	cavity	solitary	\N
<i>Megachile mendica</i>	2	ground and stem	solitary	native
<i>Megachile mucida</i>	1	ground	solitary	native
<i>Megachile rotundata</i>	5	cavity	solitary	exotic
<i>Megachile sculpturalis</i>	4	cavity and stem	solitary	exotic
<i>Megachile texana</i>	3	ground	solitary	native
<i>Melissodes agilis</i>	40	ground	solitary	native
<i>Melissodes bimaculatus</i>	137	ground	solitary	native
<i>Melissodes desponsus</i>	5	ground	solitary	native
<i>Melissodes subillata</i>	1	ground	solitary	native
<i>Melissodes trinodis</i>	1	ground	solitary	native
<i>Osmia caerulea</i>	1	cavity and stem	solitary	exotic
<i>Peponapis pruinosa</i>	22	ground	solitary	native
<i>Sphecodes atlantis</i>	1	\N	cleptoparasite	native
<i>Sphecodes cressonii</i>	1	\N	cleptoparasite	native
<i>Sphecodes sp. B</i>	1	-	-	-
<i>Triepeolus lunatus</i>	1	\N	cleptoparasite	native
<i>Xylocopa virginica</i>	12	wood	solitary	native

Table 3.3 Model results of linear regressions testing bivariate relationships between bees, temperature, and impervious surface at various buffer distances. Results with negative Adjusted R² values mean the model fit is no better than fitting a horizontal line. Results with statistically significant findings are shown in bold.

Response Variable	Predictor Variable	Coefficient	Coeff. Std. Error	t-value	p-value	Adj. R ²
Bee Abundance	% Impervious Surface 500.0-m	1.493	18.243	0.082	0.935	-0.024
	% Impervious Surface 1.0-km	5.121	21.573	0.237	0.814	-0.022
	% Impervious Surface 1.5-km	3.702	25.446	0.145	0.885	-0.023
	% Impervious Surface 2.0-km	-2.094	27.728	-0.076	0.940	-0.024
	Mean Min. Temperature	-1.413	3.412	-0.414	0.681	-0.023
Bee Richness <i>Estimated (Chao1)</i>	% Impervious Surface 500.0-m	-1.197	8.761	-0.137	0.892	-0.023
	% Impervious Surface 1.0-km	0.457	10.368	0.044	0.965	-0.024
	% Impervious Surface 1.5-km	1.000	12.224	0.082	0.935	-0.024
	% Impervious Surface 2.0-km	1.970	13.315	0.148	0.883	-0.023
	Mean Min. Temperature	-1.494	1.616	-0.924	0.361	-0.004
Bee Diversity <i>Estimated (Shannon)</i>	% Impervious Surface 500.0-m	-0.102	0.707	-0.145	0.886	-0.023
	% Impervious Surface 1.0-km	-0.071	0.837	-0.084	0.933	-0.024
	% Impervious Surface 1.5-km	-0.131	0.987	-0.132	0.895	-0.023
	% Impervious Surface 2.0-km	-0.173	1.075	-0.161	0.873	-0.023
	Mean Min. Temperature	-0.053	0.129	-0.408	0.686	-0.023
Mean Min. Temperature	% Impervious Surface 500.0-m	4.463	0.774	5.765	<0.001	0.466
	% Impervious Surface 1.0-km	5.777	0.954	6.057	<0.001	0.491
	% Impervious Surface 1.5-km	7.612	1.140	6.678	<0.001	0.541
	% Impervious Surface 2.0-km	8.178	1.403	5.828	<0.001	0.471

Figures

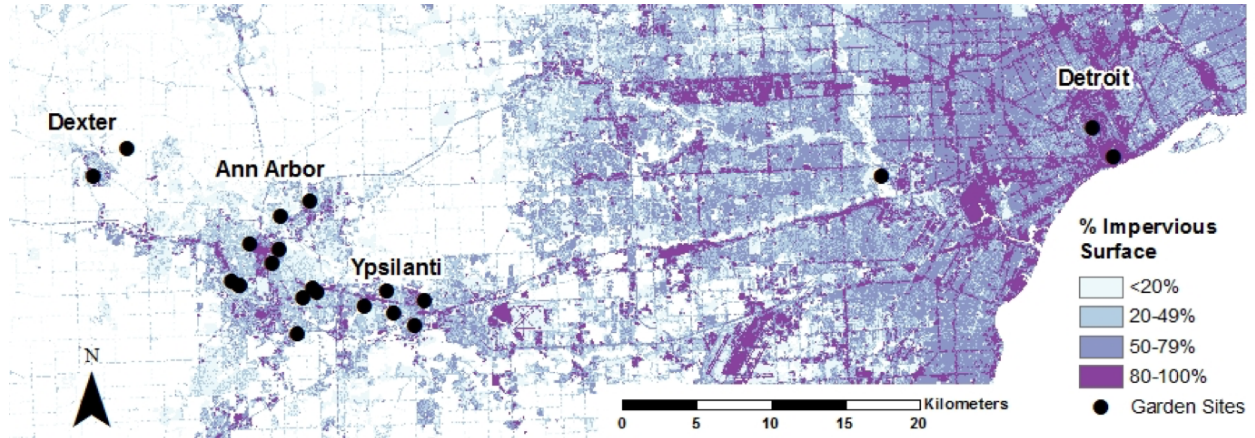


Figure 3.1 Map of garden sites sampled across southeastern Michigan’s urban gradient, U.S.A., where intensity of development is defined using National Land Cover Database classification and is based on the amount of impervious surface area.

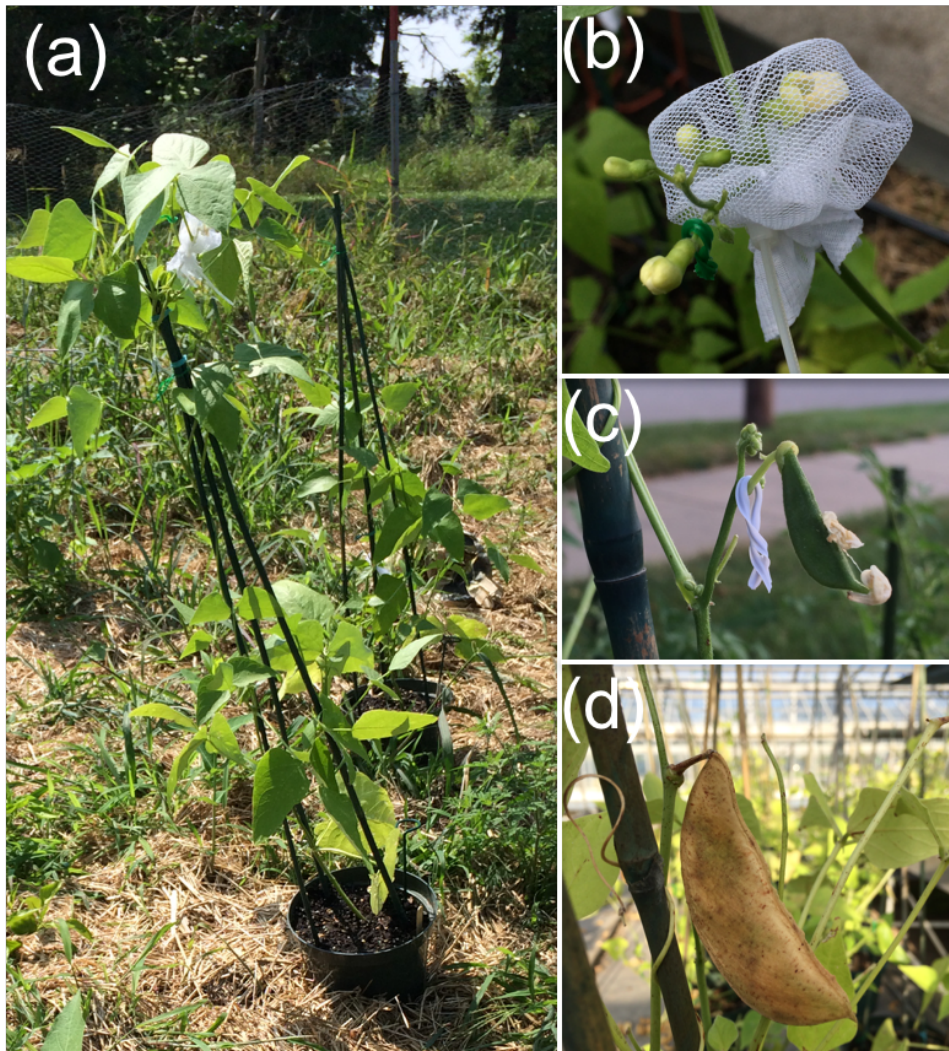


Figure 3.2 Progression of treatments on potted lima bean plants used to record effect of pollinators on urban food production. (a) Potted lima bean plants that had just begun to flower were placed in gardens in late July. (b) Buds in blocked pollinator treatment were covered throughout their flowering period, while buds in allowed pollinator treatment were tagged with green zip tie. (c) Example of pod developing from blocked pollinator treatment, tagged with white zip tie. (d) Example of dried lima bean pod ready for harvesting.

