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Bees in urban landscapes: An investigation of habitat utilization

By

Victoria Agatha Wojcik

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, & Management

in the

Graduate Division

of the

University of California, Berkeley

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Fall 2009

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ABSTRACT

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Victoria Agatha Wojcik

Doctor of Philosophy in Environmental Science, Policy, & Management

University of California, Berkeley

Professor Joe R. McBride, Chair

Bees are one of the key groups of anthophilies that make use of the floral resources present within urban landscapes. The ecological patterns of bees in cities are under further investigation in this dissertation work in an effort to build knowledge capacity that can be applied to management and conservation.

Seasonal occurrence patterns are common among bees and their floral resources in wildland habitats. To investigate the nature of these phenological interactions in cities, bee visitation to a constructed floral resource base in Berkeley, California was monitored in the first year of garden development. The constructed habitat was used by nearly one-third of the locally known bee species. Bees visiting this urban resource displayed distinct patterns of seasonality paralleling those of wildland bees, with some species exhibiting extended seasons.

Differential bee visitation patterns are common between individual floral resources. The effective monitoring of bee populations requires an understanding of this variability. To investigate the patterns and trends in urban resource usage, the foraging of the community of bees visiting *Tecoma stans* resources in three tropical dry forest cities in Costa Rica was studied. Substantial variability was noted between individual *T. stans* resources in each of the three populations. The observed variability is driven by the quality of the food resource as measured by the number of individual flowers available. Additionally, the regional landscape plays a role in general species occurrence patterns at a resource.

The urban landscape presents a heterogeneous mosaic patchwork of habitat resources. To investigate the influence of this local variability on resource usage, the foraging patterns of bees in tropical and temperate landscapes were examined. In the dry forest of Costa Rica, bee foraging on *T. stans* was studied in the cities of Bagaces, Cañas, and Liberia. In the coastal grassland region of California, bee foraging on California poppy (*Eschscholzia californica*) was studied in the cities of Berkeley, Emeryville, and Oakland. In both regions, resource abundance and spatial distribution were the main drivers of bee visitation in all taxon groups. Land use and uniquely urban landscape variables influenced the occurrence of certain bee taxa.

DEDICATION

To Sean Fine, Maria and Christopher Wojcik, and all of the busy bees out there helping to keep everything as it should be.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ACKNOWLEDGEMENTS

I would like that thank many people for their support, assistance, and guidance along the path to finishing this dissertation work. First and foremost, I would like to thank my guiding professor, Joe McBride, for his support and encouragement. I am lucky to have found such an exceptional advisor. Many sets of hands and eyes helped in collecting, cataloguing, and analyzing the data that resides within this bound copy. Thank you Meaghan Jasterbski and Laura Fine for being willing to assist in the field in Costa Rica. Thank you Steven La, Melisa Lin, and Jessica Dugan for assisting locally in California.

I am very appreciative of the funding and administrative assistance that I received. Thank you to the Margaret C. Walker Foundation for funding that allowed for special training and professional development. Thank you to the Hannah and Frank Schwabacher Foundation for funding that allowed for the field visits to Costa Rica. I am forever grateful to the Head Graduate Advisor, Kate O'Neill, and to the Graduate Affairs Staff in the Department of Environmental Science, Policy, & Management, for helping to sort out issues little and large.

Special appreciation is due to the people that were there when I needed them – especially when I didn't know that I need them. Thank you to Patina Mendez for comments and critiques and coffee breaks. Thank you to Lucy Diekmann for keeping me grounded. Thank you to Lara Roman for helping me to find a place to stay for the last little while.

Thank you to Sean Fine for helping with everything, all of the time.

GENERAL INTRODUCTION

Urban areas are a common landscape feature across the globe. In 2006, a milestone was reached – for the first time more than 50% of the world's population lived in cities (UN FPA 2008). The magnitude of the human population that lives within cities underscores the importance of this landscape type, both in terms of the impact that it has on adjacent ecosystems and the degree to which positive ecological benefits can be achieved through landscape management within a city. The continued study of urban ecosystems has verified that diverse and functional ecological communities exist within the city limits (Thompson et al. 2003; Grimm and Redman 2004; Angold et al. 2006; Alberti 2008). The actively managed ecological elements of urban landscapes, such as urban forests, gardens, and green space, create habitat that is used by humans and non-human animal species alike.

To survive, species require three main elements to be provided by their habitat: food, water, and cover. The features of the urban floral provide a multitude of habitat opportunities for species that either feed on flowers or are associated with floral ecosystems. Floral resources in urban landscapes are diverse and include an assortment of local and exotic species (Thompson et al. 2003; Thompson et al. 2004) that occur at many localities and in layers within the landscape (Rebele 1994). While vegetation occurs in many parts of the total urban green space, the majority resides in gardens that are either privately or publically managed (Smith et al. 2005, Acar et al. 2007; Loram et al. 2007). Collectively, urban gardens account for a significant proportion of the green space that is located within cities (Gaston et al. 2005; Smith et al. 2005). The structure and variability of the urban flora creates an unusually high diversity of habitat types that are subsequently used and inhabited by many different anthophilic species (Smith et al. 2006).

The anthophilic species that are found within urban landscapes are represented by mammals, birds, and arthropods. Organisms are attracted to flowers because of rewards that come in the form of food, scent, substrates, and mating sites (Kevan 2001). Notable among urban anthophiles are the bees. Populations of bees foraging at urban floral resource have been documented globally in metropolitan areas in Europe (Owen 1991; Berezin 1995; Saure 1996), North American (Tommasi et al. 2004; Frankie et al. 2005; Fetridge et al. 2008; Matteson et al. 2008), South American (Zanette et al. 2005; Loyola and Martins 2006; Nemesio and Silveira 2007), Central American (Frankie at al. 2009), and Asia (Sakagami and Fukuda 1973; Hisamatsu and Yamane 2006). The ecologically important roles that bees play in the maintenance of ecosystems services and the current challenges that they have met due to human population growth make their occurrence within cities a phenomenon that requires further investigation.

The sustainability of terrestrial ecosystems relies on the maintenance of reproductive cycles, evolutionary patterns, and ecosystem functions. Over 80% of the botanical diversity that constitutes ecosystems, defines biomes, and structures faunal communities is dependant upon animal vectors for successful reproduction (Kevan and Baker 1983). To complete their life cycle plants must achieve a pollen transfer from the male anther onto the female stigma. In the majority of cases, the pollinators of plant species are bees (Kevan and Phillips 2001). Bees are ideal pollinators because their reproductive cycle is dependant upon the collection of pollen as a food source for their developing larva (Michener 2000). As obligate floral visitors, bees have developed close-knit evolutionary relationships with flowering plants.

Many of the direct and indirect services that humans and all other living beings benefit from are a result of intimate long-standing bee-plant relationships. Two of every three bites of food consumed by humans are the direct results of pollinator activities (Buchmann and Nabhan 1996). Corn, wheat, and rice – the carbohydrate stables of most cultural diets – are wind pollinated, but the food products that provide the necessary and essential nutrients for the human diet require pollinator visitation for fruiting and reproduction. The variety of agricultural species that are pollinated by insects is high and diverse (see Free 1993 and Kevan and Imperatriz-Fonesca 2002).

The influence of pollinators on the daily lives of humans extends to the resources and products that we interact with. Many of the resources and substrates that are used to develop and advance societies are derived from the living components of ecosystems. Hardwood products, fibers, textiles, dyes, scents, plant derived chemical, and pharmaceutical products are all dependant on reproductive lineages of flowering plants (Daily 1997; Costanza et al. 1997). The aesthetic and spiritual components of human life that the activities of pollinators support must also be recognized. Cultural identities and local communities develop from the bounties seen in the adjacent environment. Our daily lives and cultural history is tied to the activities of pollinators.

Bees, and other pollinators alike, face survival challenges from anthropogenic change. A marked decline in species numbers, community abundances, and pollinator function has been experienced globally (NRC 2007). This decline is driven by an increase in human landscape change (Gess and Gess 1993; Cane and Tepedino 2001). Land use intensification in the form of agricultural and urban development diminishes and removes the nesting and foraging habitats of native bees (Kremen et al. 2002). There are regions in the world that have already experienced collapsed crop yields due to pollinator declines (Eardley et al. 2006).

Although the presence of bee communities within cities does not suggest the urban landscapes can compensate for lost wildland habitat, some of the landscape characteristics of cities provide the opportunity for colonization by bees and other pollinators, buffering some of the effects of wildland degradation. The goals of this dissertation work are to address some of the gaps that exist in the knowledge base of urban bee ecology. A literature review is used to identify the current academic and institutional capacity in the discipline of urban bee ecology. Investigations of bee-plant association in tropical and temperate urban landscapes using field observations, field experiments, specimen collections, GIS approaches, and statistical modeling are used to fill these gaps.

Chapter 1 presents a literature review of the available peer-reviewed publications that examine the ecology of bees within and around human dominated landscapes. The goal of this chapter is to identify the capacity of the current knowledge base regarding urban bees and to highlight the gaps that need to be addressed with further research. A total of 54 peer-reviewed works specific to urban bee ecology were identified using key word searches in a combination of electronic scholarly databases and world-wide-web search engines. The studies were sorted according to their date of publication and the year in which the research was conducted to produce a timeline of knowledge development. The selection of works was then examined based on the geographic region of study, the locally defined scale of investigation, and sub discipline examined. To better assess the taxonomic diversity of species and the species associations that have been studied, the taxonomic resolution of each investigation was noted as single species, multi-species, genus-level, guild-level, or community level. Finally, the previous publications were classified as surveys, comparative studies, or experimental/manipulative studies.

Many studies have examined general occurrence patterns and species presence and absence, verifying that bees are indeed residents of urban landscapes, but significant gaps in the ecosystem-level understanding of urban bee biology exist. Patterns of floral usage and preference have been described, but these trends must be quantified and compared within and between populations and regions. Monitoring tools and techniques must be defined for modified landscapes. The discipline of urban bee ecology suffers from many of the same limitations in reliable sample collection and comparability that wildland bee biology does. It is unclear if there are congruent trends in bee ecology between different urban landscapes, and across different biomes. The variability in the patchwork of land use types that makes up the urban landscape must also be examined in more detail to determine if small scale, local factors influence the success of bees in modified landscapes. A comparison between urban landscapes and a comparison of the variability of land uses within the heterogeneous urban landscape are also necessary.

The ability of urban areas to act as conservation sites for many arthropod species has been suggested and investigated. For example, threatened or rare species of beetles, butterflies, and ants have found acceptable habitat within some urban landscapes. The same habitat suitability has been suggested for the conservation of some bees, but there has not been adequate follow-up. A handful of studies examine the conservation potential that may exist in urban landscapes. Before active management steps can be taken with a reasonable degree of success, the significant gaps in knowledge must be filled. The remainder of this dissertation focuses on identifying patterns of floral usage in terms of seasonality and spatiotemporal variability, as well as on examining the drivers of floral visitation within heterogeneous urban landscapes.

In Chapter 2, the seasonal patterns of bees foraging at a constructed urban floral resource base in the city of Berkeley (California, USA) are examined, focusing on parallels between pollen and nectar availability and bee species occurrences through time. The receptiveness of newly constructed habitat to colonization by a target group of organisms is tested. The floral development of the experimental garden was mapped over the preliminary year of planting (2003) and the associated bee visitors to this newly constructed resource were recorded and collected. The occurrence of 32 bee species in association with 24 plant elements (representative of species, hybrids, cultivars, etc.) was documented. Seasonal changes in the composition of the garden fauna were highlighted. Distinct seasonal patterns, that parallel those common to the wildlands, were evident. The potential of vacant land to be transformed into functional habitat for bees with the proper provision of food resources is demonstrated.

Chapter 3 examines the patterns of resource usage exhibited by bees across multiple populations of a single resource species that are distributed within different regional land uses. The variability in bee visitation to individual *Tecoma stans* resources located in the cities of Bagaces, Cañas, and Liberia (Guanacaste, Costa Rica) that are situated within different regional landscapes in the tropical dry forest region is contrasted. The goal of this chapter is to quantify the degree of variability in bee visitation that exists between individual resources of the same floral species and to determine if this variation is linked to either the regional landscape context or the floral resource characteristics. Foraging patterns and community characteristics of bees visiting *T. stans* in three tropical cities are outlined, highlighting trends relevant to resource-based monitoring. Frequency-of-visitation counts were used are assess daily temporal foraging variation, individual resource constancy, and to assess the impacts of resource characteristics (height, number of flowers, and life form) on the abundance and richness of foragers. At least 26 species of bees forage for pollen and nectar on this floral resource, representing a range of size, nesting, and feeding guilds that are characteristic proportion of local native bee community. The hours between 0700h and 1300h exhibit peak visitation, with both taxon richness and visitor abundance. Individual bee groups have structured occurrences within these times that can be categorized as either early morning or full day. Of the resource characteristics studied, only the total number of flowers that an individual *T. stans* possessed has a significant impact on visitor abundance and taxon richness, with resources possessing more flowers also attracting more bees and more bee types. Further differential patterns of inter- and intra-tree variability are present, and are likely driven by variation in the local characteristics of the urban landscape. The regional landscape context is found to influence the presence and absence of certain bee species, while floral abundance is a key driver of resource preference. The findings of this chapter suggest that there is interplay between landscape variables and resource characteristics that requires further investigation.

The specific aim of Chapter 4 is to determine which set of landscape variables or resource characteristics play a dominant role in structuring bee foraging. The community of bees visiting the populations of *T. stans* in the cities of Bagaces, Cañas, and Liberia was once again examined. In addition to the characteristics of the floral resource, landscape variables such as the distance to the wildland-urban interface, the distance to riparian areas, proximity to open space, and the local land use were investigated. In this particular study, the investigation of bee foraging is expanded to the individual taxonomic groups that utilize *T. stans* to determine if there are any species or group specific patterns present. Resource characteristics, specifically the abundance of flowers present, were determined to be more consistently influential in structuring visitor richness patterns than the characteristics of the urban matrix. Individual bee groups display differential responses to the tested variables, with some responding exclusively to resource characteristics and others responding to landscape variables. The size of the city influenced the complexity of the model describing the richness of visitors, with increasing complexity correlating with decreasing city size. With respect to uniquely urban variables, residential land use stood out, correlating positively with increased bee visitation rates.

Chapter 5 examines larger, more developed temperate urban landscapes in the East Bay cities of Berkeley, Emeryville, and Oakland, California; looking more closely at uniquely urban variables, such as residential and commercial land use, and their influence on bee visitation to a common local native herbaceous species, the California poppy, *Eschscholzia californica.* The visitation rates of bees using the same resource in both urban and the adjacent wildland landscapes are also compared. To collect the required data, an early-season survey assessed the visitation rates of bees to patches of California poppies. Floral resource characteristics (size and density), the landscape characteristics (distance to wildland, distance to riparian areas, distance to open space, land use, disturbance), and the regional landscape context were examined for their impact on the visitation rates of eight taxonomic groups of bees that are common visitors to the California poppy. Although the mean observed visitor abundance and taxon richness of bees at urban and wildland patches do not differ significantly, individual taxa show divergent dominance patterns between the two landscapes. Generally, larger bodied species were significantly more abundant at wildland patches, while smaller bodied species were more abundant at urban patches. At the local scale, only the size and the density of the floral resource impacted visitation. Resource-level visitation patterns are found to be consistent with the previous chapter – the size and distribution of the floral resource base is the primary factor that correlates with visitation patterns at the community level and across individual bee groups.

Chapter 6 contextualizes some of the findings of the previous chapters and the findings of other authors and researchers, applying them directly to the promotion of biodiversity within constructed landscapes. Biodiversity is defined, qualified, and quantified. A discussion of the principals of increased ecosystem health and stability through increased biodiversity is followed by an overview of how this goal can be achieved within urban landscapes. The existing tools and institutions available to practitioners, in particular the USGBC LEED certification system, are examined. Case studies are considered on the basis of adherence to industry standards and biodiversity promotion success. Specific attention is paid to the development and success of green roof technologies.

The dissertation concludes by revisiting some of the significant findings and suggests next steps for the field of urban bee ecology and urban pollinator conservation.

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CHAPTER 1 – THE CURRENT STATUS OF URBAN BEE ECOLOGY: A LITERATURE REVIEW

Introduction

With the pervasiveness of urban landscapes across the globe and their rapid growth, the study of the impact that cities have on the environment and the study of the environment within cities have become growing disciplines. Urban ecology is not a novel area of study. Ecosystems within the city have been under investigation either directly or indirectly since the development of cities. Studies have assessed the both the abiotic (e.g., soil and climate) and the biotic (e.g., floral and fauna) elements within the boundaries of cities. Given the magnitude of the impact that human populations and anthropogenic forces have on ecosystems, especially with respect to biodiversity losses due to direct habitat conversion, developing a workable understanding of urban ecosystems is urgent.