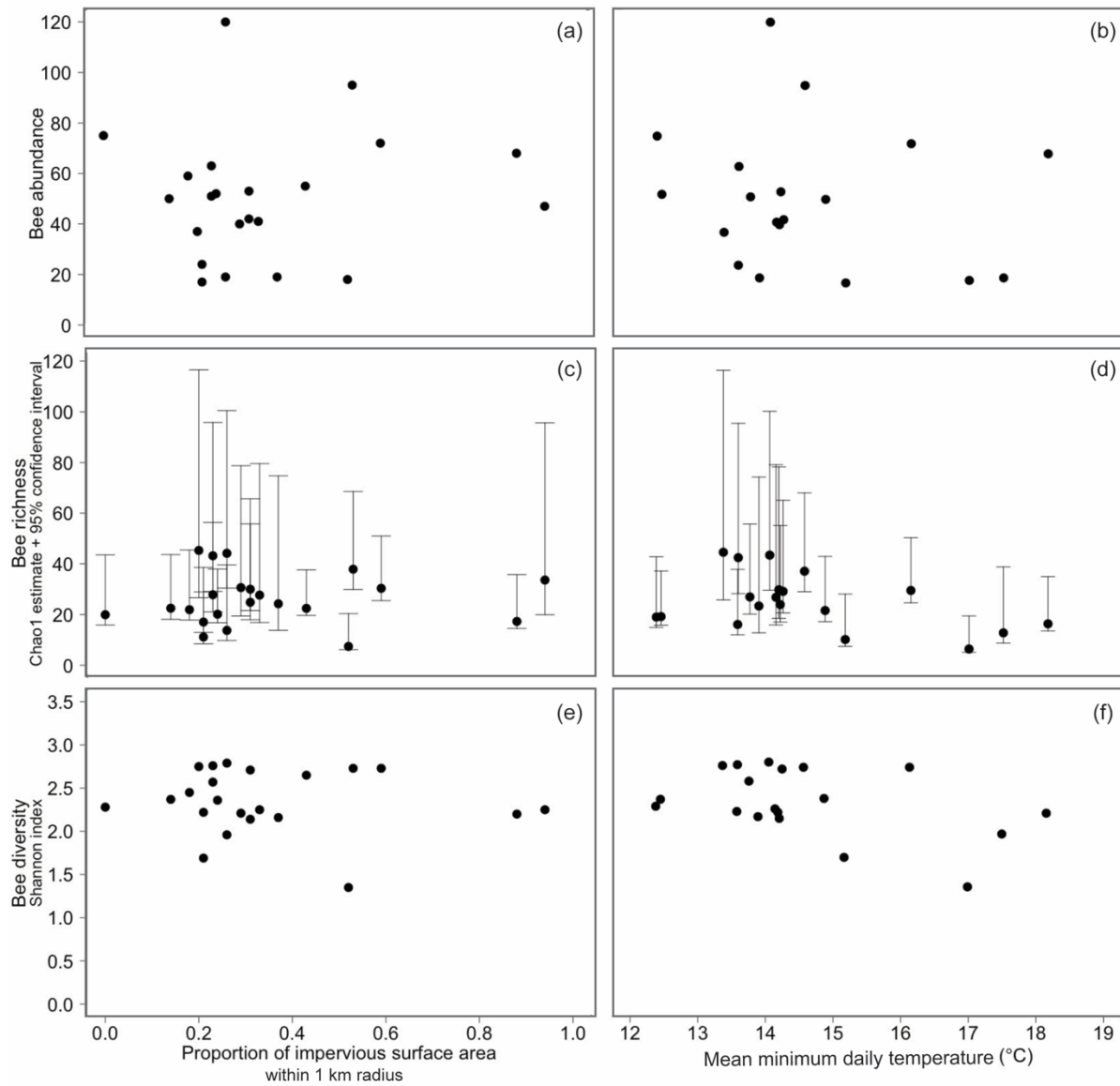


Figure 3.3 Relationships between bee community metrics and impervious surface or mean minimum daily temperature per site. Model results can be found in **Table 3.3** and show no significant effects for the relationships displayed here. Bee abundance (a, b) represents the total number of bees collected per site. Both bee richness (c, d) and bee diversity (e, f) were estimated using individual-based rarefactions. Although impervious surface was measured at four radii, only measurements made within a 1-km radius are shown here.

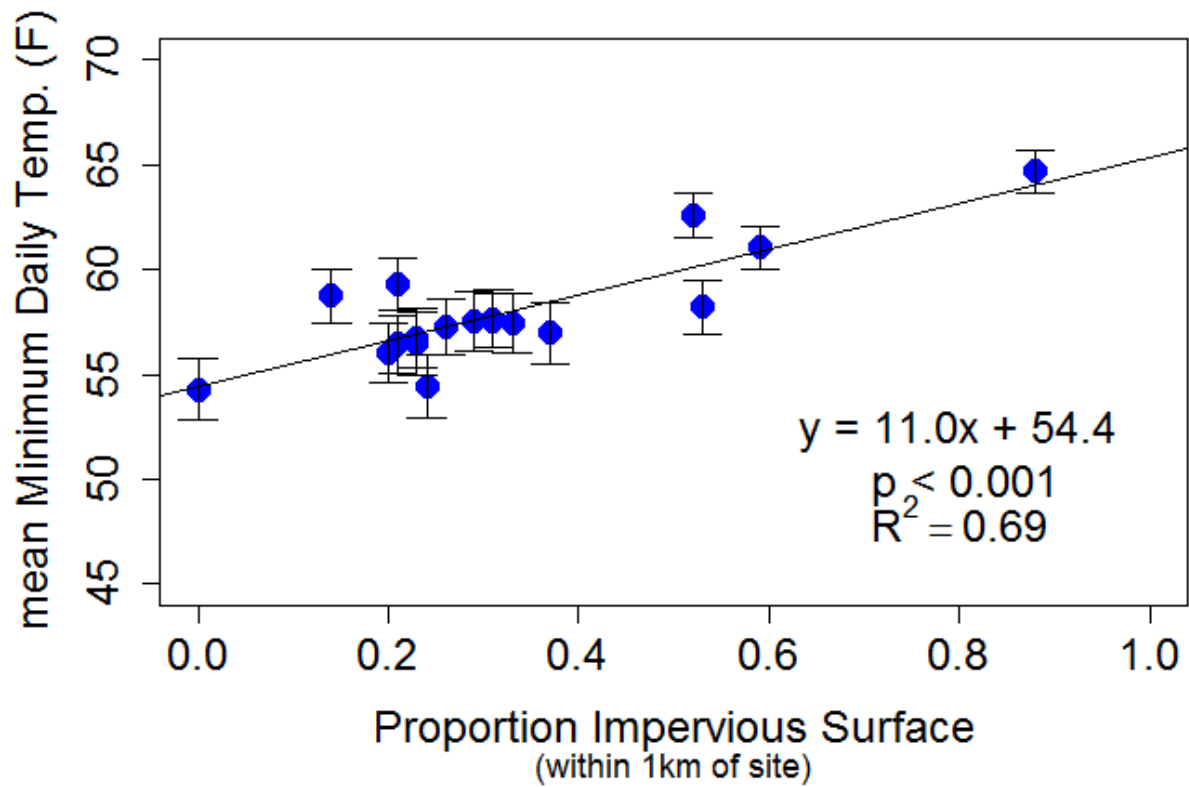


Figure 3.4 Across the urban gradient, increasingly urban sites were increasingly warmer. More specifically, garden sites with higher proportions of impervious surface within 1km had significantly higher mean minimum daily temperatures than garden sites with lower proportions of impervious surface.

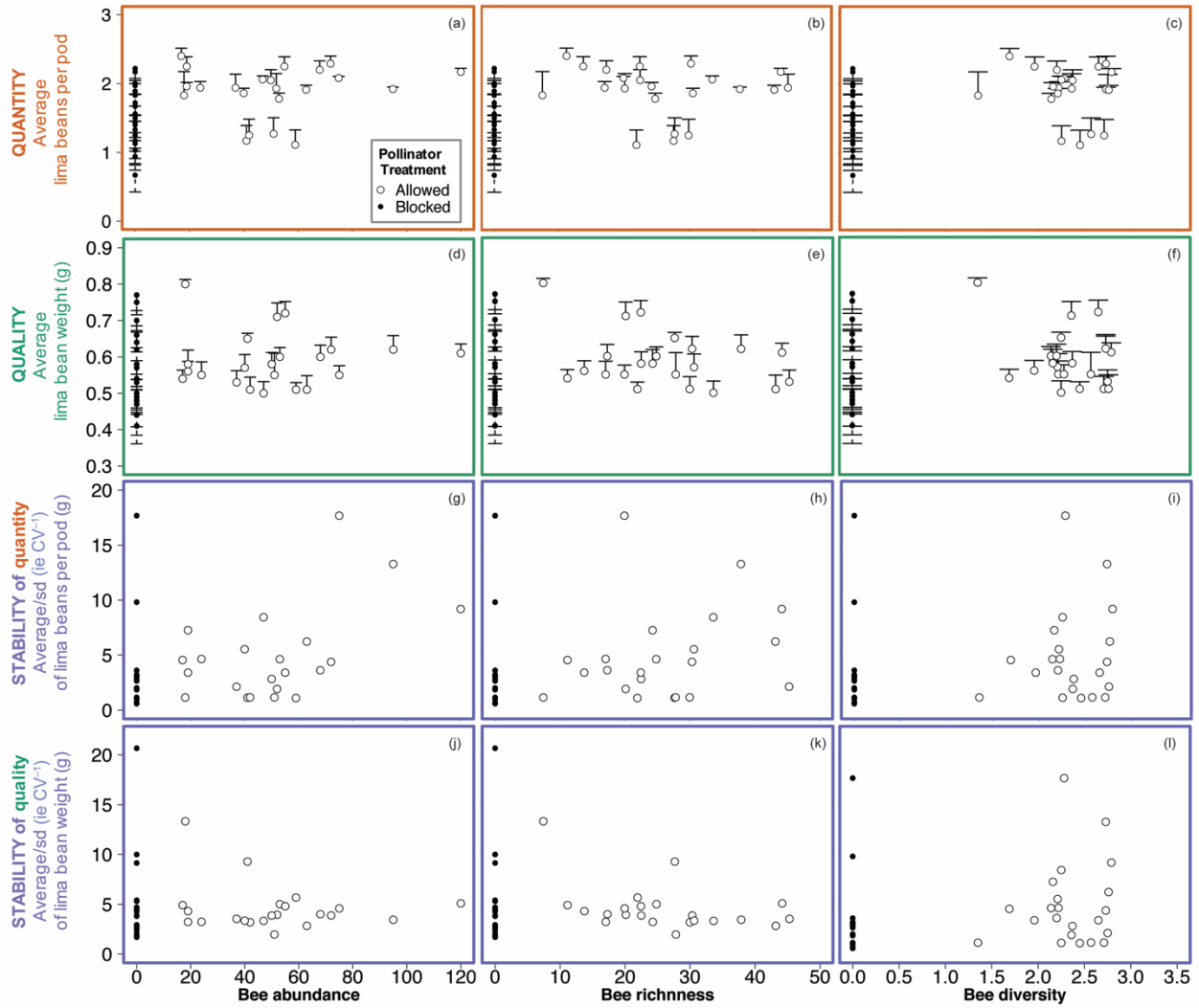


Figure 3.5 Relationships between bee community metrics (abundance, richness, and diversity) and food production metrics (quantity, quality, and stability). Bars represent standard error. The division between pollinator-allowed and -blocked treatments is shown in the legend in (a), which is applicable to subsequent graphs (b-l). All pollinator-blocked data were associated with a value of zero for pollinator abundance, richness, and diversity, and the pollinator-blocked data was therefore stacked at the zero mark for all graphs.