The greatest current global losses of biodiversity are due to human impact on the environment. Urban areas represent a significant proportion of the footprint that human beings have on local ecosystems (Murphy 1988). These dense human settlements, however, have also been proven to be sites of diverse and functional ecosystems (Bolund and Hunhammar 1999; Rebele 1994; Arngold et al. 2006). The ecological remnants and the constructed elements within a city provide important urban ecosystem services, including: air quality management; microclimate mediation and regulation; noise reduction; rainwater retention, drainage, and filtration; food provision; recreational, spiritual, and aesthetic value; and, perhaps most notably, habitat for species (Rebele 1994).

A faunal assortment occupies the urban green space. A prominent group within the urban fauna is the anthophilic arthropods – the arthropod species that are associated with flowers (Smith et al. 2006a; Smith et al. 2006b). Arthropods have been able successfully make use of and colonize many urban floral habitats. Common species groups that live off of and use urban floral resources include butterflies, flower flies, spiders, and lady beetles. One of the most recognized and ecologically important groups of flower-visiting arthropods are bees (Hymenoptera: Apoidea).

Bees are essential ecosystem service providers that are in large part responsible for the maintenance of terrestrial diversity and productivity. The associations of bees with flowering plants structure and maintain ecosystems (Kevan 1999; Kevan and Phillips 2001; Costanza et al. 1997) from which humans and other species derive direct and indirect benefits (Daily 1997; Kevan and Wojcik 2007). Massive declines in populations of bees have been noted in recent years, and they are generally driven by land use intensification – the conversion of wildland habitats into agricultural and urban landscapes (NAPPC 2006; Kremen et al. 2007; Winfree et al. 2007; Winfree et al. 2009). Declines in the abundance and diversity of bees are paralleled by declines in their pollination services. Continued and increased declines in pollination are detrimental and can result in the collapse of ecosystems – and societies.

Interestingly, urban landscapes have been shown to be acceptable and appropriate habitats for some species of bees. Urban species are often considered broad generalists and therefore not representative of keystone biodiversity; urban bees counter this trend. Rare, locally endemic, and highly specialized bee species are present as part of the urban bee fauna (Frankie et al. 2005; Winfree et al. 2007; Wojcik et al. 2008; Frankie et al. 2009b). In fact, urban bee faunas in many cities appear to be intact representations of wildland faunas. Not all species find homes within urban landscapes, but many bees do, and many of these species are ecologically important.

A subset of the estimated 24,000 bee species that occur globally (Michener 2000) are managed and integrated into commercial agricultural practices. Many managed species have been recorded in urban landscapes. Social species in particular are easily managed due to their colonial biology and general feeding habits. The same characteristics make them well suited to completing their life cycles in variable urban habitats. Honeybees and bumblebees are common urban species that have important pollination roles in agriculture, but have suffered recently from diseases that are thought by some to be associated with their management. Their urban counterparts could sever as important genetic stock for improving species vigor. Many urban beekeepers retained healthy colonies during the recent decline of managed honeybees. Similarly, important managed solitary species are also present in urban landscapes, including the Blue Orchard bee (*Osmia liginaria*), the Alfalfa Leaf-Cutter bee (*Megachile rotundata*), and species of Alkaline bees (*Andrena* spp.). Blue Orchard Bees are important pollinators of stone fruit crops, such as cherries, peaches, plums, prunes, and apricots. Alfalfa Leaf-Cutters and Alkaline bees are important pollinators of animal feeds.

The diversity and importance of the community of bees found within cities presents an opportunity for conservation and management. The conservation value of urban landscape for some arthropod species has already bee suggested. Species that are rare, important, or threatened have found refugia within anthropogenic landscapes (Watts and Larivere 2004; Pinherio et al. 2006), and many of these species, such as bees, play important ecological roles. The management of ecological systems however, requires an intimate knowledge of ecosystem level function and species-specific level biology.

As a nascent discipline, urban bee ecology must first build a knowledge capacity that can then be applied to conservation and management. The goal of this chapter is to identify the capacity of the current knowledge base on urban bees and to highlight the gaps that need to be addressed with further research. More specifically, the currently available peer-reviewed literature is examined to determine:

1) The number of references that exist in the literature;
2) The timeline of knowledge development, and in particular, if a spike in academic interest can be identified;
3) The geographic areas that have been examined, both with respect to the global region in which the study takes place and the locally defined scale of investigation (sub-city, single-city, multi-city, region, etc.);
4) A classification of the currently available literature as either sample/survey oriented, comparative, or experimental/manipulative;
5) The sub-disciplines of urban bee biology that have been examined;
6) The individual bee taxa or the taxon groups (i.e., genera, guilds, or the entire community) that have being studied.

Materials and Methods

A key word literature search was conducted using a combination of electronic scholarly databases and world-wide-web search engines. The key words used were any combination of: bee, bees, Hymenoptera, and Apoidea in conjunction with either urban, suburban, city, metropolitan, anthropogenic, landscape change, human dominated, and landscape. The reference lists cited in each paper where also searched for further relevant publications that were not acquired in the primary search. The literature search was conducted by four individuals at multiple time intervals (November – December 2008, February – March 2009, July 2009, and September – October 2009). References not available in English but available in French, Spanish, Portuguese, German, and Polish were retained because members of the research team and their associates had proficiency in these languages. Only references that were explicitly focused on the ecology of bees within and around urban landscapes were retained for further analysis.

The studies were sorted according to their date of publication and the year in which the research was conducted to produce a timeline of knowledge development. The selection of works was examined based on the geographic region of study (continent and country) and the locally defined scale of investigation (sub-city, single-city, multi-city, region, etc.). To better assess the taxonomic diversity of species and species associations that has been studied, the taxonomic resolution of each investigation was noted as single species, multi-species, genus-level, guild-level, or community level. The overall sub-discipline for each study (i.e., behavior, taxonomy, conservation, pollination, etc.) was also noted from an analysis of the key words listed by the authors. Finally, the investigations were classified as surveys, comparative studies, or experimental/manipulative studies.

Results

A total of 54 studies were identified that focused specifically on the biology of bees within, or adjacent to, urban landscapes. The publication timeline extends from 1929 through to 2009. There is a current rapid increase in both research and publication within the discipline of urban bee biology (Figure 1.1 and Tables 1.1 and 1.2). From the first identified record of bee biology within an urban context (Robertson 1929) there is a slow accumulation of studies with a decided increase beginning in the early 1970s. In the mid-1990s approximately one new publication per year. Starting in the early 2000, the number of published studies increases to about 3 new publications per year. Shortly after the year 2000 there is a clear rise in academic interest. The year 2006 signifies a significant point in urban bee ecology, with 10 publications noted. Following this peak, there is a steady flow of published works that occurs annually.

The majority of academic research concerning bees within urban landscapes comes from North America and Europe. Nearly 35% (n=19) of the publications recorded work that was conducted in North America (Figure 1.2 and Table 1.1). With the exception of 2 records (1 from Canada and 1 from Mexico), all of the studies are from the United States. Europe is also well studied, accounting for approximately 30% (n=16) of all papers. In Europe, the studies are distributed across more countries and ecoregions, however a dominant portion (n=6) are from the United Kingdom. South America is also comparatively well studied, accounting for 24% of the recorded papers (n=13). Asia and Central America are less studied, accounting for 7% (n=7) and 2% (n=1) of all studies, respectively. Globally, these particular regions are the sites of the greatest population increases and the most rapid urban growth.

The vast majority of studies examine single cities (91%, n=49). A large portion of these studies look at the city's periphery (n=25) or examine smaller scale land use within the city (n=19) such as open space, gardens, suburban landscapes, parks, etc. (Figure 1.3). The target land use of city-level studies is most often the available garden habitat within the total urban landscape. Only 4 studies considered multiple cities (Dresitadt et al. 1990; Porrini et al. 2003; Frankie et al. 2005; Frankie et al. 2009b), and only 1 was a meta-analysis that attempted to integrate information across multiple landscapes (Cane 2005).

A diversity of study focuses existed (Table 1.2) that ranged from accounts of taxonomic diversity and basic biodiversity surveys to pollination experiments and population genetic studies. When these publications are categorized as descriptive, comparative, or experimental/manipulative; more than half of the studies are descriptive of the local bee fauna. Many of these studies compare either multiple sites within the urban landscape or compare samples through time, providing a glimpse of species presence/absence or turn over. Only 5 of the studies are experimental or manipulative.

The specific discipline that dominates the urban bee literature is the taxonomic and ecological account of species at a locality. Studies provide species list for the cities of Albany, Berkeley, La Cañada Flintridge, Sacramento, San Luis Obispo, Santa Barbara, Santa Cruz, and Ukiah, CA, USA (Frankie et al. 2002; Frankie et al. 2005; Frankie et al. 2009b); Carville, IL, USA (Robertson 1929; Marlin and LaBerge 2001); Miami, FL, USA (Graenicher 1930); New York City, NY, USA (Fetridge et al. 2008; Matteson et al. 2008); Vancouver, BC, Canada (Tommasi et al. 2004); Hokkaido (Sakagami and Fukuda 1973) and Ibaraki (Hisamatsu and Yamane 2006), Japan; Bogota, Columbia (Nates-Parra et al. 2006); Belo Horizonte (Zanette et al. 2005) and Curitiba (Taura and Laroca 2001), Brazil; Berlin, Germany (Saure 1996); Liechester (Owen 1991) and Sheffield (Smith et al. 2006a; Smith et al. 2006b), UK; Warsaw (Banaszak 1982) and Turin (Pawlikowski and Pokorniecka 1990), Poland; and Moscow, Russia (Berezin 1995). Examinations of bee behavior (i.e., foraging and plant-insect interactions) within urban landscapes are also common. More specialized areas of study are rare. Only 3 studies have focused on pollination, the essential ecological service that bees provide (Liu and Koptur 2003; Silva et al. 2007; Carre et al. 2009). Studies focusing on conservation within the urban landscape area also limited, with only 3 records (McFrederick and LeBuhn 2006; Osborne et al. 2007; Fetridge et al. 2008). The most infrequent accounts are explicit studies of nesting (Barthell et al. 1998; Goulson 1999) and population genetics (Lopez-Uribe and Del Lama 2007).

The community is the predominant taxonomic level in the literature accounting for 57% of all studies (Figure 1.4). Most studies document the total number of species that constitute the local bee fauna. Individual nesting, size, and ecological guilds have also been focused on. Higher-resolution taxonomic studies are infrequent in the literature. About 24% of the examined studies focus on smaller taxonomic groupings such as guilds, families, or genera. Only 2 genera have been examined in more detail: *Bombus* (n=6) and *Euglossa* (n=3). Single species studies make up the smallest proportion of the overall taxonomic focus (19%). The biology of only 4 species has been studied in more detail within the urban landscape: European honeybees, *Apis mellifera*; African honeybees, *Apis mellifera scutellata*; *Habropoda depressa*; *and Melipona quadrifasciata.*

The vast majority of studies are limited in their temporal scale, with less than 2 years of investigation being recorded. Nine studies account investigations that range from 3 to 10 years. Only 3 studies account ecological changes that have occurred over more than a decade: Owen's 15 year study of an English urban garden (Owen 1991); Frankie et al.'s study of urbanization in Costa Rica after 25 years (Frankie et al. 2009a), and Marlin and LaBerge's 75 year re-sampling of the bee fauna of Carville Illinois (Marlin and LaBerge 2001).

Discussion

Studies have examined general occurrence patterns and species presence and absence, verifying that bees are indeed residents of urban landscapes, yet significant gaps exist in the holistic understanding of urban bee ecology. The overall mood of the works suggests that management and conservation potential exists within anthropogenic landscapes, but there is much to be done if these goals are to be achieved with a reasonable chance of success. An examination of the timeline and pace of publication in urban bee ecology indicates that it is a relatively new and growing discipline. There are areas of the globe are that are understudied, in particular Asia and Central America. Single species studies are also limited, which in turn limits the ability of conservation and management approaches that require an understanding of the autecology of a species. The bulk of the urban bee studies focus on individual cities, describing local trends in detail, but miss large-scale patterns. Larger scope regional studies, or multi-city comparisons are required to verify if the trends that are seen in a region are consistent, and such studies are less numerous. These aforementioned trends in time-span, landscape coverage, ecological knowledge, and applied research efforts are discussed in more detail.

The recent spike in interest

Prior to 2000 there is a slow pace of publication in urban bee ecology. One new publication approximately every two years is recorded during this period. Earlier still, that is prior to the 1970s, only three records provide published surveys of the bee species within cities. After 2000 this trend changes significantly, with more than two new publications per year occurring between 2000 and 2005. From 2006 to present, nearly five publications per year appear relating to urban bee ecology. The spike in academic interest toward the study of urban pollinators, and urban bees in particular, likely parallels the concurrent academic interest in pollinator conservation spurred by the San Paulo Declaration on pollinator study, management, and protection. In 1999, the Convention on Biology Diversity met in San Paulo, Brazil and convened an international working group for the protection and conservation of pollinating species and the ecological services that they provide – the International Pollinators Initiative. The result of this meeting was the creation of San Paulo Declaration on pollinator conservation (IPI 1999). Six important initiatives are highlighted in the framework of the declaration: 1 – Reducing the taxonomic impediments to adequate pollinator study and conservation; 2 – Monitoring the declines in pollinator populations; 3 – Identifying the local and global causes of pollinator decline; 4 – Quantifying the economic value that the activities of pollinators contribute to agriculture; 5 – The conservation of pollinator diversity; and 6 – Understanding the sustainable use of pollinators and their services (see IPI 1999 for a more detailed explanations of each initiative item). Although no explicit mention is made of urbanization or land use intensification in this document, and the focus is primarily agricultural, the urgency of the issues relating to pollinator and bee decline become clear. This climate of concern for bees combined with the realization of the impact that urban landscapes have on local ecosystems likely worked synergistically to focus attention on bees within and around urban landscapes.

The geographic scope of urban bee ecology

The most rapidly developing regions of the world are the least studied. The Asian continent is particularly understudied. Only Japan and Russia have had their urban bee fauna accounted for. Other Asian countries that are less economically developed and rapidly urbanizing do not have their urban bee faunas documented in the literature. Only one study exists from Central America, and this study suggests that there are significant declines in both the abundance and richness of bees associated with increased urbanization and habitat conversion (Frankie et al. 2009). The urban growth both in Central American and in Asia outpaces that of any other region in the world (UN FPA 2008). Published accounts from Africa and Australia were all together lacking. Both of these regions have diverse and endemic bee fauna that occur within areas of human settlement. In Australia, the entire Family Stenotrintidea, which is comprised of two genera and 21 known species, is endemic. These regions are in urgent needs of study.

Bee plant-associations

Patterns of floral usage and preference within cities have been described, but these trends must be quantified and compared within and between populations and regions. Recommendations for the conservation and management of bees have outlined the need to identify so-called 'magnet' resources, floral species that attract a broad range of bees across multiple landscapes that can be used for comparative assessments and studies (see Eardley et al. 2006 for more detail). Local-level work in Berkeley and Albany California has outlined a subset of plant families that are generally and broadly attractive to the local bee species, including plants in the families Asteraceae, Lamiaceae, Polygonaceae, Rosaceae, and Scrophulariaceae (Frankie et al. 2005). Frankie et al. (2009b) later compared the bee fauna of 11 California cities from different ecological zones. Their findings suggest that some bee-plant interactions are conserved across landscape types but that there is also variability between sites that are adjacent to one another. Floral resources that consistently attracted diverse assemblages of bees across the sampled cities included three plant elements (species, cultivars, varieties, hybrids, etc.) in the family Asteraceae (*Gaillardia* x *grandiflora* cultivars, *Helianthus annuus*, and *Solidago califronica*) and five in the family Lamaiceae (*Echium candicans*, *Lavandula* spp. and cultivars, *Perovskia atriplicifolia*, *Salvia* 'Indigo Spires', and *Vitex agnus-castus*). Further regional-scale comparisons are necessary to better define these trends.

Temporal variability is common to bees and occurs at daily, seasonal, and annual scales. Adult bees may feed on nectar from a wide range of plant species, but some exhibit mesolectic (Cane and Spies, 2006) or oligolectic patterns of pollen foraging (Malyshev 1936; Linsley 1958; Michener 2000). Furthermore, the individual lifespan of an adult bee is usually limited to a few weeks during specific seasons (Williams et al. 2001) underscoring the importance of the seasonal timing of appropriate floral blooms with adult flight and foraging patterns to maintain and manage communities of bees. The natural phenologies of plants are known to be modified in urban landscape either due to landscape management techniques or urban heat island effects (Lu et al.

2006; Chung et al. 2009). This might in turn alter the patterns of daily and annual occurrence of bees. The nature of these relationships is not well understood in the urban landscape.