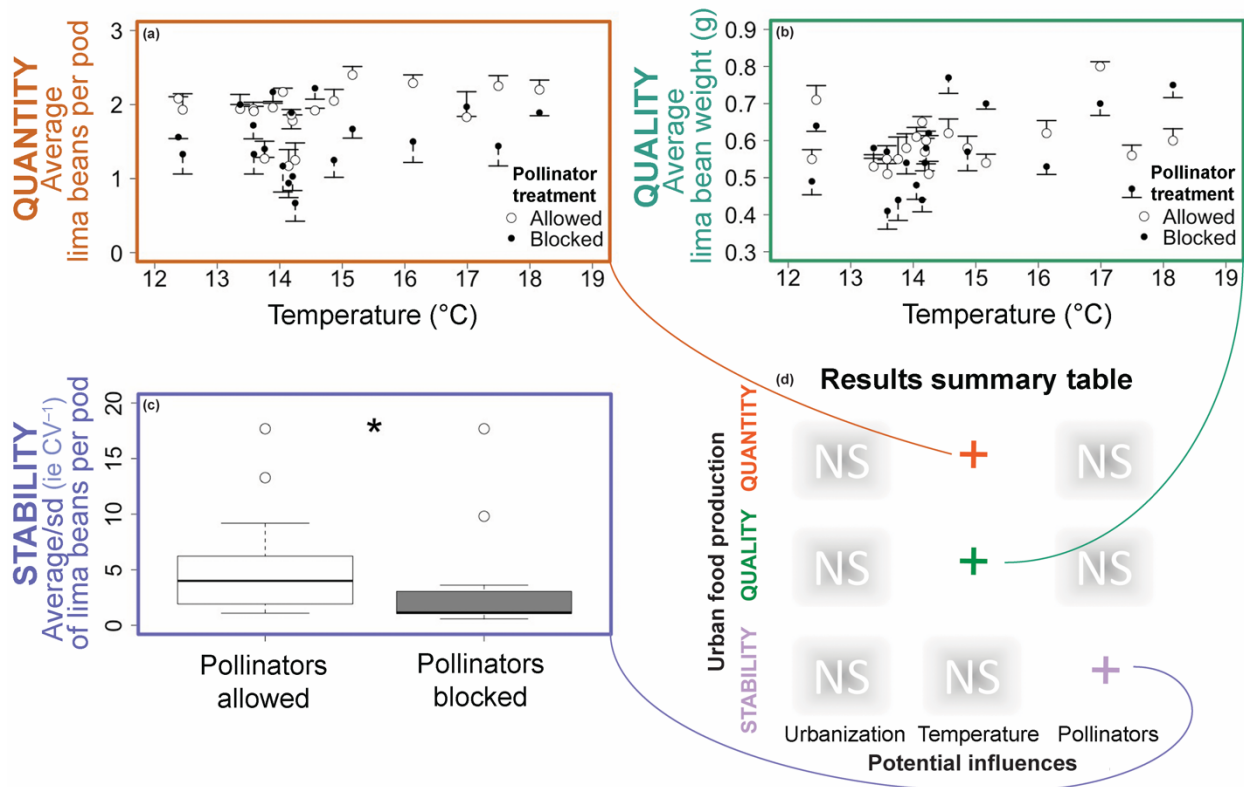


Figure 3.6 Summary of significant relationships between effects of urbanization, temperature, and pollinators on food production metrics. Mean minimum daily temperature had a small but significant, positive effect on food production quantity (a) and quality (b), while pollinator presence significantly increased food production stability (c). Stability here is measured as the inverse of the coefficient of variation (CV^{-1}), i.e. the average divided by the standard deviation (sd). Chart (d) summarizes overall results, i.e. the effect of urbanization, temperature, and pollinators on food production. Within table, NS = no significant relationship found, and + symbol means a significant positive relationship found.

Chapter 4

Experimental small-scale floral patches increase species density but not abundance of small urban bees (Hymenoptera: Apoidea)

4.1 Abstract

1. Habitat loss due to urbanization can have negative effects on bee populations. Flower plantings are often used to combat these negative effects, but less is known about the spatial scale at which flower plantings are effective, particularly in urban settings.
2. To test the effectiveness of small-scale floral additions on enhancing urban bee abundance or species density, as well as their impact from one year to the next, different quantities of potted sweet alyssum (*Lobularia maritima*) flowers were placed across sites in Ann Arbor, Michigan for two consecutive years and the resulting bee visitors were monitored.
3. Overall we found the number of flowers added at the local level was positively correlated with bee abundance and species density in an urban landscape. Both bee abundance and species density showed evidence of linear and nonlinear dynamics. At smaller flower quantities, dynamics between flower quantity and bees were clearly linear, such that incremental increases in number of flowers showed significant increases in bee abundance and species density. At larger quantities of floral additions, however, dynamics were nonlinear in that incremental increases in flower quantity had no effect on bee abundance and highly variable effects on bee species density.

4. Comparing the change in bee abundance and species density from one year to the next, we found a significant increase in bee species density in the second year of small-scale floral additions, but no significant difference in bee abundance.

5. *Synthesis and applications*: Our results show that small flower plantings can have positive effects on pollinator communities even over a short period of time, and therefore confirm that encouraging citizens to plant flowers can be an effective conservation strategy to increase urban bee diversity for certain urban pollinator populations. In addition, our finding that smaller flower plantings may have higher impacts on pollinators than larger plantings that suggests resource managers interested in pollinator conservation should consider spreading multiple, smaller floral plantings across the urban landscape, rather than pooling all resources into planting and maintaining one large flower patch.

4.2 Introduction

Wild bees are an important group of pollinators showing signals of decline (Ollerton et al. 2014; Koh et al. 2016). Given their vital role as pollinators of many wildflowers and crops (Klein et al. 2007; Ollerton, Winfree & Tarrant 2011), declines in wild bees could have cascading effects on both ecosystem function and crop yields (Kearns & Inouye 1997; Allen-Wardell et al. 1998; Vanbergen & the Insect Pollinators Initiative 2013). Bee declines have been attributed to various factors including pesticides, invasive parasites, pathogens, and habitat loss (Goulson et al. 2015). In this study we focus on habitat loss and the efforts to reverse its negative effects through the planting of additional flowers. Habitat loss is often associated with agricultural expansion, intensification, and urbanization, and negatively impacts bees by reducing the floral and nesting resources that they rely on (Goulson et al. 2015).

There is strong evidence that floral resource availability regulates wild bee abundance and diversity (Roulston & Goodell 2011), and increasing floral resource availability has therefore become a focus of pollinator conservation efforts. Floral resources are vital for bee survival—providing essential nectar for adult bees and pollen for their young (Frankie & Thorp 2009)—and numerous studies confirm the positive link between floral resource availability and bee populations (Roulston & Goodell 2011; Winfree, Bartomeus & Cariveau 2011). As a result, many U.S. federal agencies and non-profits recommend increasing floral resource to promote pollinator conservation. The U.S. Department of Transportation’s Federal Highway Administration, for example, recently released roadside management guidelines encouraging the protection of native vegetation and adjusted mowing frequencies along roadsides to benefit pollinators (Hopwood, Black & Fleury 2015). In addition, in response to former President Obama’s Executive Strategy to “Promote the Health of Honey Bees and Other Pollinators,” an initiative known as the Million Pollinator Garden Challenge was launched to incentivize the spread of pollinator flower habitats across the nation (millionpollinatorgardens.org). Non-profits such as the Pollinator Partnership and the Xerces Society for Insect Conservation stress the importance of both floral and nesting resources and encourage planting pollinator-friendly flowers in gardens and on agricultural lands (<http://www.pollinator.org/guides.htm>, <http://xerces.org/providing-wildflowers-for-pollinators/>).

Although the link between floral resources and bees is clear, the contexts in which floral additions effectively increase bee abundance and diversity are less clear, particularly for urban landscapes. Urban gardens can provide bees with both floral and nesting resources (Pawelek et al. 2009; Matteson & Langellotto 2010; Garbuzov & Ratnieks 2014), and given the trend toward increasing urbanization, urban gardens could become an important tool for pollinator

conservation (Goddard, Dougill & Benton 2010). The impact of floral additions on pollinators has been well-studied in agricultural contexts—where the impact is generally positive (Haaland, Naisbit & Bersier 2011; but see Wood, Holland & Goulson 2015)—but fewer studies have been conducted in cities, where the scales of floral additions are smaller and overall trends are not clear. Two studies, for example, found clear increases in pollinator diversity in urban areas as a result of floral additions in one main flower-rich garden (Pawelek et al. 2009; Garbuzov & Ratnieks 2014). Another study added wildflowers to amenity grasslands and found significant increases in bumble bee abundance (Blackmore & Goulson 2014). In contrast, an experiment that placed patches of native flowers within existing urban community gardens (Matteson & Langellotto 2011a), and two experiments that planted floral patches of varying sizes in urban sites found no significant differences in pollinator visitation (Yurlina 1998; per unit area, Garbuzov et al. 2015).

Several factors that are difficult to control may have contributed to the differences seen across studies. First is the issue of independent samples. Some studies place experimental floral patches within short distances of each other (e.g. 2m apart, 30–50m), which may inadvertently act as one large patch of flowers to pollinators not limited by such distances (Garbuzov et al. 2015; Yurlina 1998). Second is the issue of landscape context for both floral and nesting resources. If floral additions are placed in areas already well-populated with flowers, such as community gardens, the effects of floral additions may be negligible (Matteson & Langellotto 2011a). At the same time, if the amount of nesting resources available throughout a landscape is limited, pollinators limited by distance will remain unable to reach floral additions no matter their size (Matteson & Langellotto 2011a). Related to the second issue of landscape context is the third issue of potentially saturating relationships. There is no reason to expect that the

relationship between floral additions and pollinator communities is linear, where pollinators increase proportionally to the increase in floral quantity. Instead, it is possible that a saturating relationship exists, where after a saturation point is reached additional floral resources have little to no impact on pollinators (Feldman 2006; Ebeling et al. 2008). If this is the case, floral additions will only be beneficial to pollinators until this saturation point is reached, potentially explaining why some studies (Pawelek et. al. 2009, Garbuzov & Ratniek 2014, Blackmore & Goulson 2014) find floral additions to be effective (systems before saturation point of flowers) while other studies do not (Matteson & Langellotto 2011a) (systems after saturation point).

Our study seeks to understand whether different sizes of small, local floral additions affect urban bee communities, and tries to control for the aforementioned confounding factors. Our research questions are:

1. Does the number of flowers added at the local level affect bee abundance and species density, and what is the shape of this relationship (e.g. linear or saturating)?
2. Do flower additions at the local level affect bee abundance and species density over a temporal scale (i.e. from one year to the next)?