The autecology of urban bees

A subset of the examined studies address bee-plant interactions within urban landscapes at either the guild or the community level. Some of these studies have focused on the bee visitors to specific plants (Lui and Koptur 2003; Cane et al. 2006; Cheptou et al. 2006; Silva et al. 2007), and others have outlined the floral preferences of bee groups (Robertson 1929; Frankie et al. 2005; Hisamatsu and Yamane 2006; Frankie et al 2009b). Only four bee species have been studied in detail. Two of these species, European honeybees (*Apis mellifera*) and African honeybees (*Apis mellifera scutellata*), are non-native generalists. They are essential pollinators in commercial agricultural systems, but they are not members of the local native fauna that is suffering declines due to land conversion (see Eardley et al. 2006 and NRC 2007). Only two local native species have studied in more detail: the social *Melipona quadrifasciata* and the solitary *Habropoda depressa*.

Central and South American bee faunas are generally characterized by a higher proportion of eusocial species compared with temperate assemblages. The abundance of eusoical species in tropical landscapes also makes their dominance in tropical urban systems of interest. The floral preferences of *Melipona quadrifasciata* foraging in urban forest fragments in Belo Horizonte, Minas Gerias, Brazil have been documented by Antonini et al. (2006). *M. quadrifasciata* is known to visit 22 of the 103 flowering species that have been identified within the city. The feeding patterns of *M. quadrifasciata* individuals were identified as oligoletic, with the majority of visits recorded at species in the families Myrtaceae, Asteraceae, and Convolvulaceae. The foraging patterns of *M. quadrifasciata* in the Belo Horizonte state were similar to those found in the Sao Paulo State, but dissimilar to those in the Bahia State (Antonini et al. 2006). The variability of habitat usage by this species between landscapes verifies the need for further investigation of urban landscapes across multiple ecological regions.

The vast majority of the estimated 24,000 bee species are solitary (see Michener 2000). Within the urban landscapes, especially in temperate regions, solitary species dominate. For example, 79% of the urban bee species recorded by Frankie et al. 2005 in the Berkeley/Albany region of California were solitary in their nesting lifestyles. Yet, only one solitary species has been investigated in detail within the urban landscape. Barthell et al. (1998) examined the nesting of *Habropoda depressa* within the city limits of Berkeley, California. This species has been recorded to nest in hillsides on the University of California, Berkeley campus, and within the greater Berkeley, California area. Other studies within the Berkeley region have also documented *H. depressa* as a common visitor to urban floral (Frankie et al. 2005; Wojcik et al. 2008). Generally, nesting and the substrates that are conducive to this process within urban landscapes are poorly understood, specifically at the species level. This is also true of wildland bee ecology. It is clear, however, that a lack of appropriate nesting sites within a region limits the success of local bee species.

Pollination Services in Urban Landscapes

The act of pollination is the trademark of bees and the reason why their study and conservation has been deemed so urgent. Yet, few authors have investigated how pollination systems are manifested within the city limits. Two studies have examined the differences between patterns of bee visitation and pollination between urban and other (wildland and/or agricultural) landscapes. Lui and Koptur (2003) focused on the structure of the pollinator community and the resultant seed set in populations of the native herb *Chamaecrista keyensis* Pennall in the Florida Keys. The urban edge was shown to have an effect on the breeding system of *C. keyensis*, which is pollinated by larger bodied bees, namely *Xylocopa micans* and *Melissodes* spp. The composition of bee foragers differed between the two landscapes with an increase in the proportion of *X. micans* and a decrease in *Melissodes* spp. at the urban edge compared to the wildland. Flowers growing near to the urban edge also displayed reduced seed set. Lui and Koptur (2003) suggested that insecticide spraying under the local mosquito abatement program near urban residential areas is reducing the numbers of effective pollinators, resulting in lower seed production in *C. keyensis*.

Recently, Carre et al. (2009) examined the patterns and effectiveness of bees pollinating selected crop species adjacent to different landscapes, including wildlands, continuous agricultural, and urban areas. The presence of urban or semi-urban land use significantly affected the composition of pollinating bees at the selected crops. Their findings also suggest that concurrent patterns of community composition exist at crops located within large tracts of agricultural land and those located adjacent to urban land use. The bees that constituted the near-urban and near-agricultural communities were also more resistant to large-scale landscape change when compared to the wildland community.

Only one study has examined pollination ecology within the urban landscape. Silva et al. (2007) outlined and compared the communities of bees visiting *Tecoma stans* trees in three cities in Brazil, focusing also on seed set and fruiting in relation to bee visitation. *T. stans* was visited by 48 species across the three landscapes, and is considered a significant food source for the urban bees in those regions. Of the 48 visitors, only two were effective pollinators: *Centris tarsala* Smith and *Exomalopsis fulvofasciala* Smith. The comparative study showed that individual *T. stans* that received more bee visitation has a corresponding increase in seed set and greater fruit development. This study of urban pollinator dynamics corroborates many of the findings of wildland pollinator studies that indicated a significant correlation between seed set and increased pollinator visitation (see Kremen et al. 2004). *T. stans*, however, is not an agriculturally important species and does not provide fruit for human consumption. Many of the crops that are commonly grown in home gardens and urban community gardens are dependant upon high visitation rates by effective pollinators to set fruit, such as tomato, eggplant, zucchini, melon, and other squash species. Orchard crops, such as cherries, figs, oranges, peaches, pears, and apricots, are also pollinator dependant. The study of urban agricultural systems and the patterns and trends in pollinator effectiveness have not been presented in the literature. Similarly, no valuation of the pollination services that bees provide within urban landscapes has been made.

Finer-scale investigations of the urban systems

A comparison between different urban landscapes and within the heterogeneous urban landscape is also necessary. Studies that examine more than one land use type are limited. Urban landscapes do share many similar ecological characteristics in terms of land use patterns and disturbance regimes, but they are also situated within different ecological regions. The greater landscape context influences species occurrence patterns in wildland systems and will affect urban faunas in a similar manner. It is unclear if there are congruent trends in bee ecology between different urban landscapes. The variability in the patchwork of land use types that makes up the urban landscape must also be examined in more detail to determine if small scale, local factors influence the success of bees in modified landscapes. Small bodied species such as bee response to scale dependant factors. To gain an appropriate understanding of their ecology within any landscape requires local scale investigations.

Conservation and Management

Monitoring tools and techniques must be defined for modified landscapes. The discipline of urban bee ecology suffers from many of the same limitations in reliable sample collection and comparison that wildland bee biology does. The spatiotemporal scope of most studies is local and short. Insect populations, however, are known to have significant variability across microhabitats and over time. Wildland studies of bees visiting the same localities over time have noted significant variability and community turn over in five years of study (Cane et al. 2006). The species composition of bee guilds has also been noted to change and fluctuate over time. The degree to which bee populations fluctuate naturally is presumed to be high, and therefore recommendations of extended and detailed sampling in both urban and wildland systems are necessary. The most recent report from the NRC (2007) on the status of pollinators and previous reports by the North American Pollinator Protection Campaign (NAPPC, see www.nappc.org) recommend an increase in long-term studies, in particular studies that span more than five years, and ideally more than eight years, to more adequately assess bee population. Again, only seven of the reviewed studies have conducted examinations for periods of time longer than five years.

Many of the findings of the papers contained in this literature review suggest a positive out-look for urban bee faunas and a potential for conservation. However, only a handful of studies actually examine the conservation potential that may exist in urban landscapes. For successful management and conservation the essential habitat requirements and ecosystem interactions of a species must be acquired. For bees, especially those living in cities, much of this information is lacking. Active management steps can only be taken with a reasonable degree of success when the significant gaps in knowledge are filled. The following chapters will address some of these significant gaps.

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Figures, Tables, and Appendices

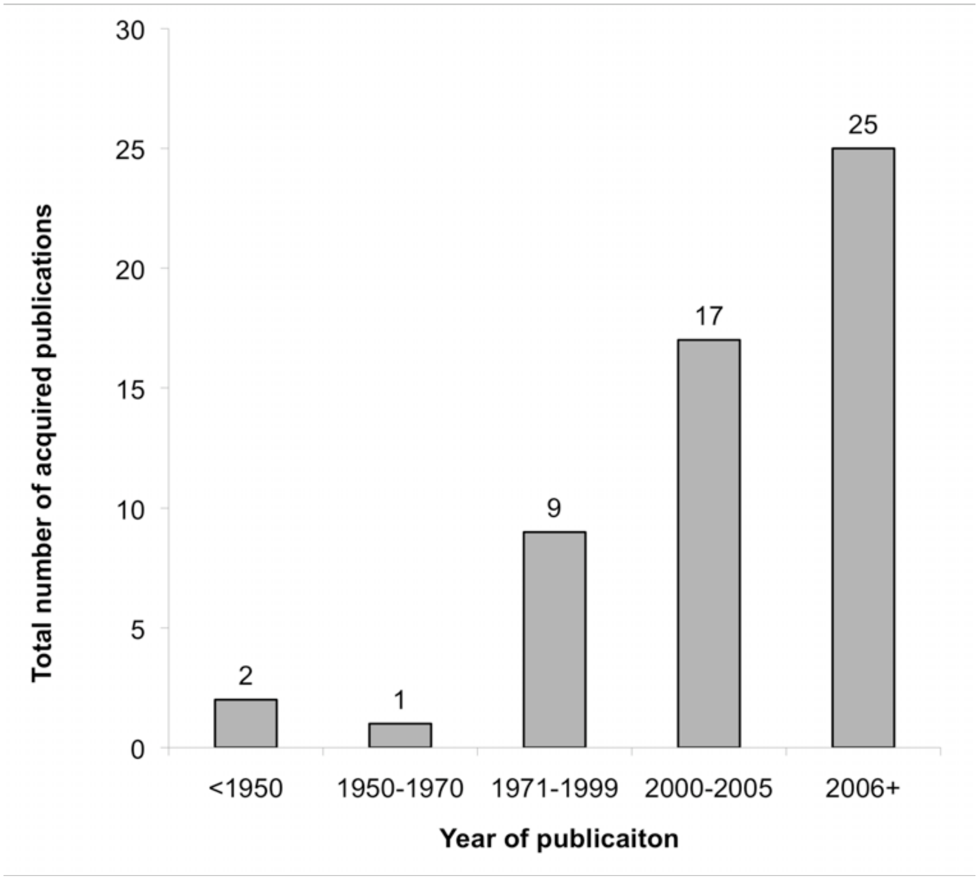

Figure 1.1: A graph showing the number of publications relating to urban bee ecology as a function of time. Publications range in date from 1929 to 2009.

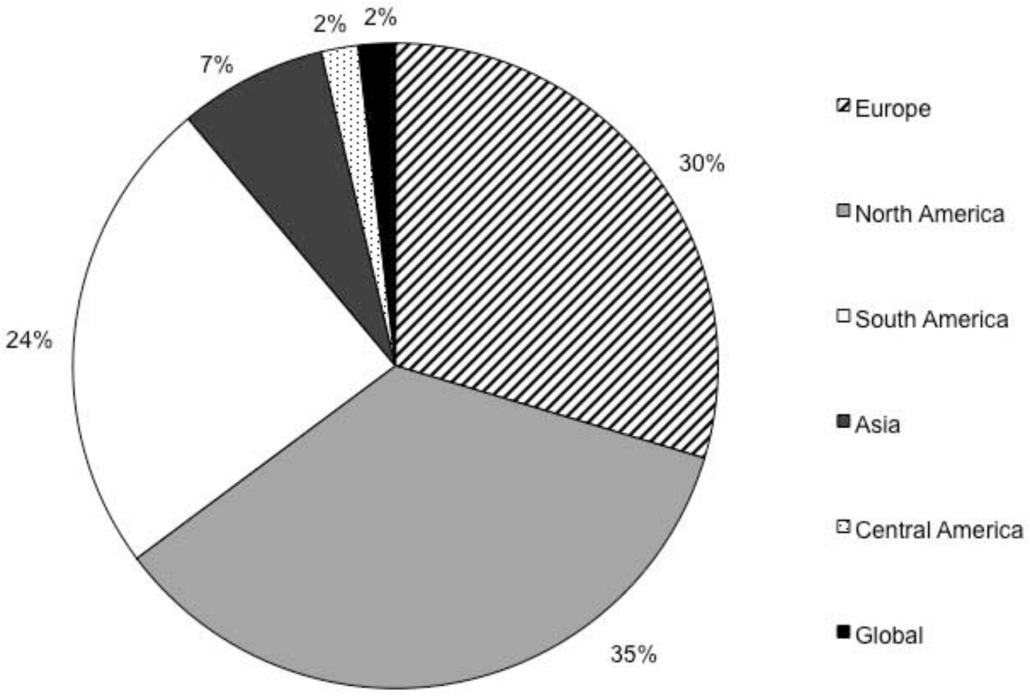

Figure 1.2: The global distribution of urban bee studies.

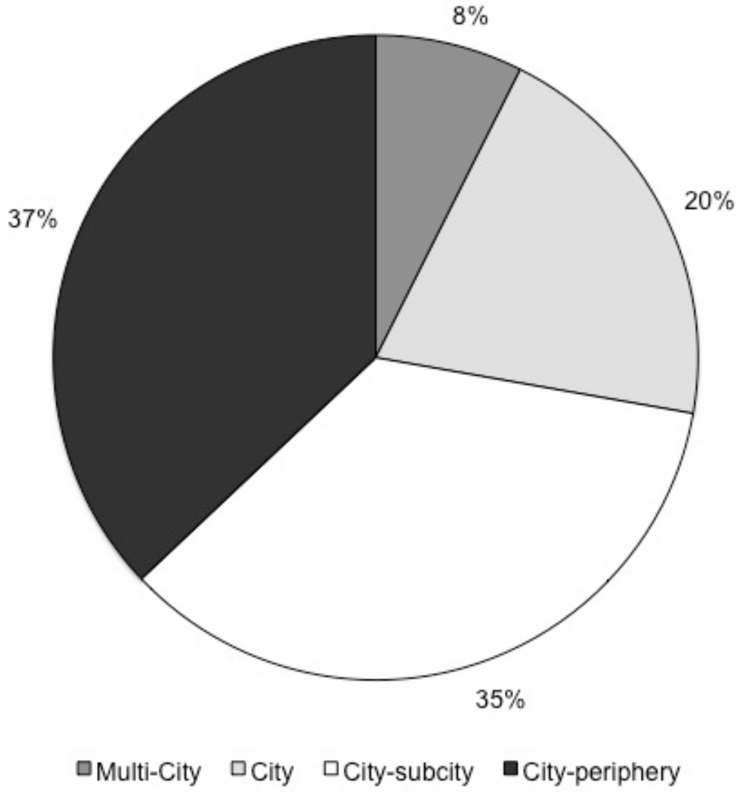

Figure 1.3: The local scale and scope of investigation represented as the proportion of studies that study the city, compare the city with the periphery, examine sub-city elements, or study and/or compare multiple cities.

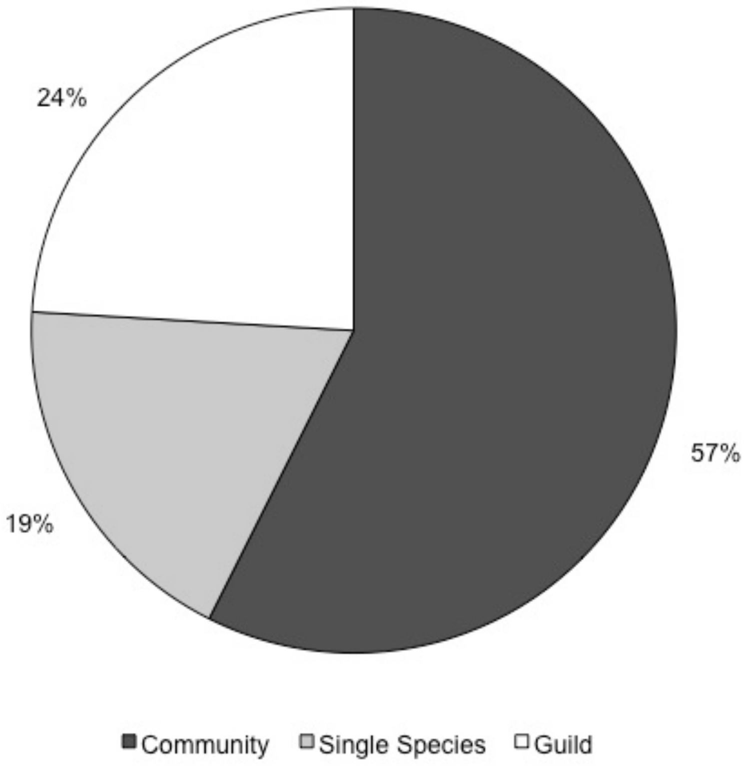

Figure 1.4: The taxonomic level of investigation present in the current list of studies of urban bee ecology. Studies are sorted as single species, guild-level, or community level.

Table 1.1: A summary tables of the catalogued urban bee ecology literature, indicating: authors, publication date, country of research, region of research (EU=Europe, NA=North America, CA=Central American, SA=South American, ASIA=Continental Asia, including Russia and Japan, and GLOBE=a multi-regional scope), and the scale of research.

Authors	Pub. Date	Country	Region	Scale
Ahrne et al.	2009	Sweden	EU	City-periphery
Antonini et al.	2006	Brazil	SA	City/sub-city
Banaszak, J	1982	Poland	EU	City
Barthell et al.	1998	USA	NA	City/sub-city
Baum et al.	2008	USA	NA	City
Berezin	1995	Russia	ASIA	City-periphery
Bhattacharya et al.	2003	USA	NA	City-periphery
Cane	2005	meta	GLB	Global
Cane et al.	2006	USA	NA	City-periphery
Carre et al.	2009	Poland, France, Germany, Sweden	EU	City-periphery
Cheptou et al.	2006	France	EU	City
Diniz et al.	1994	Brazil	SA	City
Dresitadt et al.	1990	USA	NA	Multi-city
Eremeeva and Suchchev	2005	Russia	ASIA	City
Fetridge et al.	2008	USA	NA	City/sub-city
Frankie et al.	2009a	Costa Rica	CA	City/sub-city
Frankie et al.	2002	USA	NA	Multi-city
Frankie et al.	2005	USA	NA	Multi-city
Frankie et al.	2009b	USA	NA	Multi-city
Gaston et al.	2005	UK	EU	City/sub-city
Goulson	1999	UK	EU	City/sub-city
Graenicher	1930	USA	NA	City-periphery
Hisamatsu and Yamane	2006	Japan	ASIA	City/sub-city

Table 1.1, continued:

Authors	Pub. Date	Country	Region	Scale
Jha and Vandermeer	2009	Mexico	NA	City
Kartochwil and Klatt	1989	Germany	EU	City/sub-city
Liu and Koptur	2003	USA	NA	City
Lopez-Uribe and Del Lama	2007	Brazil	SA	City-periphery
Lopez-Uribe et al.	2008	Brazil	SA	City-periphery
Loyola and Martins	2006	Brazil	SA	City-periphery
Loyola and Martins	2009	Brazil	SA	City-periphery
Marlin and LaBerge	2001	USA	NA	City-periphery
Matteson et al.	2008	USA	NA	City/sub-city
McFrederick and LeBuhn	2006	USA	NA	City/sub-city
McIntyer and Hostetler	2001	USA	NA	City
Montenegro et al.	1989	Chile	SA	City-periphery
Nates-Parra et al.	2006a	Colombia	SA	City/sub-city
Nates-Parra et al.	2006b	Colombia	SA	City/sub-city
Nemesio and Silveira	2007	Brazil	SA	City-periphery
Osborne et al.	2007	UK	EU	City-periphery
Owen	1991	UK	EU	City/sub-city
Pawlikowski and Pokorniecka	1990	Poland	EU	City-periphery
Porrini et al.	2003	Italy, Spain, Ukraine	EU	Multi-city
Robertson	1929	USA	NA	City-periphery
Romam	2005	Poland	EU	City-periphery
Sakagami and Fukuda	1973	Japan	ASIA	City/sub-city
Saure	1996	Germany	EU	City-periphery
Silva et al.	2007	Brazil	SA	City/sub-city
Smith et al.	2006a	UK	EU	City/sub-city

Table 1.1, continued:

Authors	Pub. Date	Country	Region	Scale
Smith et al.	2006b	UK	EU	City/sub-city
Steffan-Dewenter and Kuhn	2003	Germany	EU	City-periphery
Steffan-Dewenter et al.	2002	Germany	EU	City-periphery
Taura and Laroca	2001	Brazil	SA	City
Tommasi et al.	2004	Canada	NA	City
Zanette et al.	2005	Brazil	SA	City/sub-city

Table 1.2: A summary tables of the catalogued urban bee ecology literature, indicating: authors, publication date, the study focus, study type (D=descriptive, C=Comparative, E=Experimental/Manipulative), the taxon level examined (SS=single species, AHB=African honeybee, EHB=European honeybee), and the duration of the study.

Authors	**Pub. Date**	**Study Focus**	**Type of Study**	**Taxon Level**	**Length of Study**
Ahrne et al.	2009	Ecology	C	Genus: *Bombus*	1 year
Antonini et al.	2006	Behavior	C	SS: *Melipona quadrifasciata*	18 months
Banaszak, J	1982	Survey	C/D	Community	2 years
Barthell et al.	1998	Nesting	C/D	SS: *Habropoda depressa*	2 years
Baum et al.	2008	Ecology	C	SS: AHB	8 years
Berezin	1995	Ecology	C	Genus: *Bombus*	11 years
Bhattacharya et al.	2003	Behavior	C/E	Genus: *Bombus*	3 years
Cane	2005	Meta analysis	C	Community	n/a
Cane et al.	2006	Behavior	C	Guild: Dessert bees	2 years
Carre et al.	2009	Pollination	C	Community	1 year
Cheptou et al.	2006	Behavior	D	Community	1 year
Diniz et al.	1994	Pest control	D	SS: AHB	1 year
Dresitadt et al.	1990	Survey	D	Community	n/a
Eremeeva and Suchchev	2005	Ecology	C	Genus: *Bombus*	9 years
Fetridge et al.	2008	Conservation	C	Community	3 years
Frankie et al.	2009a	Re-survey	D/C	Community	25 years
Frankie et al.	2002	Behavior	D	Community	4 years
Frankie et al.	2005	Behavior/ Ecology	D	Community	5 years
Frankie et al.	2009b	Survey	D/C	Community	2 years
Gaston et al.	2005	Survey	D/C	Community	5 months
Goulson	1999	Nesting	E	SS: *Bombus terrestrius*	1 month
Graenicher	1930	Survey	D	Community	12 years
Hisamatsu and Yamane	2006	Floral usage	D	Community	8 months

Table 1.2, continued:

Authors	**Pub. Date**	**Study Focus**	**Type of Study**	**Taxon Level**	**Length of Study**
Jha and Vandermeer	2009	Behavior	C	Community	50 days
Kartochwil and Klatt	1989	Community structure	D	Community	5 months
Liu and Koptur	2003	Pollination/ Plant breeding	C/E	Community	2 years
Lopez-Uribe and Del Lama	2007	Genetic	D	Genus: Euglossa	11 months
Lopez-Uribe et al.	2008	Survey	D	Genus: Euglossa	10 months
Loyola and Martins	2006	Survey	D	Community	10 months
Loyola and Martins	2009	Survey	D	Guild: cavity nesters	10 months
Marlin and LaBerge	2001	Re-survey	C	Community	75 years
Matteson et al.	2008	Survey	D	Community	2 years
McFrederick and LeBuhn	2006	Conservation	C	Genus: *Bombus*	2 years
McIntyer and Hostetler	2001	Ecology/ Survey	C	Community	2 years
Montenegro et al.	1989	Ecology/ Foraging	C/D	SS: AHB	2 years
Nates-Parra et al.	2006a	Ecology/ Survey	D	Community	10 months
Nates-Parra et al.	2006b	Ecology/ Survey	D/C	Guild: Stingless bees	1 year
Nemesio and Silveira	2007	Survey	D	Genus: Euglossa	1 year
Osborne et al.	2007	Conservation/ Management	D	Genus: *Bombus*	15 months
Owen	1991	Survey	D	Community	15 years
Pawlikowski and Pokorniecka	1990	Ecology	C	Genus: *Bombus*	2 years
Porrini et al.	2003	Pollution assessment	C	SS: EHB	n/a
Robertson	1929	Survey	D	Community	2 years
Romam	2005	Pollution	C	SS: EHB	2 months
Sakagami and Fukuda	1973	Ecology/ Survey	D	Community	6 months
Saure	1996	Survey	D	Community	5 years
Silva et al.	2007	Pollination	D/E	Community	7 months
Smith et al.	2006a	Survey	D/C	Community	5 months

Table 1.2, continued:

Authors	Pub. Date	Study Focus	Type of Study	Taxon Level	Length of Study
Smith et al.	2006b	Survey	D/C	Community	5 months
Steffan-Dewenter and Kuhn	2003	Survey	C	SS: EHB	50 days
Steffan-Dewenter et al.	2002	Behavior	C	Guild: size	3 months
Taura and Laroca	2001	Survey	D	Community	1 year
Tommasi et al.	2004	Survey	C	Community	15 months
Zanette et al.	2005	Survey	C	Community	5 months

CHAPTER 2 – SEASONALITY IN BEES AND THEIR FLORAL RESOURCE PLANTS AT A CONSTRUCTED URBAN BEE GARDEN IN BERKELEY, CALIFORNIA.

Abstract

In mid 2003, a diverse floral resource was planted in a small urban residential plot at the University of California, Berkeley Oxford Tract with the goal of attracting local native California bee species to assess emerging patterns of diversity and seasonality. A standard procedure was used in 2004 to sample the bees and monitor their host flowers. Pollen and nectar resources were abundant and consistently available during spring, summer, and early fall months of that year. Thirty-two bee species representing 17 genera, and five families used these resources through the 2004 season. Urban bees were categorized into three seasonalities: early season, late season, and full season, represented by seven, eight, and 17 species, respectively. The results of this study indicate that newly planted urban gardens, which are designed for bees, have the potential to attract diverse seasonal bee taxa if diverse floral resources are provided throughout the growing season. Implications of these finding are discussed in terms of managing and conserving local bees in new and more developed urban gardens.

Introduction

Paralleling the current growth and expansion of urban landscapes there has been a corresponding increase in studies that examine the effect that urban growth has on native flora and fauna. Although land conversion has accounted for general declines in the abundance and the diversity of terrestrial species – a trend that is evident in arthropods such as butterflies (Blaire and Launer 1997, Tilden 1956), beetles (Spector and Ayzama 2003; Kotez and O'Hara 2003), ants (Suarez et al. 1998), and spiders (Bond et al. 2006) – there is growing evidence that urban areas can provide good habitat for some groups of invertebrate organisms. Habitat resources present in urban landscapes may not be equivalent to wildland habitat in terms of overall quality, patch size, connectivity, resource distribution, and resource phenology, but they can have a subset of appropriate characteristics that allow some species to colonize, reproduce, and persist.

High floral diversity is a characteristic of many urban landscapes (Gaston et al. 2005a and 2005b; Acar et al. 2007; Loram et al. 2007) and has been shown to attract an array of anthophilic species (Smith 1989), including bees (Hymenoptera: Apoidea). Faunal surveys have documented communities of bees in cities in North America (Hostetler and McIntyre 2001; Tommasi et al. 2004; Frankie et al. 2005, Cane et al. 2006), Europe (Saure 1996; Eremeeva and Sushchev 2005), South America (Nates-Parra et al. 2006a; Nates-Parra et al. 2006b) and Asia (Sakagami and Fukuda 1973) in association with urban floral resources. These studies indicate that some bees are finding a niche within highly modified and human dominated urban landscapes.

The issue of seasonality in bees, and the corresponding seasonality of their associated floral hosts, emerges as one attempts a more detailed examination of how bees survive, reproduce, and persist in urban areas. In most studies, inventories of urban bee communities have focused on bee-plant associations, or more specifically on how resource presence affects bee occurrence. The seasonal structure of bees in the urban landscape and how seasonal resource availability affects bee communities over time has received only limited attention.

A seasonal floral resource base that provides pollen and nectar at the appropriate times is essential for survival and reproduction in bees. The ability to acquire adequate nutrition and to provision a nest for larval development is dependant upon the availability and productivity of flowering plants. Adult bees may feed on nectar from a wide range of plant species, but some exhibit mesolectic (Cane and Spies 2006) or oligolectic patterns of pollen foraging (Malyshev 1936; Linsley 1958; Michener 2000). Further, the individual lifespan of an adult bee is usually limited to a few weeks during specific seasons (Williams et al. 2001; Shepherd et al. 2003) underscoring the importance of the seasonal timing of appropriate floral blooms with adult flight and foraging patterns to maintain and manage communities of bees.

A current literature search of seasonal bee emergence patterns yields predominately single species level or generic level studies. Linsley (1958) presents an overview of community level seasonality nested within a larger synopsis of solitary bee ecology, but the scope is global and the scale is broad. Ginsberg (1983) studied the seasonality and phenology of the bee community at an abandoned field site in New York, noting patterns of emergence that he classified into distinct flight seasons, as well as seasonally specific floral usage. Bee seasonality and floral resource development at an urban garden site in England was examined in detail by Owen (1991), providing evidence of within- and between-year patterns in community composition linked to floral phenology. Maintaining bee visitation throughout the season in urban environments has also been shown to be dependant on floral resource presence (Owen 1991; Tommasi et al. 2004; Cane et al. 2005; Cane et al. 2006), yet little research has been done to document patterns of floral seasonality and the associated seasonal diversity of bees visiting an urban resource.

The Oxford Tract Garden at the University of California, Berkeley campus, was designed to provide a continuous, consistent, and locally appropriate (Frankie et al. 2005) floral resource base during the known flight times of bees in Berkeley, California. Floral resources were managed to maintain blooming from April through to October in 2004. Detailed records of flowering and bee visitation were collected monthly during this time period. The results of this study provide a quantitative analysis of floral resource phenology and corresponding patterns of seasonality and emergence of bees observed in the first full year (2004) of garden development. The research presented in this chapter addresses two specific goals:

1) To examine the phenology of numerous selected plant types, noting the patterns of pollen and nectar availability during the initial 2004 growing season.

2) To outline the patterns of emergence and seasonality in the community of bees using the designed resource.

Materials and Methods

Site Description

The Oxford Tract is located at the periphery of the University of California, Berkeley campus, at 1751 Walnut Street, Berkeley, CA, 94720 (122°16'3.531"W; 37°52'41.672"N). The immediate surroundings include low-rise multi-unit residential buildings to the north, east, and west and a small open field to the south that is used for agricultural trials. Nearby to the southwest is downtown Berkeley, which is characterized by mid-rise commercial buildings with moderate to heavy traffic flow throughout the day. The land use type surrounding the Oxford Tract is residential in the form of single-family housing (City of Berkeley 2004). Approximately five kilometers west is the San Francisco Bay, and 1.2 kilometers east is Tilden Recreational Area (a part of the East Bay Regional Park District; 122°14'34.815"W; 37°53'33.184"N). Tilden Recreation Area is an open space reserve characterized by northern costal scrub, oak woodland vegetation, and grassland vegetation, however it as been disturbed through the introduction of numerous invasive species. The north and south sides of Berkeley are bordered by the cities of Albany and Oakland respectively. Land use does not changed significantly across these municipal borders. Floral resources that provide pollen and nectar resources required by native California bees are commonly found in private residential gardens as well as some community gardens within the Berkeley city limits (Frankie et al. 2005).

Garden Construction

The bee resource garden was constructed in a 6-meter by 30-meter (180 square meter) plot at the north end of the Oxford Tract. Garden plants were selected based on their known attraction to local bees from earlier survey work in the Albany/Berkeley residential neighborhoods (Frankie et al. 2005). This survey focused primarily on ornamental plants, most of which were exotic species. Native California bees have been observed visiting approximately 200 species of flowering plants in the Berkeley/Albany area of which 129 have been found to have measurable attraction to bees (Frankie et al. 2005). Plants from among these were used to develop the Oxford Tract Garden. Most of the plants were acquired from local nurseries. The plants were identified to species, subspecies, varieties, cultivars, and hybrids. As such, the term plant element was used to refer to each unique plant type used in this study. The first planting at the Oxford Tract Garden began in bare soil in July 2003 (Figure 2.1). The addition of plants continued in 2004, until 78 plant elements were established (Figure 2.2). Floral resources were aggregated in patches of approximately 1.5 meters square, corresponding to the unit of measure used in bee visitation counts (frequency counts) by Frankie et al. (2005). The selection of plant elements was also based on the need for adequate spring floral resources, as well as summer/early fall flowers for attracting diverse bee taxa throughout the entire 2004 season. The garden was maintained through watering and pruning to ensure constant flowering. During exceptionally hot and dry periods the plants were watered daily. No synthetic chemical fertilizers or insecticides were used at this site.

Phenology Data Collection

Plant elements were monitored once a month, on the same day that the bee collections were made, for their degree of flowering. Three categories of flowers were established: full flowering (ff), partial flowering (pf), and no flowering (nf). Full and partial flowering distinctions were made based on horticultural experience and knowledge of individual plant elements. A no flowering (nf) designation was made when plants were in a vegetative state, when there were only flower buds, or when all of the flowers were spent. When calculating the resource availability for each collection day, only the plant elements that were in full flower (ff) were included. The observations occurred during the middle of the month for a period of seven months. During the 2004 growing season 40 of the 78 installed plant elements flowered. Only these 40 plant elements were used in the analysis.