While we are unable to control all factors in our field experiment, here we attempt to account for issues of independent samples, landscape context, and potential non-linearity by: selecting sites separated by distances larger than the foraging range of target pollinators (addressing the issue of independent samples), placing our floral additions adjacent to parking lots—a space where floral and nesting resource availability should be uniformly low—but still documenting landscape floral and nesting resource levels to account for potential effects (addressing the issue of landscape context), and focusing our experiment on small pollinators, in the hopes of providing a full gradient of floral resources—from too little to too much (to explore the possibility of a non-linear

or saturating relationship). Over two summers, we manipulated floral resources across urban and suburban areas in Ann Arbor, in southeastern Michigan, U.S.A., and monitored the local pollinator response.

4.3 Methods

Sampling Locations

This study was conducted in the summer of 2015 and 2016 at 16 sites in Ann Arbor, Michigan, U.S.A. (**Figure 4.1, Table 4.1**) a city with a population of close to 114,000 (U.S. Census Bureau, 2010 data). In an effort to make sites more comparable within a heterogeneous urban landscape, all selected sites bordered paved parking lots, which provide little to no floral and nesting resources for bees. All sites were on or near University of Michigan property. Sites were distanced more than 200 m apart (mean 819 m; range 235 m - 3,182 m) to minimize interactions between small pollinator populations, which are estimated to have foraging ranges no greater than 200 m (pers. comm. Jason Gibbs, Greenleaf et al. 2007).

Flower Treatments

The number of sweet alyssum flowers (*Lobularia maritima*, Easter Bonnet Lemonade variety clones from C. Raker & Sons Inc., Litchfield, MI, USA) was manipulated across the landscape to test effects on pollinator communities. Sweet alyssum was chosen because of its common use in landscaping, long flowering period and small flower size, which attracts mostly small pollinators such as halictid bees, especially in the genus *Lasioglossum*, and syrphid flies. We wanted our flower choice to target *Lasioglossum* bees because of the diversity of *Lasioglossum* species found in urban areas; targeting this genus ensured that we would be able to

examine both bee richness and abundance as a response to floral additions. Restricting the study to small pollinators increased the likelihood of our experiment simulating the full spectrum of nectar required by the observed pollinator community—from potentially not enough nectar to more than enough. Focusing on small pollinators also increased the likelihood of sampling independent communities across our sites, given that small pollinators are assumed to have smaller foraging distances (Greenleaf et al. 2007).

Ten pots of soil (Sun Gro Horticulture Professional Growing Mix, Agawam, MA, USA; NSI Blow Molded Container Pots, Trade Size 3, 11” wide, A.M. Leonard, amleo.com) were placed at each site in a 2 by 5 pot configuration (approximately 1.7 x 0.6 m area), with either 0, 3, 6, or all 10 pots filled with sweet alyssum flowers. Sites that had pots with 0 sweet alyssum flowers in 2015 (our control) were changed to have 1 pot of sweet alyssum flowers in 2016, because after establishing that 0 pots lead to 0 bees in 2015, we wanted to understand how floral quantities even smaller than 3 pots of flowers affected bees. There were four replicates of each treatment: five sites had 10 pots filled with sweet alyssum flowers, four sites had 6 pots, four sites had 3, and the remaining five sites had 0 or 1 pot filled with flowers. The number of soil-containing pots was kept constant across all sites to keep potential added nesting habitat equal across all treatments, as *Lasioglossum* spp. can be ground-nesting and have been shown to nest in potted plants (Tonietto et al. 2011). This minimized the possibility of confounding the effect of floral additions with the effect of nesting resource additions. Each flower pot was watered with Blumat watering probes (Blumat 23308 Bottle Adapter for Automatic Plant Watering, Austria, amazon.com) attached to 1.5L clear plastic bottles.

Since sweet alyssum flower vitality varied across sites throughout the season and between years, we calculated an estimate of the actual number of sweet alyssum flowers

available each instance pollinators were sampled. To obtain this estimate, a random flowering pot was selected at each site, where first the total number of flowering stems were counted, and second the number of flowers on six different flowering stems at equidistant points around the pot were counted. The final estimate was then calculated by taking the average numbers of flowers from the six flowering stems and multiplying it by the total number of flowering stems.

Towards the end of each summer, this estimate was slightly modified to accommodate the increasing number of flower pots with sections no longer flowering. The variability across pots led us to mark the ‘quality’ of each flower pot as zero (0 to extremely few flowers), low (1/3 of pot flowering), medium (2/3 flowering), and high (fully flowering) in the months of August 2015, July 2016, and August 2016. To obtain final estimates of sweet alyssum flower quantity for the aforementioned months, we incorporated this ‘quality’ data by first multiplying the number of flowers estimated in the randomly selected pot (mentioned above) by the inverse of the quality ratio assigned to that same randomly selected pot (to obtain the estimated number flowers for a high quality flower pot at that site). If, for example, a randomly selected pot at one site had 120 flowers, but was perceived to be of low quality (1/3 of the pot was flowering), 120 would be multiplied by 3 to get an estimate of the number of flowers for a high quality (1/1 or fully flowering) pot at that site, in this case 360 flowers. To attain a count of the total number of flowers available at each site, the ‘quality’ ratios (0, 1/3, 2/3, or 1) for all pots at the site were summed, and then multiplied by the high quality estimate (in our example, 360).

Finally, on the last sampling date in August 2016, we found five sites where all potted sweet alyssum flowers had died; we believe this was a result of an unusually warm summer.

Pollinator Measurements

Pollinators were sampled at each site in 15-minute intervals once a month for 3 months (June-August) each year. Each month pollinators from all sites were sampled on the same day and by the same collector, and data were collected on mostly sunny or partly-sunny days, with a few observations on mostly cloudy days. To sample pollinators, all insects entering the perimeter of pots were collected. Bee specimens were separated and pinned for identification to species by Jason Gibbs. All specimens—bees and non-bees—are stored in the Insect Division of University of Michigan's Museum of Zoology.

Surrounding landscape floral and nesting measurements

Floral surveys of the surrounding landscape were conducted within a day of pollinator sampling to measure surrounding floral resource availability. At each site three 100-m transects were extended, starting from the center of the sweet alyssum flower pot location and extending in either a north, southeast, or and southwest direction. At the 0-m, 50-m and 100-m points on each transect, the area within a 20m radius of each point was surveyed for flowers (**Figure 4.1** insert). To survey flowers, the number of flower morphospecies (richness) and the proportion of space covered by flowers (abundance), and the relative sizes of the flowers present were estimated. The proportion of space covered by flowers within the 20 m area was quantified in increments of 5% at the lower range of floral cover (where the majority of the data fell) and then 25% at the higher range (i.e. 0%, 5%, 10%, 15%, 20%, 25%, 50%, 75%, 100% floral cover). After collection, data on surrounding floral landscape cover were converted from percent cover (%) to physical area (m^2) for each transect, and summed across all transects per site. Flower sizes were categorized as small (equivalent to average size of frequently mowed hop clover, *Trifolium*

campestre), medium (average size of white clover, *Trifolium repens*) or large (average size of standard daisy, e.g. *Leucanthemum vulgare*).

The amount of suitable nesting habitat in the landscape was estimated within 120-m of each site. This scale was selected to match the extent of area covered by floral surveys, and because of its relevance to the smaller scale at which the pollinators observed are assumed to operate (Greenleaf et al. 2007). Within each 120m radius, a grid of 2.5m cells was created atop an aerial image base layer in ArcMap software (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Any edge cell whose area was not 50% within the radius was eliminated. Presence of nesting resources was recorded for each cell in the field.

The nesting resources considered in each cell included: bare soil exposed to light for at least part of the day, dead wood, slope (recorded as presence of an inclined surface), rock ‘mulch’ (aggregations of rocks greater than approximately 1 cm, sometimes used in university landscaping), and areas of herbaceous plants. Dead wood and slope were considered because both have been cited as factors in nesting preferences for certain halictine bees (Sakagami and Michener 1962). Rock ‘mulch’ was considered because of a study finding *Halictus rubicundus* bees preferred to nest in areas between landscaped pebbles rather than bare dirt (Cane 2015).

To calculate each site’s nesting habitat availability, each cell marked with the presence of nesting resources was given a value of 1 per nesting resource available, and values were summed across all cells within the grid. There were two situations that were exceptions to this rule: (1) When bare soil bordered clumps of trees or forests, we found the amount of area ever exposed to light often varied. In these situations, if a part of the bare soil patch was never exposed to light, we marked two thirds of the cells along the patch with a value of 1, and the remaining third of

the cells with a value of 0. If most of the bare soil patch was never exposed to light, we marked one third of the cells with a value of 1, and the remaining two thirds with a value of 0. (2) For the dead-wood measurement, we considered any piece of wood potentially large enough for a bee to nest in. Since we were unable to account for every piece of dead wood in forested areas with our method, we assigned a value of 1 to a cell if we directly observed a piece(s) of dead wood in a location identifiable on our map of cells. Otherwise doing field surveys of forests—where individual cells were hard to pinpoint on our map—we used a value of 0.05 in each cell as an estimate of the general potential contribution of the urban forest.

Analysis

In our analyses, we treated bee abundance and bee species density (number of species found across equal unit areas, see Gotelli & Colwell 2011) as our response variables, and number of sweet alyssum flowers, landscape nesting availability, landscape floral availability, time (hh:mm) of sampling, month, and year as predictor variables. Site was included as a random effect. Neither bee richness nor bee diversity rarefaction curves were constructed because most sites had fewer than 20 individuals per sample, and therefore did not meet minimum requirements for rarefaction analysis (N. Gotelli, pers. comm.).

For exploratory analysis, we first plotted each response variable against each predictor variable and ran simple regressions to test for significant predictor variables. We then used a paired t-test in R (R Core Team 2015) to compare sweet alyssum flowers between years. One data point proved to be an extreme outlier in number of sweet alyssum flowers and heavily skewed subsequent models (causing a third of trend line to be based on one data point) and was therefore excluded from subsequent analyses.

Both research questions (1.) Does the number of flowers added at the local level affect bee abundance and species density, and what is the shape of this relationship, e.g. linear or saturating?; (2.) Do flower additions at the local level affect bee abundance and species density over a temporal scale, i.e. from one year to the next? were answered using a generalized additive model with the mgcv package in R. A generalized additive model is similar to a general linear model or generalized linear model, but the generalized additive model can incorporate nonlinear forms of predictor variables (Clark 2016); this feature makes it ideal for our research question, where we question the linear assumptions of the flower predictor variable. In each generalized additive model, either bee abundance or species density was chosen as the response variable, number of sweet alyssum flowers as the nonlinear predictor, landscape nesting availability, landscape floral availability, time (hh:mm) of sampling, month and year as linear predictors, and site as a random variable. Since all three measures of landscape floral availability (total landscape floral area, floral area of small flowers, and floral richness) were highly correlated, three separate models were run, each including one of the landscape floral availability measures, and the model with the lowest AIC value was selected.