Bees were sampled once each month from April through to October 2004 on ‘good bee days’ – days characterized as sunny with daily high temperatures equal to or greater than 18 °C, with high atmospheric pressure, and little or no wind. Two methods were used to collect bees: passive pan-trapping and active aerial net collections at flowers. Efforts to collect bees earlier in 2004 were hampered by unseasonably cool weather and prolonged rainfall in March and early April.

Pan-Trapping

Bees were pan-trapped passively by attracting them to brightly colored bowls filled with soapy water. Fifteen 177-milliliter (6 ounce) Solo™ bowls were used as pan traps. They were segregated into three color groupings: fluorescent blue, fluorescent yellow, and plain white. The fluorescent blue and yellow pans were spray-painted. The liquid in the pan traps was a mixture of water and Blue Dawn™ liquid soap (one tablespoon soap to one gallon water). Pan traps were placed near the floral resources in full sun and where spaced approximately three meters apart. Trap colors were alternated with a fixed pattern of white, yellow, blue, followed again by white, yellow, blue, etc. The traps were set out at 1000h and collected at 1400h. Throughout the day, the liquid content of the traps was monitored and was topped-off with more liquid as necessary. At the end of the collecting day the contents of the pan traps were strained, rinsed, and placed in labeled plastic bags for temporary storage. The contents of all of the pan traps of each color were combined. The collection methods follow the Bee Inventory Plot protocol, http://online.sfsu.edu/~beeplot/, (LeBuhn et al. 2003) with modifications made for use in a small urban plot.

Sampling at Flowers

Aerial nets were used to collect bees actively from flowering plant elements. Only bees that made contact with the reproductive parts of flowers were collected. Netting occurred from 1000h to 1400h. Collectors moved from resource to resource catching foraging bees with as little disturbance as possible. After one netting attempt was made at a resource, the plant element was left to recover for a period of at least 15 minutes. Netted bees were placed in kill-jars charged with cyanide. Once deceased, the bees where placed into marked plastic containers for temporary storage. At the end of each collection day the specimens were removed from temporary storage, pinned, and labeled in the laboratory. Bees were stored in Schmidt boxes and sent to the University of California, Davis to be identified by Robbin W. Thorp. These specimens are now stored in a voucher collection at the University of California, Berkeley.

Results

Floral Resource Phenology

The Oxford Tract Garden was designed to produce a continuum of diverse floral resources during the main growing season from April through October, 2004. Figure 2.3 displays the abundance of pollen and nectar resources recorded during this time period. Floral resources remained constantly available with their numbers increasing slightly in mid-summer. In every month there were numerous pollen/nectar and nectar only plants. There was only one plant in this study on which bees foraged for pollen only – the California poppy, *Eschscholzia californica*. The numbers of floral resource plants ranged from a low of 20 in April to a high of 31 in both June and July. Throughout the season, the average number of available floral resources was 25.29 (± 1.61 S.E.). Plants that provided nectar and both pollen and nectar resources were the dominant type for the entire season (see Figure 2.3 and Appendix 2.i). Seven plant elements flowered in portions of both seasons, however, only the following plant elements flowered for most of each season: *Bidens ferulifolia*, *Cosmos bipinnatus*, *Gaillardia* x *grandiflora*, *Lavandula* spp., and *Limonium perezii*. The first three plants listed provide a mix of pollen and nectar resources, whereas *Lavandula* spp. and *Limonium perezii* provide only nectar.

Bee Collections

During the 2004 season 405 individual bees were collected representing five families (Apidae, Andrenidae, Colletidae, Halictidae and Megachilidae), 17 genera and 32 unique taxa (see Appendix 2.ii for a species list). Of these 32 species, 29 were identified to species, whereas three were identified to morphospecies. Bees were most numerous between June and September, displaying two peaks of abundance with 89 and 92 individual specimens respectively. Though bee numbers dropped between these two months in July and August, they were still higher than the average monthly abundance of 58 (± 8.73) bees.

Individual bee species recorded in this study can be classified into three seasonal patterns based on when they emerge: early season (April to June), late season (July to October), and full season (occurring from early spring into the fall). Early season bees included *Andrena nigrocaerulea* and *Osmia* sp. 3. Records for these individuals came from single samples. Common late season bees included *Hylaeus punctatus*, *H. rudbeckiae*, and *Xeromelecta californica*. The full season bees were represented by *Apis mellifera*, *Agapostemon texanus*, *Anthophora urbana*, *Megachile perihirta*, *M. rotundata*, and *Halictus tripartitus*. Species richness in the early and in the late seasons was nearly identical with 24 and 25 species respectively. Seven species were unique to the early season and eight species were unique to the late season, whereas 13 species occurred in both seasons (see Appendix 2.ii).

Individual bee groups, such as families and genera, also showed a seasonal trend. Bees in the genus *Andrena* are a common early season group, but had very low numbers in our collection – only one individual was collected in April. Similarly, the genus *Osmia* was represented by a single individual. The family Apidae showed a trend of steady increase through the season with a peak in late summer. The family Halictidae had a similar pattern of increase, but with an earlier abundance peak in late spring/early summer (May-June). Numbers of the family Colletidae were low in the spring as they are a late season group with peak abundance in September. The family Megachilidae persisted throughout the full season with distinct peaks in abundance in June and in September.

Trends in bee abundance can also be sorted into social, solitary univoltine, and solitary multivoltine classes based on the numbers of generations of each species. Social bees have multiple generations of workers throughout most of the year, which explains their full season presence. Their numbers are expected to build up through the season, peaking in summer. Three species of social bees sampled were represented by enough individuals to examine this seasonal pattern. *Halictus tripartitus* and *Lasioglossum kincaidii* both showed steady increase into June followed by a decline (see appendix 2.ii). *Lasioglossum incompletus* had a similar pattern, but the abundance of this species peaked in July. *Apis mellifera*, *Bombus californicus*, *B. melanopygus*, *B. sitkensis*, *B. vosnesenskii*, *Halictus ligatus*, and *H. rubicundus* were not represented by enough individuals to demonstrate this seasonality.

Hylaeus rudbeckiae exemplified the trend expected from a univoltine species. It was present from June to October with a distinct peak in abundance occurring once during the season in September, followed by a decline (see appendix 2.ii). The other univoltine species collected were represented by three or fewer samples (*Andrena nigrocaerulea*, *Ceratina acantha*, *Diadasia enavata*, *Megachile fidelis*, *M. inimica sayi*, *M. lippiae*, *Osmia* sp. 3, *Sphecodes* sp. M1 and M2, and *Xeromelecta californica*), or had a sporadic occurrence (*Anthidium maculosum* and *Hylaeus punctatus*).

Solitary multivoltine individuals were the most abundant group in every month except April. Their abundance increased rapidly from May to June and remained high into September, dropping sharply in October. Table 2.1 summarizes the temporal occurrence of males and females in seven potentially multivoltine species. Overlapping generations make it difficult to determine multivoltine patterns from pan-trap samples or from observations at flowers, however, the data suggest bimodal patterns of flight for *Agapostemon texanus*, *Anthophora urbana*, *Coelioxys rufitarsis*, and *Megachile rotundata*. Other species with suggestive bivoltine patterns include *Megachile brevis* and *M. perihirta*. The latter is a host for the cuckoo bee *Coelioxys rufitarsis*. *Megachile apicalis* is known only from two individuals collected on the same sample day.

Discussion

The Oxford Tract Garden, numerous native, and some non-native, bee species used the new urban floral resource patch throughout its first full growing season. Bees visiting the resource represented a subset of those known to frequent urban floral resources in the surrounding residential neighborhoods (Frankie et al. 2005). Further, the patterns of urban plant phenology and associated seasonal patterns of bee occurrence emerged in the study. Three distinct seasonal categories of bees were recorded: early season bees that emerged from April to early June; late season bees that exhibited peak abundance towards the end of July through to September before declining in October; and full season bees that emerged as early as April and were present until the end of our sampling season in October.

Patterns of floral resource diversity and abundance had an influence on the seasonal diversity and abundance of the three groups of bees using the constructed floral resource, indicating the important role that seasonal resource structure plays in bee foraging. Pollen and nectar providing plant elements were in bloom from April to October, however, early season floral resource richness was slightly lower than mid and late summer richness, resulting in a low representation of the early season bees that are associated with these species. In particular, spring bees in the genera *Andrena* and *Osmia*, showed low numbers in the sample. Monitoring by Frankie et al. (2005) and earlier studies of bees in the Berkeley Hills and at the University of California Berkeley Campus (Linsley 1944; Linsley and MacSwain 1955, 1957, 1959; and Thorp 1969) established that many species of *Andrena* and some species of *Osmia* occur there early in the year. *Habropoda depressa* Fowler was also recognized as a common spring occurrence on the main University of California, Berkeley campus by Barthell et al. (1999). In 2004, this species was readily observed on campus and in the surrounding residential neighborhood, but was altogether lacking from the collection. Low numbers of *Andrena* and *Osmia* at the Oxford Tract Garden are likely due to a lack of appropriate floral resources during the flight times of these bees. *Habropoda depressa* activity in the early season was likely limited by a lack of suitable nesting sites – sloping ground and shaded vertical banks (Barthell et al. 1999) – near the Oxford Tract Garden.

Seasonal floral resource development has continued with seasonally specific and specialist-oriented plantings to target bees that were poorly represented in 2004. In the first full year of study, 40 plant elements flowered from April to early October. Since then the total diversity and duration of resource availability has increased; the numbers of early and late season flowering species have also been balanced. The proportion of native plant species preferred by local native bees has also increased as more knowledge is acquired about the host plant preferences in of bee foraging in urban gardens. The most recent floral survey of the garden catalogued 112 plant elements that flowered from early March into late October in 2007. During this three-year time period an increase in bee visitation in the early and the late seasons, as well as an increase in species diversity, was observed indicating that more established gardens attract a more diverse community of early, late, and full season bees. The Oxford Tract Garden requires further development to attract a larger proportion of the bees known to be foraging in the urban residential neighborhoods of Berkeley, California.

Comparing these findings to the existing published work describing community level patterns of seasonality in bees reveals some similarities in seasonal species composition and distribution. Ginsberg's 1983 study of a wildland community of native bees in Ithaca, New York outlines three phenologies of native bees: spring, early summer, and late summer/fall; adding a fourth non-native full season category represented by *Apis mellifera*. In Ginsberg's assessment, spring foragers were represented by *Andrena* spp. and univoltine halictids, and the same groups compose the urban early-season category at the Oxford Tract Garden. *Andrena* species were also described as representative spring taxa in the urban garden studied in Leicestershire, England by Owen (1991). Ginsberg's early summer bees were represented by multivoltine species and primitively social halictids, a trend that is once again paralleled in the Oxford Tract Garden results (see Table 1.1 and Appendix 1.ii). The late summer/fall group described by Ginsberg outlines a replacement of the spring univoltine species by a late season assemblage and a peak in *Bombus* spp. foraging. The Oxford Tract Garden results contain a corresponding replacement of univoltine bees, however *Bombus* spp. numbers show a decline from spring to fall (see appendix 2) similar to what was observed in the urban garden study by Owen (1991) where *Bombus* spp. numbers rose in spring and tapered off towards the end of the season throughout 15 years of sampling. *Bombus* spp. abundance and diversity appeared to correlate with floral resource abundance and the ability of queens to forage and establish colonies (Owen 1991). Work underway more locally in California on wild bee habitat management in agricultural landscapes is assessing three seasons of bees for management with seasonally appropriate floral resources (Claire Kremen, personal communication). Not surprisingly, the seasonal categories described in this work are most similar to the Oxford Tract Garden findings.

Characteristics common to urban floral resources such as high diversity (Angold et al. 2006; Smith et al. 2006; Loram et al. 2007) and prolonged bloom periods (Lu et al. 2006; Wilby and Perry 2006; Niel and Wu 2007) appear to alter the foraging behavior and the flight times of bees. Cane et al. (2005) observed this effect in urban Tucson, Arizona where native bees used urban resources after wildland resources were out of season. Another manipulator of floral blooming within the urban landscape is common garden management that includes greenhouse propagation, planting decorative varieties out of season, pruning, dead-heading, increased irrigation, and nutrient supplementation. Some of these techniques have been used for aesthetic management at the Oxford Tract Garden, and subsequently extended flowering and corresponding bee visitation in native (*Encelia californica*, *Penstemon heterophyllus*, *Erigeron glaucus*, *Grindelia hirsutula*, *Eschscholzia californica*) and non-native (*Cosmos* spp., *Bidens* sp., *Linaria* sp., *Coreopsis grandiflora*, *Salvia* spp., *Duranta recta* and *Gaillardia* sp.) bee-attractive plant elements has been noted. Smith et al. (2006) suggested that individual gardens form interconnected tracts of habitat within the urban landscape and with the surrounding natural landscape that can facilitate species movement between the two areas. If populations of these bees are moving between habitats as resources change or if there are localized wildland and urban populations will require further investigation.

The results in this study are based on both pan-trapping and netting at the resources. An analysis shows that nearly 23% of the sampled bees where caught in pan traps (n=92). Removing pan traps from the study would have only slightly changed the species richness results, as only three of the 32 species were caught exclusively by pan trap. These species are *Diadasia enavata*, *Ceratina acanthi,* and *Sphecode*s sp. Extended sampling using both pan traps and floral netting is required to determine if sampling at flowers alone is a sufficient method with which to address questions regarding species richness in an urban garden setting. Abundance numbers would have varied greatly without the pan traps. Species in the genera *Lasioglossum*, *Halictus*, and *Hylaeus* were caught in large numbers (more than 50%) in pan traps. The total number of bees sampled in the season would have decreased from 405 to 313 if only floral samples were considered. Accurate abundance assessments, especially within groups such as families and genera, require both collection techniques.

Urban gardens have the potential to be important conservation and management tools for native bee communities if they are constructed and managed with the needs of bees in mind. There are key elements responsible for attracting and maintaining a diverse community of bees within the urban landscape. Diverse floral resources experience higher levels of visitation from bees (Pontin et al. 2006); diverse urban gardens are the same in this respect (Frankie et al. 2005). Bees exhibit strong preference patterns for floral hosts (Frankie et al. 2005) and this makes it possible to target species for management with resource provisioning. The seasonal composition of a floral resource base is a major factor in attracting the full range of local species as foraging patterns over the season are known to correlate with resource availability both in wildland (Ginsberg 1983) and urban environments (Tommasi et al. 2004; Cane et al. 2005 and 2006). More detailed knowledge of urban bee seasonality will possibly enable the design and management of garden resources to attract economically or agriculturally important species and potentially extend the seasons of these bees to meet productivity requirements within cities.

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Figures, Tables, and Appendices

Figure 2.1. The bare soil of the Oxford Tract site in 2003 prior to the first garden planting. The buildings of urban residential Berkeley can be seen in the background. Photo credit G.W. Frankie.

Figure 2.2. The Oxford Tract garden seen in 2004 after one year of planting and garden development. Photo credit G.W. Frankie.

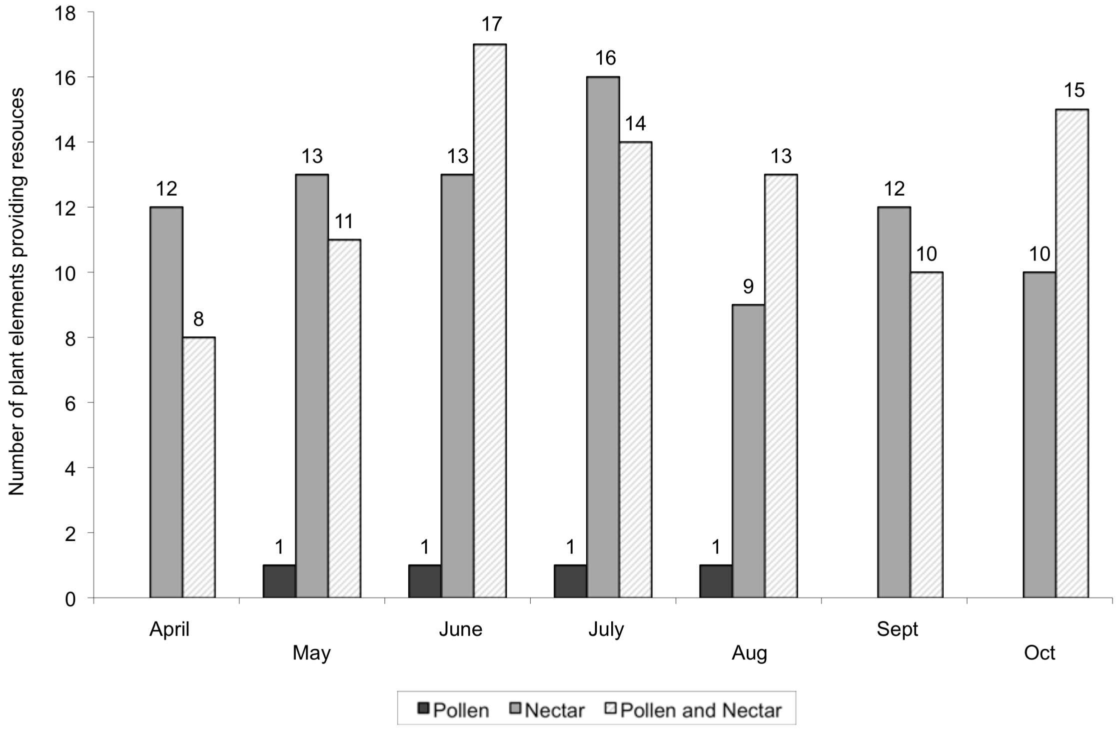

Figure 2.3. The number of Pollen and Nectar resources in full flower (ff) each month during the 2004 season at the Oxford Tract Garden.

Table 2.1. Male and Female bee numbers collected at the Oxford Tract garden from April to October for seven putatively multivoltine species.

	April		**May**		**June**		**July**		**Aug**		**Sept**		**Oct**	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f
Agapostemon texanus Cresson	—	—	—	—	—	2	—	—	1	—	3	—	3	3
Anthophora urbana Cresson	—	—	1	2	—	2	1	3	—	3	5	—	3	—
Coelioxys rufitarsis Smith	—	—	—	1	1	2	—	1	2	—	5	5	—	—
Megachile apicalis Spinola	—	—	—	—	—	—	—	—	—	—	2	—	—	—
Megachile brevis onobrychidis Cockerell	1	—	—	—	—	—	1	2	—	1	4	5	2	2
Megachile rotundata (Fabricius)	—	—	—	1	3	14	—	3	—	—	1	5	—	2
Megachile perihitra Cockerell	—	—	4	4	9	6	13	4	8	8	4	2	6	3
Melissodes robustior Cockerell	2	—	2	4	4	2	5	10	5	8	3	5	—	—

Appendix 2.i. The pollen (P) and nectar (N) resources present at the Oxford Tract Garden in the 2004 Season. The * symbol indicates a native California species, the † indicates an annual.

P/N	N	P
Spring (Apr-Jun)		
ASTERACEAE	**LAMIACEAE**	**PAPAVERACEAE**
Bidens ferulifolia (Jacq.) Sweet	_Agastache_ spp.	_Eschscholzia californica_* Chamisso
Calendula spp.	_Lavandula_ spp.	
Coreopsis tinctoria Nuttall	_Marrubium vulgare_ Linneaus	
Cosmos bipinnatus† Cavanilles	_Salvia chamaedryoides_ Canvailles	
Gaillardia spp.	_Salvia mellifera_* Greene	
Grindelia sp.*	**LOASACEAE**	
BRASSICACEAE	_Mentzelia lindleyi_*† Torrey & A. Gray	
Brassicaceae† (mustard) spp.	**PLUMBAGINACEAE**	
HYDROPHYLLACEAE	_Limonium perezii_ (Stapf) F.T. Hubbard	
_Phacelia grandiflora_*† A. Gray	**POLEMONIACEAE**	
_Phacelia tanacetifolia_*† Bentham	_Gilia achilleifolia_*† Bentham	
_Phacelia viscida_*† (Bentham) Torrey		
ONAGRACEAE		
_Clarkia unguiculata_*† Lindley		
RHAMNACEAE		
Ceanothus 'Ray Hartman'*		

P/N	N	P
Summer (Jul-Oct)		
ASTERACEAE	**APIACEAE**	**PAPAVERACEAE**
Aster x frikartii Silva Tarouca & C.K. Schneider	_Eryngium_ spp.	_Eschscholzia californica_* Chamisso
Bidens ferulifolia (Jacq.) Sweet	**GERANIACEAE**	
Calendula spp.	_Geranium incanum_ 'Sugar Plum'	
Coreopsis grandiflora Hogg ex Sweet cultivars	**CONVOLVULACEAE**	
Coreopsis lanceolata Linneaus	_Convolvulus arvensis_ Linneaus	
Coreopsis tinctoria Nuttall	**CRASSULACEAE**	
Coreopsis verticillata Linnaeus	_Sedum telephium_ Linneaus	
Cosmos bipinnatus† Cavanilles	**LAMIACEAE**	
Cosmos sulphureus† Cavanilles	_Agastache_ spp.	
Gaillardia x _grandiflora_	_Lavandula_ spp.	
Grindelia spp.*	_Marrubium vulgare_ Linneaus	
_Helianthus annuus_*† Linneaus	_Salvia chamaedryoides_ Cavanilles	
_Helianthus gracilentus_*A. Gray	_Salvia uliginosa_ Bentham	
Madia elegans ssp. _densifolia_ (Greene) D.D. Keck*†	_Thymus vulgaris_ Linnaeus	
Tithonia rotundifolia† (Miller) S.F. Blake	**PLUMBAGINACEAE**	
BRASSICACEAE	_Limonium perezii_ (Stapf) F.T. Hubbard	
Brassicaceae† (mustard) spp.	**POLYGONACEAE**	
VERBENACEAE	_Eriogonum fasciculatum_* Bentham	
Caryopteris x clandonensis hort. ex Rehd.	_Eriogonum grande_ var. _rubescens_* (Greene) Munz	
Caryopteris incana 'Bluebeard'	_Eriogonum latifolium_*Smith	

Appendix 2.ii. The seasonal distribution of urban bees collected on host plants and with pan traps in the 2004 season at the Berkeley Oxford Tract Garden. The * symbol indicates bees collected only in the early season (April to June) and the † symbol indicated bees collected only in the late season (July to Oct). The ‡ symbol denotes species not native to California.

	25-Apr	**14-May**	**15-Jun**	**21-Jul**	**19-Aug**	**16-Sep**	**14-Oct**	**Season Total**
Apidae								
Anthophora urbana Cresson	—	3	2	4	3	5	3	*20*
Apis mellifera‡ Linnaeus	—	1	3	1	4	2	2	*13*
*Bombus californicus** Smith	—	1	—	—	—	—	—	*1*
*Bombus melanopygus** Nylander	1	—	—	—	—	—	—	*1*
*Bombus sitkensis** Nylander	—	1	—	—	—	—	—	*1*
Bombus vosnesenskii Radoszkowski	—	3	6	1	1	—	1	*12*
Ceratina acantha† Provancher	—	—	—	—	—	1	—	*1*
*Diadasia enavata** Cresson	—	—	1	—	—	—	—	*1*
Melissodes lupina† Cresson	—	—	—		1	6	—	*7*
Melissodes robustior Cockerell	2	6	6	16	13	8	—	*51*
Xeromelecta californica† Cresson	—	—	—	—	2	1	—	*3*
Andrenidae								
*Andrena nigrocaerulea** Cockerell	1	—	—	—	—	—	—	*1*
Colletidae								
Hylaeus punctatus‡ (Brulle)	—	—	4	—	—	1	1	*6*
Hylaeus rudbeckiae (Cockerell & Casad)	—	—	1	1	3	13	2	*20*
Halictidae								
Agapostemon texanus Cresson	—	—	2	—	1	3	4	*10*
Halictus ligatus Say	1	—	—	—	1	1	—	*3*
Halictus rubicundus† (Christ)	—	—	—	1	—	—	—	*1*
Halictus tripartitus Cockerell	7	1	17	15	8	5	1	*54*
Lasioglossum incompletus (Crawford)	4	1	4	6	1	3	—	*19*
Lasioglossum kincaidii (Cockerell)	2	4	7	5	4	3	—	*25*
Sphecodes sp. M1†	—	—	—	—	—	1	—	*1*
Sphecodes sp. M2*	—	1	—	—	—	—	—	*1*
Megachilidae								
Anthidium maculosum Cresson	2	—	—	1	—	2	4	*9*
Coelioxys rufitarsis Smith	—	1	3	2	2	10	—	*18*
Megachile apicalis‡ Spinola	—	—	—	—	—	2	—	*2*
Megachile brevis onobrychidis Cockerell	1	—	—	3	1	9	4	*18*
Megachile fidelis† Cresson	—	—	—	—	1	1	1	*3*
Megachile inimica sayi† Cresson	—	—	—	—		1	—	*1*
Megachile lippiae† Cockerell	—	—	—	—	—	2	—	*2*
Megachile perihirta Cockerell	—	8	15	17	15	6	9	*70*
Megachile rotundata‡ (Fabricius)	—	1	18	2	—	6	2	*29*
*Osmia sp. 3**	1	—	—	—	—	—	—	*1*
Monthly Bee Total	22	32	89	75	61	92	34	405

CHAPTER 3 – PATTERNS AND DYNAMICS OF BEES VISITING *TECOMA STANS* RESOURCES IN TROPICAL URBAN LANDSCAPES: A MICRO SCALE ANALYSIS OF BEE RESOURCE USAGE IN CITIES.

Abstract

Foraging patterns and community characteristics of bees visiting *Tecoma stans* in three tropical cities were studied, outlining trends relevant to resource-based monitoring. Frequency-of-visitation counts were used to assess daily temporal foraging variation, individual resource constancy, and to assess the impacts of resource characteristics (height, number of flowers, and life form) on visitor abundance and taxon richness. At least 26 species forage for pollen and nectar from this floral resource. These species represent a range of size, nesting, and feeding guilds and are a characteristic proportion of the local native bee community. The hours between 0700h and 1300h display peak visitation in both taxon richness and visitor abundance. Individual bee groups have structured occurrence within these times that can be categorized as either early morning or full-day. Of the resource characteristics studied, only the total number of flowers that an individual *T. stans* possessed had a significant impact on the visitor abundance and the taxon richness of foragers. Resources possessing more flowers attracted more bees and more bee types. Further differential patterns of inter- and intra-resource variability are present, and are likely driven by micro-scale variation in the local urban landscape.

Introduction

As urban areas grow, making the city a significant global land use type, the nature of bee-plant relationships within these modified landscapes becomes of particular interest. Urban bees (Hymenoptera: Apoidea) have been studied globally in recent years examining community composition with respect to general land use patterns (Fetridge et al. 2008; Saure 1996; McIntyre and Hostetler 2001; Tommasi et al. 2004; Cane et al. 2006; Nates-Parra et al. 2006; Matteson et al. 2008) as well as floral host usage and preferences (Hismatsu and Yamane 2006; Antonini et al. 2006; Frankie et al. 2005a). Collectively these works have shown that suitable foraging habitat resources exist within urban landscapes for a subset of bee species. Cities may also have conservation potential, providing refugia through parklands and green space (McFrederick and LeBuhn 2006). Additionally, urban foraging and nesting resources can compensate when those in the wildland are diminished or disturbed (Cane 2005; Cane et al. 2006; Frankie et al. 2009). The ability to reliably measure and monitor bee communities in the urban niche is the next step in facing the challenges of continued urbanization and pollinator management.

In the tropical dry forest region of Costa Rica, urban development linked to an increase in tourism, international business, and agriculture is transforming natural lands into cities. Corresponding changes in bee community composition have been noted, both in remnant wildlands (Frankie et al. 1997) and at the interface of development and the natural habitat (Frankie et al. 2009). Given the intensity of landscape change and the importance of pollinators, such as bees, there is a need to document and more accurately measure their populations across a range of landscape types and spatiotemporal scales (Eardley et al. 2006).

The challenge of monitoring bee communities comes from their small size, seasonal variability, range of guilds with varied life strategies, and mobile nature. Targeting known resource plants is an appropriate strategy for assessing the local community, but it can be complicated by the need to access multiple plant species, thus increasing variability in analysis. The lack of resource availability within the area of interest can also affect monitoring efforts. Moreover, the use of a single plant can limit the ability to detect most of the species in the community, as individual bees tend to have narrow ranges of hosts on which they forage. In ecosystems in which there is a better understanding of the local flora and fauna, magnet resources – individual plant species or genera that attract a representative range of the known bees species – have been used to outline the general patterns and characteristics of local bee communities across broad landscapes (see Frankie et al. 1997; Frankie and Vinson 2004; Minckley et al. 1999; Cane et al. 2005; and examples in Eardley et al. 2006). While not measures of absolute richness or diversity, such assessments provide a glimpse of larger community trends and basic taxon presence and absence, and can serve as rapid biodiversity assessment tools.

The visitation of flowers by bees plays a fundamental role in maintaining angiosperm reproduction (Kevan 1999), evolutionary processes (Fenster et al. 2004), and ecological diversity (Daily 1997). Long-standing evolutionary relationships have developed patterns in the breadth of resource usage and in the dynamics of foraging, often optimizing resource exploitation with the heavy metabolic demands of flight. As such, associations between bees and flowering plants are distinct and predictable – seasonality, host-specificity, and daily flight times are patterned. Bees show fidelity for individual foraging sites, visiting sites along repeated circuits known as "traplines" (Heinrich 1976). Individual species occur seasonally (Linsley 1958; Ginsberg 1983; Wojcik et al.

2008) and partition daily foraging to reduce competition and increase resource exploitation (Gottlied et al. 2005). In tropical systems in particular, abundant floral resources occur at many strata in the savanna and forested ecosystems. Corresponding vertical stratification, or structural niche partitioning, has been suggested in tropical pollinator systems as different bee species exploit these diverse resources (Roubik 1993). A more refined understanding of the resource usage strategies that bees employ will provide a baseline of information for bee conservation and management, especially as anthropogenic influences increase.

Tecoma stans Kunth (Bignoinaceae) is a common mass-flowering woody perennial found across Costa Rica, and much of the tropics. In urban environments, *T. stans* is prominent in home gardens, city squares, and lining city streets. It has been used extensively as a decorative ornamental because of its year-round production of striking yellow trumpet-shaped flowers. In the three urban landscapes under study in this chapter (Bagaces, Cañas, and Liberia), *T. stans* is ubiquitous and well distributed. *T. stans* also presents substantial variability in life form and structure, particularly in urban landscapes where human management, such as pruning, results in individuals that range from low-growing shrubs, to full hedges, and tall trees. Preliminary observations indicated that *T. stans* attracts a wide range of bee species from many genera, and guilds and many foraging strata. The ubiquitous distribution, structural variability, and observed high attractiveness suggests that *T. stans* could be a potential in-situ magnet resource suitable for future ecological studies on the impact of urbanization on bee populations, as well as a general tool for long term monitoring in these landscapes.

The study presented in this chapter examines the characteristics and patterns of the bee community using *T. stans* across varied spatiotemporal scales. Also addressed are some of the factors and variables that need to be considered if this species is to be used as a monitoring tool. The specific research questions addressed are as follows:

1) Which bee species and guilds are using *T. stans* as a resource in urban landscapes and what are the life history characteristics of this community?
2) Are there finer scale patterns of richness and abundance displayed by the bees foraging on *T. stans* throughout the day and over time?
3) To what extent is there variability in bee visitation within individual trees over time and between trees in the population, both in terms of the taxon richness and the abundance of bees attracted?
4) To what extent do the characteristics of a tree, including life form, height, and the number of total flowers, impact the abundance and richness of bees recorded as foragers?
5) Are broader patterns of visitation and community composition seen when individual study sites located within the tropical dry forest region are compared?

Material and Methods

Site description

The cities of Liberia (10°37'47.19"N, 85°26'17.75"W), Bagaces (10°31'34.29"N, 85°15'17.73"W), and Cañas (10°25'35.95"N, 85°05'28.02"W) lie in a row along Central America

Highway 1 in the Guanacaste province of Costa Rica (Figure 3.1). The surrounding landscape of tropical dry forest is fragmented by ranching and agriculture. Urbanization and growth in this region are above that national average with the population doubling in the past decade (INEC 2000). A recent census puts the population Liberia, the provincial capital, at 39,242 (34,469 urban; 4,773 rural), Bagaces at 9,261 (3,645 urban; 5,616 rural), and Cañas at 18,798 (16,512 urban; 2,286 rural) (INEC 2000). The area covered by Liberia is approximately 7.97 km^2, Bagaces, the smallest city, covers approximately 0.76 km^2, and Cañas covers approximately 2.98 km^2 (Urban land coverage calculated in ArcMap 9.3, © ESRI Inc. 2009). At the landscape level, Bagaces and Liberia lie in closer proximity to the biological reserve network of Lomas Barbudal and Palo Verde. The remaining surrounding land is used primarily for cattle grazing. Cañas resides within an intensive crop production region.