For the first research question we focused on the effect of the nonlinear predictor number of sweet alyssum flowers and observed the shape of the modeled curve. If the number of sweet alyssum flowers proved to be a significant predictor variable in the generalized additive model and the resulting trend line showed semblance of a saturating relationship, we tested for further evidence of a positive saturating relationship by first identifying a potential saturation point—or point of transition from linear to nonlinear relationship—in the trend line, and second testing for a linear relationship before and after the perceived saturation point with a linear mixed model. To better scale variables within the linear mixed model, values of sweet alyssum flowers were

divided by 10,000. If the linear mixed model was significant before the saturation point but not after, we interpreted this as further support—although not complete confirmation—of a saturating relationship.

For the second research question, we focused on the effect of the year predictor variable in the generalized additive model, to determine whether there was a significant change in bee abundance or species density from 2015 to 2016, given the effect of the remaining predictor variables. In addition, we re-ran each generalized additive model using the same predictor and response variables, but excluding data from the four ‘control’ sites (which had 0 and 1 pots of flowers in 2015 and 2016, respectively) in case the change in number of flower pots biased trends seen between years. We found no differences in yearly trends from original models using the full data set, and therefore proceeded with original models’ results.

4.4 Results

Overall bee community and sweet alyssum flower trends

In 2015, 194 bees were collected and identified to 11 unique species. In 2016, 147 bees were collected and identified to 15 unique species (**Figure 4.2**). In both years, the dominant species was *Lasioglossum ephialtum*, comprising 86% of all bees captured in 2015 and 58% in 2016 (**Figure 4.2**). Most bees collected were ground-nesters and native species (**Figure 4.2**).

Despite planting the same quantities of sweet alyssum flowers each year at each site, the summer of 2016 was unusually warmer and we observed increased sweet alyssum mortality. In 2015, the mean number of sweet alyssum flowers estimated across sites was $10,479 \pm 14,661$ s.d., while in 2016, the mean number was $4,666 \pm 5,178$ (paired t-test, $t = 3.125$ $p = 0.003$).

1. Does the number of flowers affect bee abundance and species density, and what is the shape of this relationship?

In the best-fit generalized additive model, the number of sweet alyssum flowers significantly affected both overall bee abundance ($F(3.214, 3.915) = 3.188, p = 0.019$) and bee species density ($F(7.733, 8.522) = 5.347, p < 0.001$; **Figure 4.3, Table 4.2**). Upon visual inspection of each model's trend lines, neither showed a clean and distinct saturating function; however, both models appeared to follow a similar pattern, where at low floral densities the bee response showed a positive and linear trend, yet at mid-range and higher floral densities, bee response showed flatter or variable trends. We therefore identified the point of transition—between linear increase and lack of clear, linear increase—for each model as 11,000 sweet alyssum flowers for bee abundance and 4,000 for bee species density (**Figure 4.3**). For both bee abundance and bee species density, we found a significant linear positive relationship before the point of transition (abundance, 3.985 ± 1.481 s.e., $t = 2.692, p = 0.009$; species density, 4.266 ± 1.306 s.e., $t = 3.265, p = 0.002$), and no significant relationship with sweet alyssum flowers was found after the point of transition (abundance, 0.436 ± 0.760 s.e., $t = 0.574, p = 0.577$; species density, 0.007 ± 0.175 s.e., $t = 0.041, p = 0.967$).

2. Do flower additions at the local level affect bee abundance and species density over a temporal scale, i.e. from one year to the next?

In the generalized additive model, year did not significantly affect bee abundance ($-0.775 \pm 0.956, t = -0.81, p = 0.421$), but did have a positive, significant effect on bee species density ($0.636 \pm 0.316, t = 2.01, p = 0.049$; **Figure 4.4, Table 4.2**).

Additional findings

A few of the additional predictor variables included in our models also produced notable results. For bee abundance, the variation among sites was significant (**Table 4.2**). This may be explained by one site with particularly high bee abundance values (site RH in **Figure 4.5**), and the four sites with 0 or 1 pot of sweet alyssum flowers that had consistently low bee abundances (sites ARB, NC53, OSEH, and WT in **Figure 4.5**). For species density, both time (hh:mm) of sampling and month were significant effects. Time showed a slightly negative effect, meaning that slightly fewer bees were collected later in afternoon, as compared to the morning. Sampling month had the expected significant effect on bee abundance, in that more bees were collected in the warmer months of July and August as compared to June. We also verified that neither floral or nesting resources at the landscape level significantly affected bee abundance (total floral area, -0.001 ± 0.001 s.e., $t = -0.979$, $p = 0.332$; nesting, -0.004 ± 0.007 s.e., $t = -0.589$, $p = 0.558$) or species density (floral area of small flowers, -0.0002 ± 0.0003 s.e., $t = -0.895$, $p = 0.374$; nesting, 0.0001 ± 0.002 s.e., $t = 0.103$, $p = 0.918$, **Table 4.2**, **Figure 4.6**).

4.5 Discussion

Overall our results are encouraging for urban planners and conservationists interested in green infrastructure, demonstrating that even over short time periods (one year), small-scale floral additions can make effective contributions to conservation of pollinator species in urban areas. To summarize our findings, our analysis of the relationship between floral additions and bees showed signals of a saturating relationship, with significant linear increases at smaller scales of floral additions, but not at larger scales. From one year to the next, small-scale urban floral additions significantly increased pollinator species density but did not have a significant

effect on pollinator abundance. Neither of the landscape-level measures of nesting or floral resources significantly correlated with bee responses.

Lasioglossum ephialtum dominated the bee community visiting sweet alyssum flowers in Ann Arbor, Michigan; they are small-bodied ground-nesters native to North America and are expected to be primitively eusocial (Gibbs et al. 2012), but as with many native bees, little has been documented on their behavior, life history, and preferred habitats. Although only recently described, it is considered a common species across its range (Gibbs 2010) and is commonly found in urban areas—even on green roofs (MacIvor *et al.* 2015)—and may also be successful outside of urban habitats (J.Gibbs, *pers. comm.*).

Our results on the functional relationship between floral additions and bees suggest that the relationship is nuanced, but has important implications for decisions on effective patch sizes for pollinator conservation. Past studies have explored similar questions of saturating relationships between floral resources and pollinators, with varying results. One study, for example, tested whether flat, linear, saturating, or sigmoidal models best fit the relationship between plant density and pollinator visits, and found pollinator visits were best explained with a saturating function model (Feldman 2006). In Matteson’s study of bees in New York City gardens, however, he found a linear—not saturating—relationship between garden floral area and bee richness (Matteson 2007). Yet, another experimental study done near Jena, Germany, found bee species richness followed a saturation curve with blossom cover, while bee abundance increased linearly (Ebeling et al. 2008). We found evidence of direct linear increases in bee abundance and species density at smaller ranges of floral additions, but a non-linear and more variable response at higher ranges of floral additions. In other words, in the context of our field experiment with small bees, adding 3,000 sweet alyssum flowers showed more significant effects

on bee species density than adding 1,000 sweet alyssum flowers, but at the higher end of the scale, adding 15,000 sweet alyssum flowers did not attract significantly different species density as 40,000 flowers. Our result suggests that, at least for small bees in urban landscapes, there is a semblance of a saturating relationship in which additions of independently spaced, smaller patches of flowers may have greater overall impacts than planting one large patch of flowers.

In the second year of floral additions, we found no significant change in bee abundance from the previous year. This finding contradicts the established direct relationship between floral resources and bee communities (Roulston and Goodell 2011), but matches some previous studies where floral additions had no significant impact on bee visitation (Yurlina 1998; Matteson and Langellotto 2011). These past studies suggested the lack of impact might have stemmed from floral additions that were either too close together or too small in size, or that other limiting factors such as nesting availability were not addressed. Our study made an effort to address these factors by explicitly spreading sites out beyond the foraging range of target pollinators, providing a range of thousands of flowers, and incorporating both nesting and floral landscape resources data into our models. We believe the lack of impact found in our study was associated with problems in flower mortality in the second year, when roughly half of the flowers placed across sites died in 2016. Ann Arbor—like much of the U.S.A.—experienced “much above average” temperatures from June to August of 2016 (NOAA.gov). Sweet alyssum flowers prefer cooler summer temperatures, and the above-average heat aligned with increased mortality of sweet alyssum flowers in the second year. Extending this type of study across larger time scales would reduce the impact of unique years, or at least allow more confidence in the patterns that emerge over time. Floral additions placed next to blueberry fields, for instance, only showed significant changes in wild bee visits during the third year of sampling (Blaauw and Isaacs 2014a).

Despite collecting 24% fewer bees in 2016, we found a significant increase in bee richness between years. In 2016, we collected five new bee species, in addition to nearly all of the species seen the previous year. One of the species collected in 2016, *Lasioglossum michiganense*, is parasitic (J.Gibbs, *pers. comm.*). Although little is known about the behavior and preferences of many of the species collected here, we assume the patterns seen here are rooted in the distribution of each species across the landscape. Species seen in both years of sampling may have already been established in nests within flying range of our floral additions; if newly emerged reproductive females of those species exhibit preferences to nest near or in their natal nest, we assume the existence of adequate floral resources in the landscape—especially supplemented by our floral additions—would encourage them to remain within range of our sites. The species newly collected in 2016, however—with the exception of *Apis mellifera*, whose distribution is likely more influenced by human activity—may have originated in nests slightly outside the foraging range distance of our floral additions, but upon emerging in the spring may have wound up nesting and reproducing at a location within range of our floral additions. Nesting behavior and distribution of these bees remains a huge gap in the literature, but is vital information if we are to understand the mechanisms behind bee dynamics across urban landscapes.

The main implications of our results are that small scale flower plantings in urban areas can be effective, even over short time periods, and that for targeted pollinator species or groups, there may be optimal ranges of flower addition sizes that maximize pollinator response. These results contradict previous findings suggesting that only larger areas of floral plantings are effective in increasing pollinator diversity (Blaauw and Isaacs 2014b), and suggest instead that actions taken in smaller areas—e.g. at the individual scale of an urban home garden—can be

effective. A study examining pollinator services throughout the city of Chicago reported a similar result, finding that when models simulated increased flower plantings by residents in their home gardens, pollination services significantly increased throughout the city (Davis et al. 2017). We recommend that urban natural resource managers focus on spreading multiple, smaller flower plantings out across urban landscapes, rather than concentrating resources into one large floral patch. The benefits of individual flower gardens in urban areas has been documented elsewhere, such as in Chicago, IL, where more densely populated neighborhoods had a greater diversity of flowering plants, which correlated to increased bee abundance, richness, and visitation in the densely populated neighborhoods (Lowenstein et al. 2014). While our results are encouraging, they are most relevant to small halictids in temperate urban areas, and the urban pollinator ecology field would benefit from similar additional studies with different species with different natural history traits, varying floral species, and studies focused on longer temporal dynamics.

4.6 Acknowledgements

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Michigan's Center for Statistics, Computing, and Analytics Research (CSCAR) for multiple statistical consultations.

4.7 References

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Tables

Table 4.1 Geographic coordinates of sampling sites. All sampling sites were located on or near University of Michigan property.

Site Name	Initials	Latitude	Longitude
Art and Architecture	AA	42.28866247	-83.71665934
Arboretum/Markley	ARB	42.28009998	-83.72865717
Briarwood Building	BB	42.24338118	-83.74319834
Eisenhower Blvd Complex	EBC	42.24544126	-83.73187618
Elbel Field	EF	42.27113898	-83.74462477
326 East Hoover	EH	42.26651371	-83.74583719
Fire House Station 6	FH	42.24281686	-83.75122275
Kellogg Eye Center	KEC	42.28867223	-83.73885612
NC 53 Commuter Lot	NC53	42.29512801	-83.70724837
NCRC East Side	NCRC-E	42.29860953	-83.70848599
NCRC West Side	NCRC-W	42.30111588	-83.70133803
Occupational Safety and Environmental Health	OSEH	42.26454326	-83.74366339
Revelli Hall	RH	42.26902286	-83.74444458
State Street Commuter Lot	SS	42.24868936	-83.74004108
Varsity Drive	VD	42.2354232	-83.72801208
Wolverine Tower E	WT-E	42.24311439	-83.73507714

Table 4.2 Results of the two generalized additive models used to analyze trends in bee abundance and bee species density. Each model included the same linear predictor variables (landscape nesting availability, landscape floral availability, time of sampling, month, year), one nonlinear predictor variables (number of sweet alyssum flowers), and one random effect (site). A * indicates a significant effect.

Response variable	Predictor variables	Estimate	Std.Error	t	p-value
Bee abundance	(Intercept)	1567.000	1927.000	0.813	0.420
	Landscape nesting availability	-0.004	0.007	-0.589	0.558
	Landscape floral area	-0.001	0.001	-0.979	0.332
	Time (hh:mm) of sampling	-0.020	0.018	-1.118	0.268
	Month (June)	0.844	1.147	0.736	0.465
	Month (August)	2.296	1.329	1.728	0.090
	Year	-0.775	0.956	-0.811	0.421
Nonlinear Predictor variables		edf	Ref.df	F	p-value
	Number of sweet alyssum flowers	3.214	3.915	3.188	0.019*
	Site, <i>random effect</i>	8.584	14	1.846	0.001*
Response variable	Predictor variables	Estimate	Std.Error	t	p-value
Bee species density	(Intercept)	-1281.000	637.700	-2.008	0.049*
	Landscape nesting availability	<0.001	0.002	0.103	0.918
	Landscape floral area of small flowers	<0.001	<0.001	-0.895	0.374
	Time (hh:mm) of sampling	-0.014	0.006	-2.437	0.018*
	Month (June)	1.142	0.395	2.896	0.005*
	Month (August)	1.500	0.444	3.378	0.001*
	Year	0.636	0.316	2.011	0.049*
Nonlinear Predictor variables		edf	Ref.df	F	p-value
	Number of sweet alyssum flowers	7.733	8.522	5.347	<0.001*
	Site, <i>random effect</i>	3.125	14	0.33	0.144

Figures

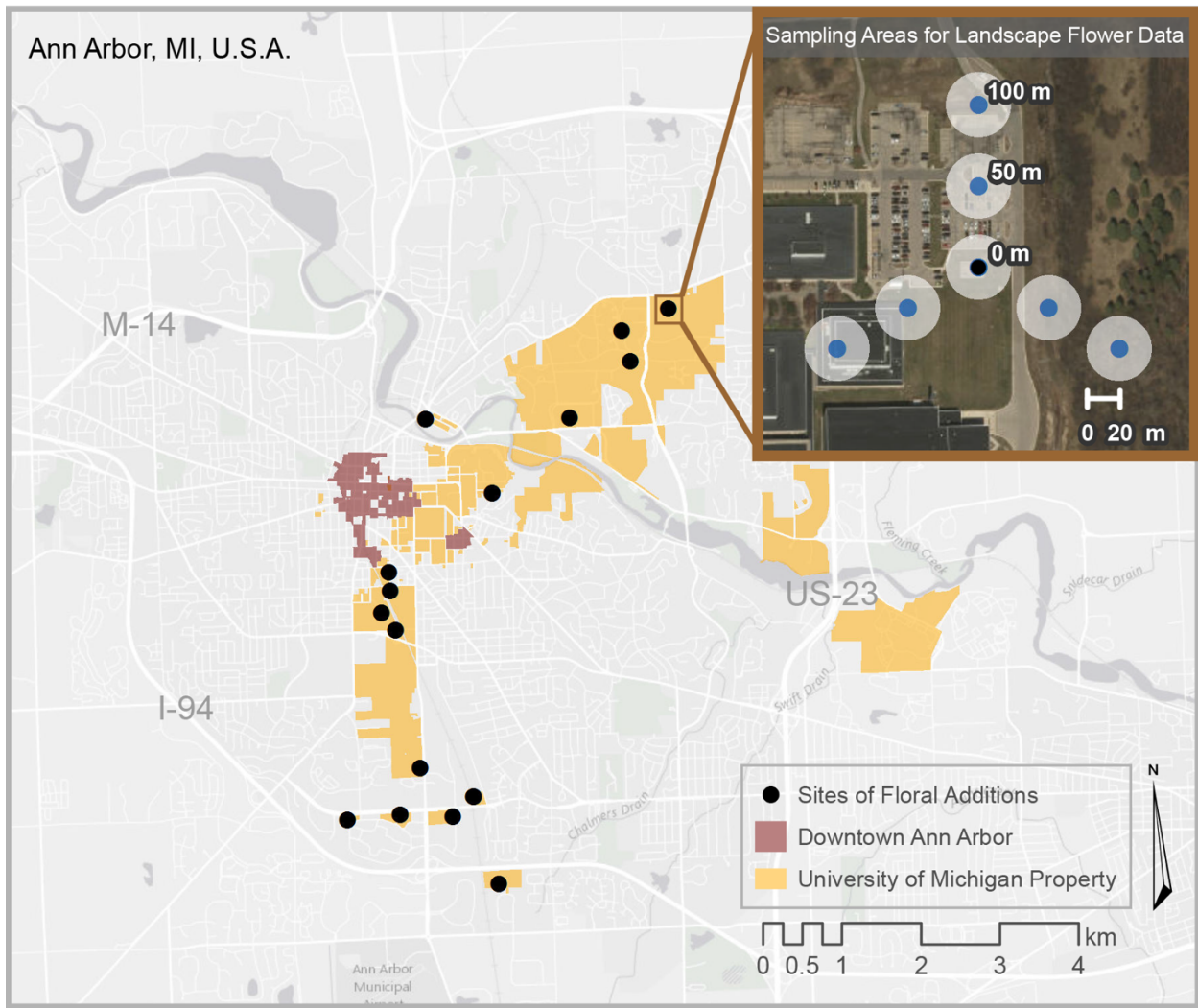


Figure 4.1 Map of sites where floral additions were placed within Ann Arbor, Michigan. Inset map shows one sampling site in detail, where potted sweet alyssum flowers were placed in the center (black dot) and landscape flower resource data was taken within 20 m (white circle areas) of sampling points spaced 50 m (blue dots) along three 100 m transects from the center. Source of base layer: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community.

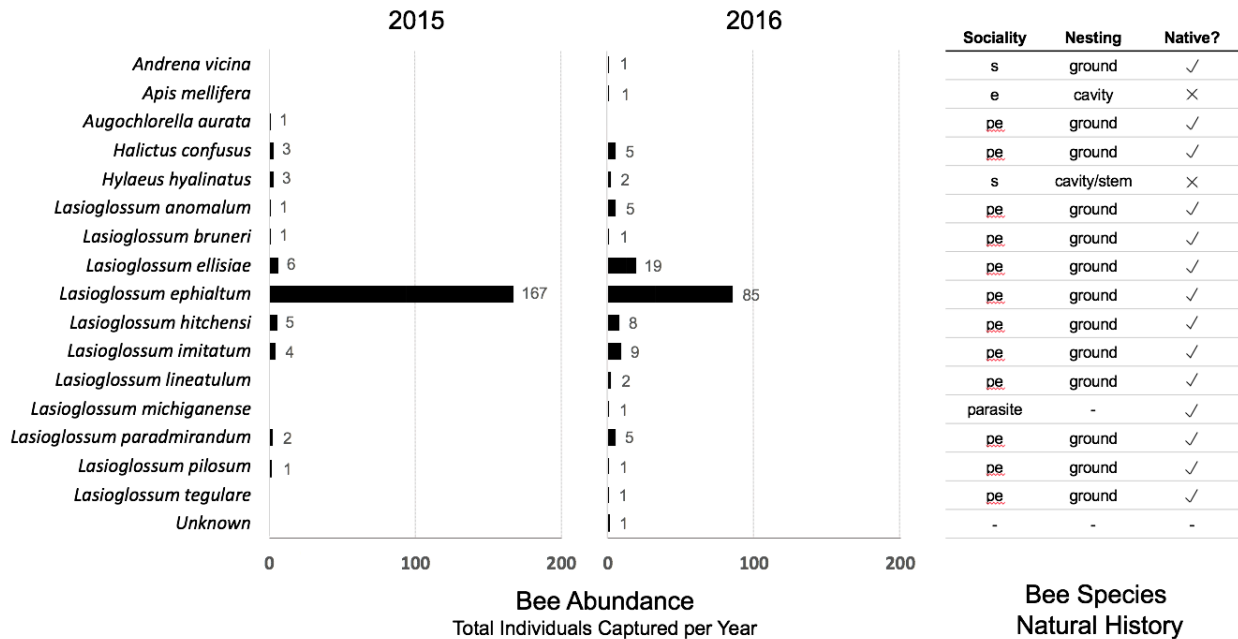


Figure 4.2 Total bee abundance found across sites in 2015 and 2016 with associated natural history of each species. *Lasioglossum ephialtum* dominated the bee community captured each year, although other species saw slight increases from 2015 to 2016. Most bees captured are considered native in Michigan and are ground nesters, and one parasitic species was found. In bee species natural history descriptions, ‘s’ refers to solitary, ‘e’ to eusocial, and ‘pe’ to primitively eusocial.