Floral resource description

Tecoma stans Kunth (Bignoinaceae) is common along city streets and on private land in all three cities as well as throughout the wildland in this region. Its native range in the Americas extends from the south central and southeastern United States (Arizona to Florida) to the Antilles and down into Argentina (Hammel 2005; Zuchowski 2007). *T. stans* is also present throughout Mexico, however, it varies significantly in leaf and flower morphology with the leaves significantly more pinnate and elongated and the flowers are much smaller in size with a longer corolla tube. Populations of *T. stans* are also present in South Africa, southern India and throughout Polynesia and Micronesia (see the Rancho Santa Anna Botanical Garden and Herbarium collection). In Costa Rica, *T. stans* is most often found on the Pacific slopes from the Guanacaste province into the central mountain region and in the greater San Jose area of the Puntanenas province (Hammel 2005). Its natural habitat includes both dry and moist forests, at elevations from zero to 1,300 meters above sea level (Zuchowski 2007). Figure 3.2 presents an example of two typical urban *T. stans* resources lining a residential street in the city of Cañas. Individuals can reach a height of 10 meters (Zuchowski 2007), but are commonly shorter in urban landscapes. Although *T. stans* flowers year-round, the most intense flowering occurs between November and March.

Resource Classification

Each resource in the study was marked and numbered using a hand-held Garmin Vista C *e*trex GPS unit. A digital photograph of each individual resource was also taken. Each *T. stans* was given a unique alphanumeric identifier that included the first letter of the city in which it grew (B=Bagaces, C=Cañas, and L=Liberia) followed by TS denoting "*Tecoma stans*" (a parallel study is using multiple species in these urban areas) and a unique number. The height, life-form, and the total number of flowers on each tree in this study were assessed. Height was estimated to the nearest 25 centimeters using either a meter measure or through photographic scaling with the author (measuring 158 cm) as a reference. The *T. stans* individuals in this study where then grouped into three size classes: small (up to 1 meter tall), medium (greater than 1 meter, but less than 3 meters tall), and large (taller than 3 meters). Life-form was categorized as a shrub, hedge, or tree corresponding to the following criteria: shrubs appeared as low-growing (generally shorter than 1 m) individuals that lacked a clear dominant axis; hedges ranged in height and were predominantly characterized by having top-to-bottom foliage coverage; trees where those individuals that had a distinct dominant axis (trunk) and a crown of foliage and flowers.

The number of flowers that an individual *T. stans* possessed was estimated using a stratified sub-sample of the inflorescences in the canopy. The canopy of each resource was fractioned into a manageable sector based on the overall resource size (either 2, 4, 8, or 10 sectors). The number of fractioned sectors was then used as an expansion factor (k) to calculate the estimated number of inflorescences (i) and the subsequent total flowers per resource (total flowers). The total number of inflorescences in one randomly selected sector was counted (i). A random subsample of the enumerated inflorescences was then selected and the total number of flowers contained in each inflorescence was counted, and averaged over the total sample (f). The calculated average number of flowers per inflorescence was then multiplied by the number of inflorescences and the expansion factor as follows:

$$\text{total flowers} = f \times i \times k,$$

where i is equal to the number of enumerated inflorescences in a random sector; k is the expansion factor that is equal to the number of sectors; and f is the estimate of mean floral abundance per inflorescence. All calculations were performed in Microsoft Excel 2008. In the case of some individual resources that possessed very few flowers (BTS12, BTS45, CTS5, CTS7, CTS36, LTS39, LTS42, LTS49, LTS58, and LTS65) the total number of flowers was enumerated using a census. Individual *T. stans* were then classified into three categories of floral resource abundance: low (less than 100 flowers per individual), medium (from 100 to 300 flowers per individual), and high (more than 300 flowers per individual).

Bee visitation counts

Between July 2007 and March 2009, 2,088 bee visitation counts documenting richness and abundance were conducted at 121 *T. stans* resources. A standardized 1-meter by 1-meter square observation frame was visually projected onto an easily observable and unobstructed area of the floral resource. The visitation rates of bees to all of the flowers within this visual frame were recorded for the duration of the three minutes that were timed with an electronic stopwatch. Bee visitation counts were taken approximately every 45 minutes between the daylight hours of 0600h and 1800h. Efforts were made to randomize the observation frames over repeated visits each resource to achieve a more representative account of bee visitation at each sample resource. Each hour was defined from the beginning of the hour (00 minutes) to 59 minutes past the hour; for example, the 1300h time block included the time period between 1300h and 1359h. Visitation was recorded only if a bee entered the corolla of the flower. Identification was based on general morphology, coloration, and flight pattern. Generalized flight patterns and overall gestalt were used to indentify bee visitors on-the-wing. Eleven distinguishable taxonomic categories of visitors were observed: African honeybee (AHB, *Apis mellifera scutellata*), Stingless bees (STB, *Trigona* spp.), Centris (Centris spp., and others), Eulema (*Eulema* spp.), Epicharis (*Epicharis* spp.), Euglossa (*Euglossa* spp.), Halictid (members of the family Halictidae), Mesoplea (*Mesoplea* spp.), Melitoma (*Melitoma* spp.), Xylocopa (*Xylocopa* spp.), and small bees (when a closer designation could not be made). Abundance was recorded as the total number of individual bees that were observed per count. Taxon richness was the recorded as the number of different distinguishable taxonomic categories recorded per count.

Representative samples of foraging bees were collected with aerial netting for more refined taxonomic identification. The bee collections where labeled and stored in Schmidt boxes. The identification of the collections was assisted by Dr. Laurence Packer and Jason Gibbs of York

University, Toronto, Canada and Dr. Ricardo Ayala of UNAM, Mexico. The majority of the collection resides at the University of California, Berkeley Essig Museum of Entomology. Collection request can be made directly to the collections manager.

Statistical Analysis

To determine if significant daily patterns of taxon richness and visitor abundance were present, bees from all visitation counts (n=2088) were sorted into 12 one-hour blocks, and analyzed using Multivariate ANOVA using a Bonferroni adjusted α of 0.004 (0.05/12=0.004), to account for multiple comparisons. A Bonferroni adjusted Tukey's HSD (α=0.004) was used to verify significance between groups and the direction of variability between multiple comparisons.

Variability in abundance and taxon richness within individual resources over multiple samples and between all resources in the population was compared using repeated measures ANOVA ($n_{resource}=42$, $n_{repeats}=3$, $\alpha=0.05$). Variances of repeated samples were tested with Mauchly's test of Sphericity and the degrees of freedom were corrected as needed. Visitation data was analyzed collectively as well as by city to investigate site-specific variability. Multivariate ANOVA was also used to establish if taxon richness, visitor abundance, and individual bee groups differed between the three cities studied. A Bonferroni adjusted α of 0.016 (0.05/3) was used in this comparison. A further sub-sample of four trees (Two in Bagaces numbered BTS3 and BTS5; and two in Liberia numbered LTS1 and LTS17) for which more detailed repetitive observation were made over a two year period were also compared for changes in daily visitation rates and richness using ANOVA. Tukey's HDS was used to investigate patterns of variability between years (2007 versus 2008) and seasons (wet and dry) in these four individuals.

The main and interaction effects of resource characteristics (height, life-form, and floral abundance) on bee abundance, richness, and the occurrence rates of the four dominant taxon groups (Centirs, Halictid, AHB, and STB) were examined using multivariate ANOVA, with a Bonferroni adjusted α of 0.016 (0.05/3). All of the multivariate tests were further analyzed with Tukey's HSD to determine the direction, magnitude, and level of the observed differences. All statistical analysis was run in SPSS 16 (Rel. 16.0.0, 2007 Chicago: SPSS Inc.).

Results

Throughout this two-year study period 7,417 bees where examined across 2,088 individual observations. Bees collected represent 26 species in 20 genera and two families (see appendix 3.i). The species are diverse in their feeding styles, nesting habitats, and levels of sociality. A list of the associated life history characteristics is presented in appendix 3.i (see Michener 2000 for more species specific details).

Three groups of native bees accounted for 90.36% of the total visitors recorded: Centirs, STB, and Halictid. Centris was the most abundant at 52.10%, followed by STB at 19.43% and Halictid at 18.86%. Non-native AHB (*Apis mellifera scutellata*) accounted for 5.68% of the total records. Figure 3.3 presents the proportions and patterns by city. Bagaces and Liberia have corresponding proportions of Centris, STB, Halictids, and AHB. Cañas has a higher proportion of Centirs and fewer AHB. Halictids are also more abundant than STB in Cañas. The remaining seven groups accounted for less then 2% each of the total visitors in the entire sample: Eulema, 1.12%; Xylocopa, 0.89%; Euglossa, 0.69%; Epicharis, 0.44%; Mesoplea, 0.19%; small bee, 0.16%; and Melitoma 0.15%.

Most visitors to *T. stans* in the urban landscape are solitary, ground nesting species, however, cavity, twig, and wood nesters, as well as eusocial and communal species are present. Eusocial stingless bees (in the genera *Trigona* and *Nanotrigona*) were also represented in this collection. At the species level *Centris eurypatana* is dominant, constituting 46.8% of all bees collected. *Ancyloscelis sp.* accounted for 13.1% and *Nannotrigona perilampoides* for 14.9%. All other species accounted for less than 5% each of the total sample. Bees classified as 'small bee' are most likely *N. perilampoides*, *Tetragonisca angustata*, *Plebeia* spp., or *Ceratina* sp. as these where the dominant small species identified from aerial samples.

Daily foraging patterns

There is an overall trend of higher bee visitor numbers in the morning hours, which drops off after 1300h. Taxon richness follows the same trend. Figure 3.4 displays the patterns of foraging between the hours of 0600h and 1800h, indicating visitor abundance and taxon richness. Data are presented as the number of bees per count, averaged across all counts taken during each time block. The mean abundance of bees per three-minute count across all measures was 2.45 ± 0.04 (mean ± SE). Mean taxon richness across all measures was 0.99 ± 0.03. While bees were present throughout the entire monitoring period, there are significant differences in visitor abundance ($F_{11,2076}$=5.931, p=0.00) and taxon richness ($F_{11,2076}$=9.629, p=0.00) over time. A period of higher abundance between 0600h and 1400h, with a mean of 3.38 ± 0.02 bees per count compared to lower abundance after 1400h (where there are 0.58 ± 0.06 bees per count) can be differentiated. The taxon richness of bee types per count within these two abundance periods is significantly different ($p<0.004$), with an average of 1.29 ± 0.01 bees per count between the peak hours that falls to an average of less than one bee type per count after 1400h (0.40 ± 0.05), and only two bee types (Centris and Trigona) are recorded as visitors during this period.

Seven of the 11 bee groups had significant patterns of occurrence throughout the day (Table 3.1). These daily patterns can be sorted into two categories, those restricted to the early morning and those that forage for the entire day. The most distinct patterns of occurrence can be seen in the groups Xylocopa and Euglossa (Figure 3.5). Their early and restricted occurrence exemplifies the early morning pattern; from the beginning of the day their numbers decline rapidly, disappearing after 1200h. Trigona and Centris exemplify full-day foraging patterns (Figure 3.6). While their abundances are different with Centris being present in higher numbers, their occurrence pattern is congruent. Halictid bees, while present most of the day, are most abundant between the late-morning hours of 0900h and 1100h. The AHB visitors restrict their foraging to the morning hours and are not present after 1200h. The remaining groups have sporadic occurrences with low numbers that do not fit any distinctive pattern (data not shown).

Intra- and inter-resource variability

There is variability in the degree to which individual resources in the population attract bees, both in terms of the number of bees and bee types attracted per individual count and in mean attractiveness over time. The number of bees counted in each individual three-minute count ranged from 0 to 34, with a mean of 3.55 (± 3.57). The number of bee groups encountered per count ranged from 0 to 4, with a mean of 1.35 (± 0.98). Table 3.2 displays these trends and the range of visitation seen in each city. Inter-resource variation rates were statistically significant for both visitor abundance (repeated measures ANOVA, $F_{1,441}$=0.005744, p=0.000) and taxon richness (repeated measures ANOVA, $F_{1,441}$=0.003596, p=0.000). This trend was consistent when samples were analyzed by city. The measures of intra-tree bee visitor abundance and taxon richness exhibited contrasting trends when cities were analyzed independently and when all cities were grouped together. In the combined city analysis, the bee abundance did not vary significantly from measure to measure on the same resource (repeated measures ANOVA, $F_{2,882}$=0.517, p=0.596). The individual analysis of Liberia keeps to this trend ($F_{1,294}$=2.289, p=0.103), but Mauchly's Sphericity is violated and the values from this F-test is not reliable. When Bagaces and Cañas are analyzed independently, however, there is significant variability between the individual samples on the same resource ($F_{1,294}$=4.982, p=0.007; $F_{1,294}$=5.505, p=0.004, respectively).

Intra-resource variation in bee richness displays an opposite trend. Across all cities, variability is significant between individual measures on the same resource (repeated measures ANOVA, $F_{2,882}$=2.329, p=0.098). This is also the case in Bagaces ($F_{1,294}$=4.416, p=0.013), but not in Cañas ($F_{1,294}$=1.491, p=0.227) and Liberia ($F_{1,294}$=4.113, p=0.170). In addition, there was significant interaction between the measures of bee taxon richness and visitor abundance and the individual resource (p<0.000), which suggest that other variables might be structuring the patterns of bee visitation to *T. stans* in urban landscapes.

The four resources for which more detailed repetitive samples where available differed significantly between individual measures for both abundance (BTS3: $F_{8,128}$=8.232, p=0.000; BTS5: $F_{14,84}$=8.458, p=0.000; LTS1: $F_{7,48}$=2.671, p=0.020; BTS17: $F_{6,35}$=4.104, p=0.003) and richness (BTS3: $F_{8,128}$=3.816, p=0.000; BTS5: $F_{14,84}$=3.230, p=0.000; LTS1: $F_{7,48}$=3.116, p=0.009; BTS17: $F_{6,35}$=4.659, p=0.001). The observations were spread over a 24-month period and occurred both in wet and dry seasons. No underlying pattern corresponding to seasonality or sample year is evident within this comparison (see figures 3.7-3.10).

Individual bee group occurrence between cities

Abundance and taxon richness in 10 of the 11 bee groups sampled varied significantly between the three sample cities (p<0.016). Appendix 3.ii shows the results of the between-city comparisons for each of the 11 bee groups, visitor abundance, and taxon richness in more detail, indicating the magnitude of the observed difference. Only Euglossine bees did not show any significant variation between the three cities (p>0.095, Appendix 3.ii). The average abundance of bees per count was highest in Cañas and lowest in Bagaces (see Table 3.2). The overall taxon richness per count was greatest in Liberia, followed by Cañas, and once again lowest in Bagaces (see Table 3.2). This trend in richness corresponds to the relative size of each cites, with the largest city having the greatest richness.

Resource characteristics and bee foraging

The abundance and richness of bees visiting an individual *T. stans* resource was significantly influenced by the number of flowers that a resource had (p<0.00), and not by the height or life form characteristics (Table 3.3). To a lesser extent, the interaction between total flowers and life form influenced the abundance of bees visiting a resource ($p<0.10$), but not the total number of bee types. Figure 3.11 displays the general trends seen in the abundance and richness of bees observed per count as a function of resource characteristics. There is no observed variability between the visitor abundance and taxon richness attracted based on resource life form. Although medium and tall resources attract more bees and more bee types than shorter resources, this difference is not significant.

The previously indicated significant effect of the number of flowers that a resource possessed on both the visitor abundance and the taxon richness is one of increasing bee occurrence with increasing flowers. The three floral resource classes are also significantly different in order of increasing floral abundance for both bee visitor abundance and taxon richness (Tukey's HDS; $p>0.05$). When the four dominant bee groups where examined for their individual response to resource characteristics, more specific patterns were seen (Table 3.4). The foraging rates of Centris and STB are not significantly impacted by any of the resource characteristics or their interactions. The foraging rates of Halictids are impacted by the life form and the total number of flowers possessed by a resource ($p<0.010$), as well as by the interaction between the two ($p=0.001$). ABH are significantly influenced by the total number of flowers a resource has ($p=0.000$), and by the interaction between life form, height, and total flowers ($p=0.007$). The patterns seen at the level of total bee abundance and richness are likely driven by the responses of Halictids and ABH to resource variability. While the individual city within which each resource was located had a significant influence on the foraging rates of some bees, an alternative ANOVA of the previously tested resource characteristics and city as an additional variable did not show any significant interaction with any of the variables or variable combinations and the city ($p>0.10$, data not shown).