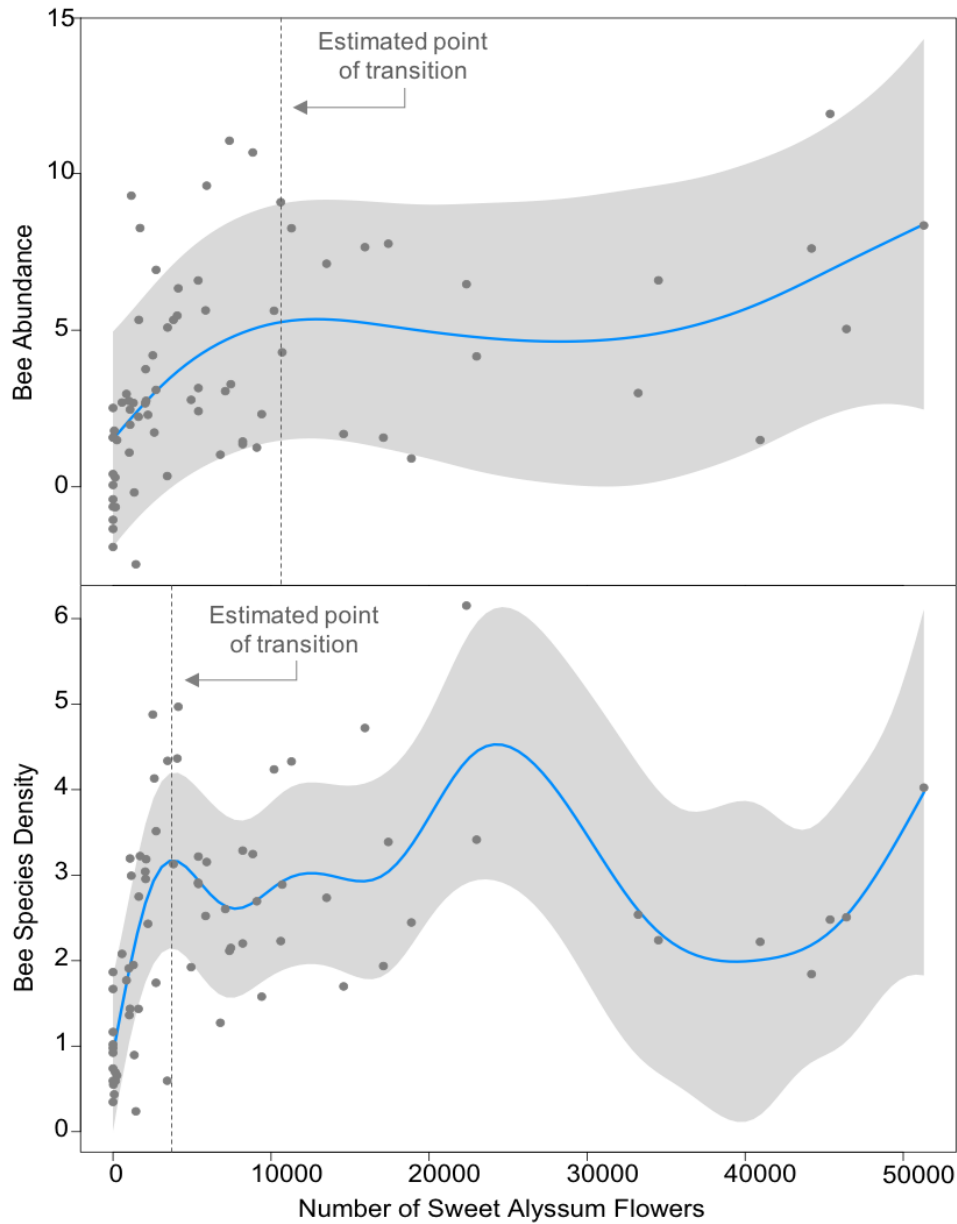


Figure 4.3 Partial residual plots of generalized additive model results, showing the fitted trend line in the relationship between flowering sweet alyssum quantity on (a) bee abundance and (b) bee species density. Graphs do not show raw data, but instead show modeled bee data, given other independent variables included in the model. Visually estimated points of transition between linear and nonlinear portion of the trend line are also shown.

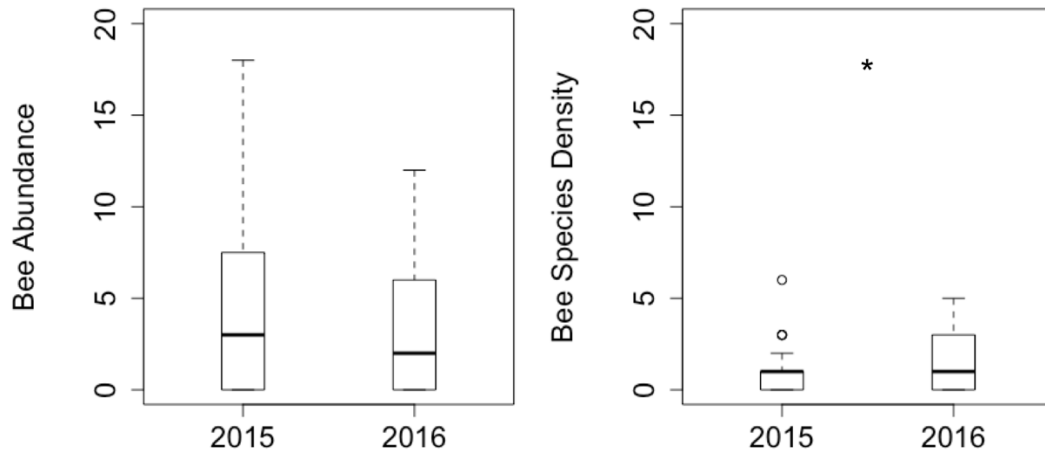


Figure 4.4 Bee abundance and bee species density in the two years of study. Abundance did not differ significantly between years, but bee species density increased significantly.

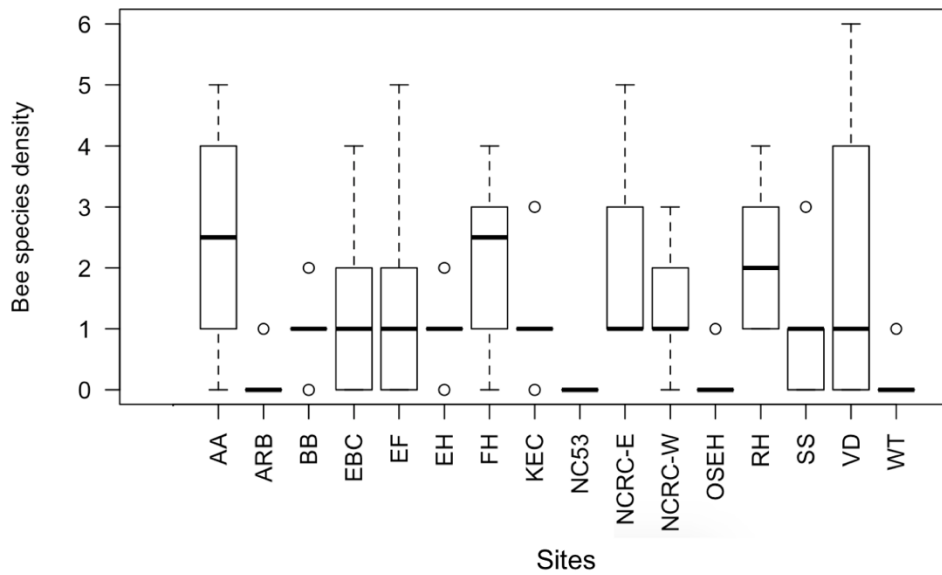
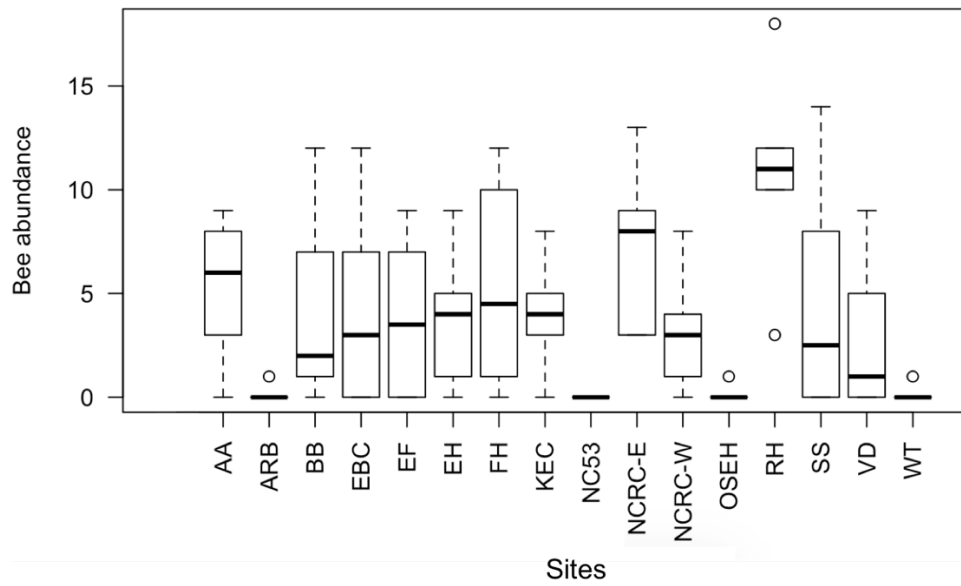


Figure 4.5 Variation in bee abundance and species density across sites. The sites ARB, NC53, OSEH, and WT had 0 or 1 pots of flowers in 2015 and 2016, respectively, and shared consistently low bee abundance and species density throughout the two years of sampling.

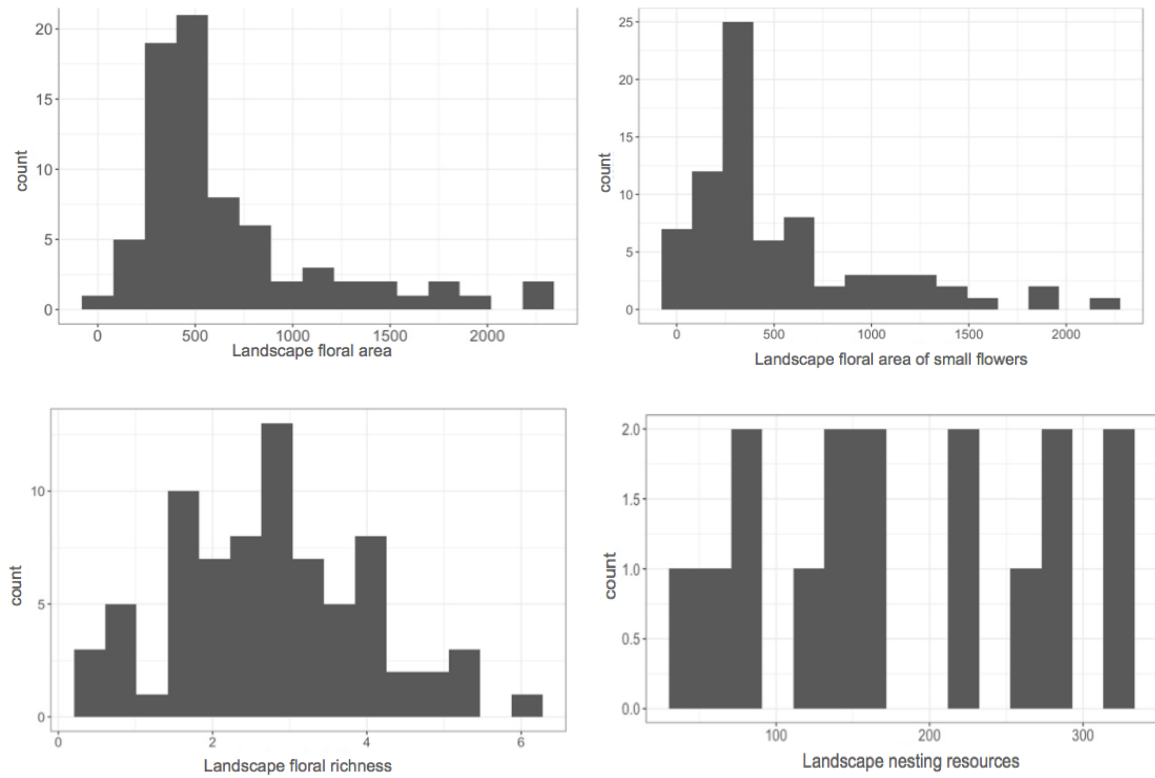


Figure 4.6 Frequency distributions of floral and nesting resources at the landscape level. Histograms showing the variation observed in the floral and nesting resources observed. Floral resource histograms include data from all 6 sampling periods across the 16 sites, whereas the nesting resource histogram uses only one data point per site—since nesting resource measurements were only taken once.

Chapter 5

Conclusion

In response to signals of bee declines (Winfree 2010; Potts et al. 2016) and projected increases in urbanization (Seto et al. 2012), this dissertation explored the links between urbanization, wild bee populations, and their ecosystem services in urban landscapes.

Chapter 2 investigated whether a change in scale could improve pattern-detection of bee responses to urbanization. First, current patterns of bee responses to urbanization were established through a mini-literature review, and second, coarse- and fine-resolution land cover data were compared to test whether the use of fine-resolution revealed new insights. The literature review showed the number of studies examining bee abundance and richness patterns has increased in recent years, and similar to reviews of urban bee response to other anthropogenic land cover changes, studies showed great variation and mostly neutral responses (Roulston and Goodell 2011; Winfree et al. 2011). Studies included in the mini-review utilized a wide range of scales, making comparisons between studies less straight-forward, yet the most common resolution scale used was coarse (30m). In our study, when fine-resolution land cover data was created and compared to coarse-resolution data, the fine-resolution land cover data detected land covers associated with bee resources—such as barren land cover—that coarse-resolution land cover data did not detect. This detection allowed the variation between these landscape features and bee response data begin to emerge, signaling that once enough sites can be analyzed to provide sufficient statistical power, relationships that were otherwise obscured with coarse-resolution data could now be analyzed. This result confirms that if we are to clarify

the sources of variation seen across current studies of urban landscape effects on bees, there is a need to match the scales at which landscapes are quantified to the scales at which bees operate.

Chapter 3 examined urban bee function by testing how increasing urbanization changed the ecosystem service of pollination in urban agriculture. It showed that food production in urban agriculture is impacted by both changes in microclimatic conditions and the presence of pollinators. In a classic urban heat island effect, increasingly urban sites experienced warmer temperatures, which positively affected urban food production quantity and quality. Food production stability, however, was not affected by temperature, and instead increased with the presence of bees. These results suggest that the increasing temperatures predicted with climate change may have positive effects on agriculture in temperate regions. These results also confirm a benefit of preserving pollinators in urban areas, especially given the unpredictability associated with climate change, as pollinators can stabilize potential fluctuations in yield.

Chapter 4 examined urban bee management by testing the effect of small-scale flower patch additions on urban bee populations. It showed that small flower plantings can positively increase species density of pollinators in urban areas, even over short periods of time. In addition, for small bees, adding smaller quantities of flowers had a greater impact than adding larger quantities of flowers. These results show that urban bee management is nuanced, and requires a more nuanced understanding of the details in relationships between bees and their resources. In addition, these results show both that encouraging citizens to plant flowers can be an effective conservation strategy for pollinators in urban areas as well as that spreading smaller plantings of flowers throughout urban areas may be more effective than concentrating all flower resources in one area.

Synthesis

In light of global changes associated with the Anthropocene, the need to design sustainable cities—where human needs are balanced with the maintenance of ecological functions—is ever-growing (Steffen et al. 2015b; Nilon et al. 2017). Steffen et al. (2015) illustrated the remarkable rate of urbanization best when they stated: “On current trajectories there will be more urban areas built during the first three decades of the 21st century than in all of previous history combined (Seto et al. 2012).” Bees are critical to ecological functions—even in cities—and show some signs of decline in highly industrialized regions such as North America and Europe (Winfree 2010; Potts et al. 2016). These declines bolster common assumptions that urbanization has negative consequences for biodiversity (McDonnell and Hahs 2008; Hall et al. 2017).

Yet, this dissertation reinforces the relatively new notion that urban landscapes are not inherently incompatible with bees (Hall et al. 2017). First, through the fine-resolution land cover analysis, I confirm that urban areas can contain both flowering and nesting resources for bees, and that we can track the location of those resources at a landscape scale. Second, I find that urban agriculture can benefit from wild pollinators, as we saw significantly positive impacts on lima bean food production stability across urban agriculture gardens. Finally, I show that small actions—such as planting a few pots of flowers—can positively impact wild bee abundance and species density in urban areas. A recent essay by various urban bee ecology researchers similarly argues that cities may be ideal locations to conserve bees, both for their potential to maintain pollinator diversity and provide ecosystem services, as well as for educational value (Hall et al. 2017).

The breadth of studies presented in this dissertation can be used as a foundation for future work in urban bee ecology. Take the application of the patch-corridor matrix model to bees in urban landscapes, for instance. In the patch-corridor matrix model, assumptions made about a population in a focal resource patch depend on an awareness of the number and sizes of the resource patches nearby. The development and use of fine-resolution land cover presented in this dissertation allows for more accurate detailing of the number and size of bee resource patches throughout the landscape, identifying patches of habitat that have been missed in previous studies. This more accurate detailing should increase the explanatory power of landscape-resource on the distribution of bee species in future urban studies. In addition, the ability to be spatially explicit about locations of bee resource patches in urban areas opens the door to further inquiries about the effects of distance between patches, connectivity, and dispersal ability on urban bee populations—areas that have been less explored in urban bee ecology.

My findings of urbanization effects on urban agriculture also encourage an expansion in the focus of gradient analyses studies. Past studies of urbanization gradients mostly focused on the distribution of organisms across a gradient (McDonnell and Hahs 2008), where a change in the distribution of organisms could suggest an accompanying change in ecosystem function. In my study of how bees and food production change across an urban gradient however, I found no significant effects of urbanization on the distribution of bees across the gradient; yet, regardless, I found that the function of pollination varied significantly across the gradient. This result only emerged by measuring the function of pollination directly—rather than, again, simply looking at the distribution of organisms—and by measuring an additional factor such as temperature. This work shows that future gradient analyses, particularly in urban bee ecology, can produce results with broader implications by incorporating measures beyond levels of urbanity, such as abiotic

factors, land-use legacies, and socio-economic information (Ramalho and Hobbs 2012). To understand how to create more sustainable cities, where crucial ecosystem services such as food production can be maintained, it is crucial to understand how the complex factors of urban areas interact to alter ecosystem functions and services.

Perhaps the largest limitation of this dissertation—and most current urban bee ecology research—is its nearly singular focus on the distribution of flower resources as the primary factor structuring urban bee communities. While this focus is well-founded in ecology—since individual species cannot persist in spaces without their essential resources (Begon et al. 2006)—it is clear that additional factors also impact bee populations.

These additional factors span a wide range of disciplines. In the realm of natural sciences, for example, competition among bee species, interactions with parasites, and the chemical side-effects of pesticides have been shown to affect bees (Goulson et al. 2015; Lindström et al. 2016). In the realm of the social sciences, factors such as local policy, infrastructure, socio-economic factors, people’s perceptions of insects and plants, and decisions about pesticide-use could also affect bee communities (for example, see Iuliano et al. 2017). Social factors have been much less studied yet should be considered just as relevant to urban bee ecology, especially when bees are being studied in highly heterogeneous areas dominated by humans, where human perceptions, behavior, and politics affect every meter of land.

Therefore, I believe future work needs to prioritize an understanding of how these additional factors impact urban bee populations, and then work on integrating these perspectives together. To start, I believe an emerging research priority should be the social and ecological impacts of pesticide-use in urban areas. An increasing amount of research has linked bee declines to pesticide-use in agricultural settings (Goulson et al. 2015; Woodcock et al. 2017), yet

very few studies have addressed the impact of pesticides on bees in urban areas (*but see* Larson et al. 2013). Ecological and sociological bodies of knowledge should be applied to understanding how much cities and individual gardeners apply pesticides to landscaped areas, and what impact this is having on wild bee populations.

Finally, the information gathered by urban bee ecology researchers must be communicated with the practitioners who can apply the information in urban landscapes; this requires increased collaboration between ecologists and professional design practitioners (Hunter and Hunter 2008; Nassauer and Opdam 2008). Urban areas and the processes within them are inherently linked to surrounding ecosystems (Grimm et al. 2008), and working together, we can envision the creation of more vibrant, healthy urban ecosystems that balance human needs and preserve ecosystem functions.

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