Discussion

The tropical dry forest of Costa Rica is known for its bee diversity. More than 250 native bee species are found in the wild lands in this region (Frankie et al. 1983). Mass-flowering angiosperms that are common in the savanna and mesic habitats provide ideal forage. In turn these bees provide essential pollination services to nearly 70% of the flowering plants growing in this region (Frankie et al. 2004). *Tecoma stans* resources in the three studied cities attract a sub-sample of the wildland bee community – twenty-six species with diverse life histories. The species present on *T. stans* range in body sizes, floral usage patterns, and nesting habits (see Appendix 2.i). These bees use *T. stans* as a pollen and nectar source, and in some cases, as a mating site (i.e., some *Centris* species). The balance of guilds attracted, high temporal attractiveness, and annual blooming suggest that *T. stans* might be an appropriate target resource that can highlight trends in the local bee community. Patterns and variability in the overall attractiveness of individual trees has been established and the implications for sampling and monitoring in relation to these trends are discussed in further detail.

The patterns in the bee community

The pollination systems of small and large bees in this region have been linked to different resources. Small bees are often generalist feeders while larger bodied species show more specialization in resource usage (Frankie et al. 1983). The plant life forms preferred by small bees are herbaceous (Frankie et al. 1976). The opposite is true for large bees, which feed predominantly on trees, especially those with large, showy, symmetrical flowers (Frankie et al. 1976). Both large- and small-bodied foragers are using *T. stans*; allowing the study of patterns in both systems on a single resource. Other local floral species attract both large and small bees (e.g., *Andira inermis* and *Tabebuia rose*), however, their landscape level distribution is more limited, and blooming periods more truncated.

Foragers using *T. stans* possess oligolectic, mesolectic, and polylectic feeding habits (see appendix I and Michener 2000 for more species specific information) presenting the opportunity to examine broad trends across guilds and groups using this single resource. The dominant group of bees in this study, the large bodied *Centris* species, have been documented as dominant foragers on other mass-flowering species in this region, generally accounting for two thirds of total diversity (Frankie et al. 1997; Frankie et al. 2009). *Centris* species feed broadly on other members in the family Bignoniaceae (Coville et al. 1986). Examples in these cities include; *Crescentia alata, Cordia dentata, C. inermis, Tabebuia ochrace,* and the previously mentioned *T. rosea.* It has been suggested that oligolectic and mesolectic large bees within this region display resource tracking and high fidelity for an individual tree as determined by a mark recapture study (Frankie et al. 1976). The variability in overall tree attraction may be driven by the foraging patterns seen in this dominant group.

Nesting habits of the bees identified from *T. stans* in this study are equally varied, and include cavity dwellers, twig and wood excavators, and ground nesters. Diverse nesting habits in urban bee communities are not surprising given the increased complexity and heterogeneity found in the urban matrix. Other studies, however, have noted a smaller proportion of ground nesting species due to habitat fragmentation and a possible lack of available open space in some urban fragments (Cane et al. 2006). Bees with ground nesting habits are the dominant type in this study, represented in the highest proportion by members of the genus *Centris*. The three cities examined possess specific local land use features that may account for the high proportion of ground nesting species. Streams that have not been culverted flow through, or at the periphery of, each city. Exposed stream banks serve as good potential nesting sites for common ground nesters such as Centris and Halictid species. In addition, the municipal storm-drain system found in the study cities is not an engineered concrete pipe, but instead a network of shallow trenches dug out along paved roadsides that channel water to nearby riparian areas. The exposed ground provides a network of well-drained soil that may be appropriate for nesting. Females of *Eulema* spp. were noted on several occasions walking along the bottoms of the dry drainage ditches in Liberia, supporting their usage of this exposed ground for nesting.

Clear patterns are present in both the richness and the abundance of foragers using this resource throughout the day. Two foraging periods are evident on *T. stans*: full day and early morning. Full day foragers include STB and Centris bees. Early morning foragers include AHB, *Xylocopa* spp. and especially *Euglossa* spp. In addition to having the broadest foraging times, Centris and STB taxa were found to forage on every resource that showed measureable bee activity in this sample. The occurrence of *Xylocopa* spp., *Euglossa* spp., *Eulema* spp., and other less numerous species was not common on all resources. An adequate assessment of species richness in urban faunas requires observations throughout the day and across multiple resources to account for rare visitors, as well as the variability in the attraction of individual resources.

Patterns in resource variability

The population of *T. stans* examined here showed variability in bee attraction, that to some extent can be explained by the greater landscape content within which sub-samples were found, suggesting that the surrounding landscape impacts the larger structure of urban bee communities. Regional trends did not hold true when examined at the city level. At a finer resolution, individual resources within the three cities were found to vary significantly in both the number of bees and the number of bee groups attracted. Inter-resource variability in bee visitation has been documented in local species in the family Bignoniaceae, namely, *Tabebuia rosea* (Frankie et al. 1982) and *T. ochracea*. The same is seen in some members of the family Fabaceae within this region, including *Dalbergia retusa*, *Gliricida sepium* and *Andira inermis* (Frankie et al. 1997; Frankie et al. 2005b). Suggested causes include: the quantity and quality of bloom; variation in both the volume and sugar content of nectar (Kevan 2001); inconsistencies in seasonal phenology, especially advanced or delayed blooming (Frankie et al. 2005b); variability in secondary compounds found in nectar (Roubik et al. 1995); competition for pollinators in the surrounding floral community; and the characteristics of the surrounding urban matrix (Cane et al. 2006).

Resource characteristics and differential bee foraging

Foraging strategies of bees are optimized, balancing resource acquisition with competition and energy consumption. This results in the development of patterns and techniques to facilitate efficient resource acquisition including: temporal flight patterns, feeding specialization, trap-lining behavior, and resource partitioning by landscape location and vertical stratum. While vertical stratification has been suggested by many tropical bee biologists (Roubik et al. 1982; Roubik 1993; Gumbert and Kunze 1999), in this particular system there were no significant patterns with respect to resource high or life form. Instead, the number of flowers that a resource possessed, a measure of resource abundance, was a significant driver of bee abundance. Resources with more flowers attracted more bees, irrespective of their height and life form. This trend was driven, in particular, by AHB and by Halictid taxa. The visitation rates of Centris taxa and STB were not influenced by resource characteristics and structure, which is consistent with wildland studies of foraging in these species groups (Roubik et al. 1982). The same study, however, did not establish any relationship between floral abundance and bee foraging.

Characteristics of the surrounding urban matrix may be structuring bee visitation at different spatial scales. Bagaces and Liberia have the most similar patterns of bee visitation and both are situated within similar regional land use; cattle grazing in modified grasslands punctuated by native dry forest species. Nearby are the biological reserve systems of Lomas Barbudal and Palo Verde. Cañas is different, sitting in the center of agricultural intensification. On a finer scale, Bagaces and Liberia are interspersed with more streams and riparian areas than Cañas. An investigation of the factors responsible for inter-tree variability in urban landscapes continues, focusing on factors unique to anthropogenic systems as well as the interplay between local and regional landscapes.

Differential visitation over time on the same resource is evident, and needs to be taken into consideration for monitoring. Mark-recapture studies in the region also (Frankie et al. 1976) indicate that bees tend not to switch resources during individual foraging days. Migration to nearby conspecifics was suggested in cases when either the original forage tree displayed lower attractiveness, or when a local neighbor displayed increased attractiveness. The factors mentioned previously as influencers of inter-resource attractiveness can function to alter the attractiveness of the same resource over time. Temporal patterns of sunlight and moisture availability, other climatic factors, bloom disturbance, and the mass visitation of a resource by pollen and nectar foragers can subsequently impact the perceived quality of the resource. Peaks of nectar flow that are either cyclical, or influenced by temperature and humidity have been noted in some tropical species (Frankie et al. 1974). For example, *G. sepium* exhibits intense nectar production peaks (so much so that an observer standing under a tree in peak nectar production will experience a 'nectar rain'), with corresponding increases in bee visitation. These patterns appear to cycle every three to five days. The dynamics of nectar flow and day-to-day bee visitation rates for *T. stans* are unknown and under investigation. Abiotic factors including wind, rain, and intense heat can affect flower retention and wilting. If bees are responding to floral quality and quantity as mentioned above, this may impact the numbers of bees recorded from day to day, especially if climatic variables are not consistent. In this particular region, however, daily patterns of temperature and humidity are relatively stable. Bees might be judging resource 'quality' with another metric.

Patterns in richness are likely driven by the sporadic occurrence of rare species. When these patterns were examined in each city, more consistent day-to-day patterns of richness were seen in Bagaces and Liberia, mentioned above as cities situated within a more natural landscape context. Larger scale landscape characteristics may also structure patterns of richness seen through time. Attempts to more adequately catalogue species richness will require more extensive sampling over a four to five year period due to both natural variability in pollinator populations (see Eardley et al. 2006 and the 2006 NRC report on Status of Pollinators in North America) and large scale cycles of seasonal variability common to the tropics (see also Frankie et al. 2005b and 2009 for a regionally specific explanation).

Monitoring considerations

In modified urban landscapes, *Tecoma stans* is an attractive resource plant that serves as a forage for bees in many guilds common to the wildland bee community. Individual resources have been shown to vary significantly in their ability to attract foraging bees. Resource characteristics and resource abundance are driving this trend in differential foraging to some extent. The careful selection of a diverse population of *T. stans* individuals is then required to achieve a balanced sample for effective monitoring. A comparative analysis of the community and species composition sampled using other standardized bee collecting methods, such as the bee inventory plot (LeBuhn et al. 2003), which employees a combination of passive pan traps and active aerial netting, would also verify if *T. stans* does indeed attract a representative sub-sample of the local community. Currently, such detailed data on the local bee species and their relationships is lacking, as is generally the case globally. Documenting and fully understanding the diversity of bees across all ecosystems is a daunting task that struggles from declining taxonomic expertise and funding constraints. Furthermore, a comparative sample of wildland and urban *T. stans* resources would provide insight into larger patterns of urban versus wildland bee community composition.

The dominance of *T. stans* in the urban flora due to its aesthetic value has provided a potential network of resources with monitoring possibilities. While there are some other species in this region that attract more species of bees (e.g., *Andira inermis* in Frankie et al. 2005b; Frankie et al. 2009), or that have higher rates of visitation (e.g., *Tabebuia rosea* and *T. ochracea*) the wide distribution of *T. stans* throughout urban landscapes and across the tropics, as well as year-round flowering, make it a good monitoring choice, especially if the goal is larger-scale landscape comparison. To truly determine if *T. stans* stands out as a potential magnet resource, a more detailed comparative study of the other highly attractive species in the area is needed.

Since *T. stans* resources are located on both public and private land within urban landscapes an opportunity for community based conservation and citizen science presents itself. A particularly high capacity for locally based conservation initiatives exists in this region of the Guanacaste province. Locals living in the study cities have a history of community involvement in local biodiversity conservation (see Frankie and Vinson 2004). Amigos de Lomas Barbudal, an early conservation organization, was started in conjunction with local participation and was instrumental in the development of the Lomas Barbudal Biological Reserve System. Subsequently, a culture of environmental education and outreach has grown to include the Center for Conservation of Nature in Bagaces (Centro para la Conservacion de la Naturaleza) and many other conservation efforts that have been linked to local government, schools, and universities.

Acknowledgements

Funding was provided by the Margaret C. Walker Fund in partnership with the Essig Museum of Entomology, at the University of California, Berkeley. I am very grateful to Dr. Laurence Packer and Jason Gibbs of York University, Toronto, Canada and Dr. Ricardo Ayala of UNAM, Mexico, for their assistance with specimen identification. I would like to thank Laura Fine and Meaghan Jastrebski who provided field assistance and good company throughout the dry season. I would also like to thank Steven La, Lindsay Kwong, and Casey Bodden for assistance in data management. Additionally, the hospitality of the Sandoval-Argon family made the research experience wonderful.

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Figures, Tables, and Appendices

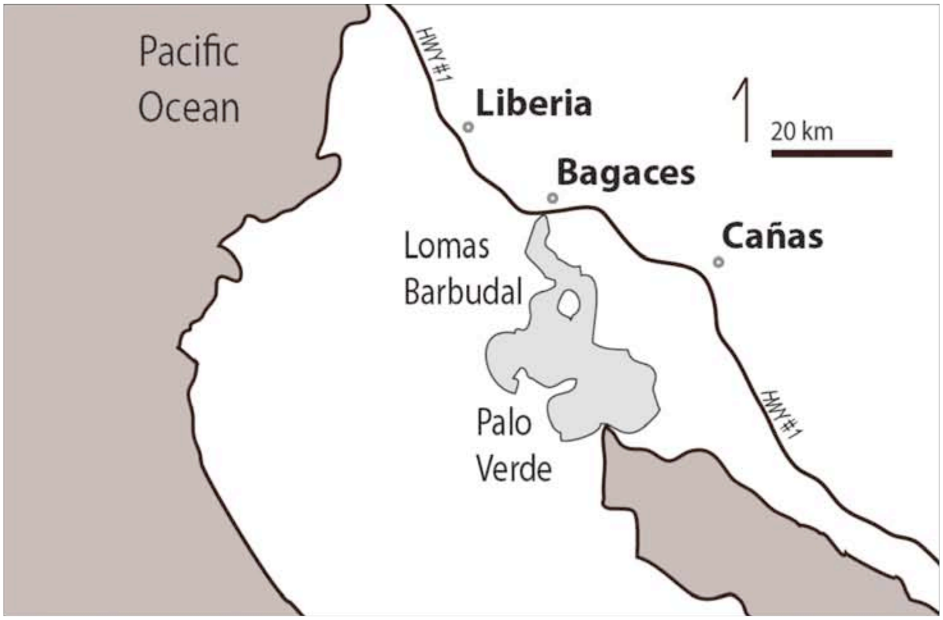

Figure 3.1: A map of the study region in the Pacific northwest of Costa Rica indicating the location of the study cities with reference to Central American Highway #1 and the nearby Biological Reserves of Palo Verde and Loma Barbudal highlighted in the lighter grey.

Figure 3.2: Two typical *Tecoma stans* trees lining a residential street in Cañas, Costa Rica. Photo credit: Victoria Wojcik.

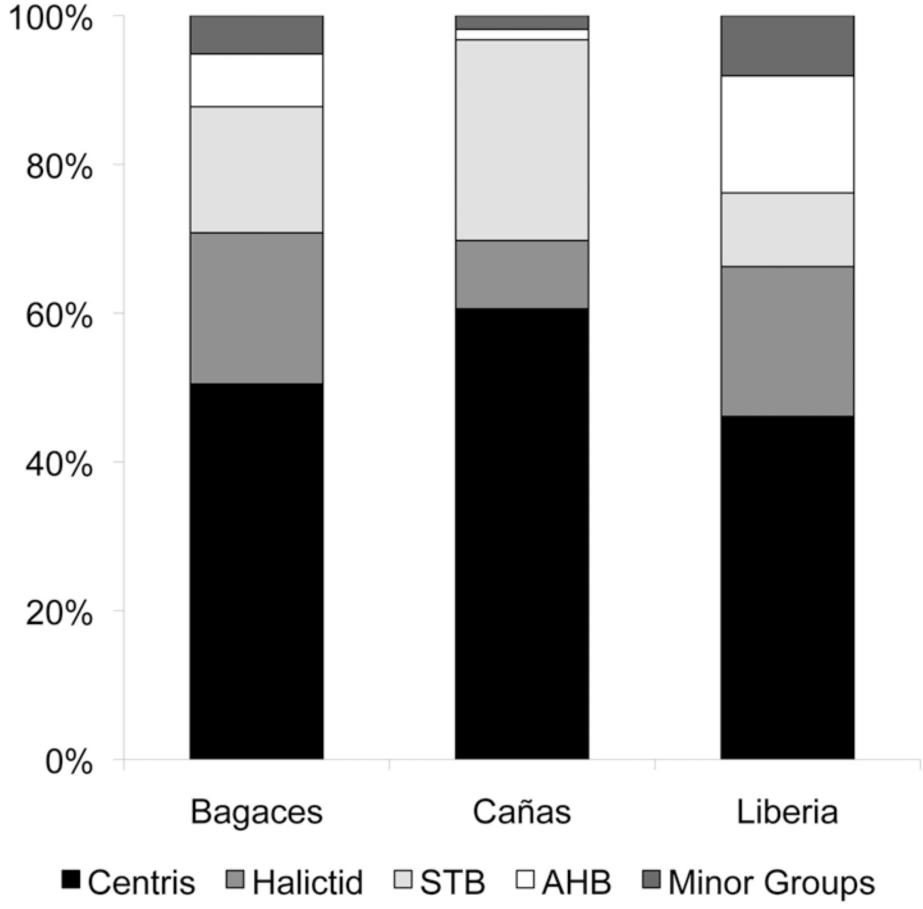

Figure 3.3: The representative proportions of the dominant bee groups from the total recorded foragers to *T. stans* trees in the cities of Bagaces, Cañas, and Liberia. "Minor Groups" represents those bees that accounted for less than 2% of the total abundance found at each site, and in each case included: Xylocopa, Epicharis, Euglossa, Eulema, Mesoplea, Melicta, and small bees.

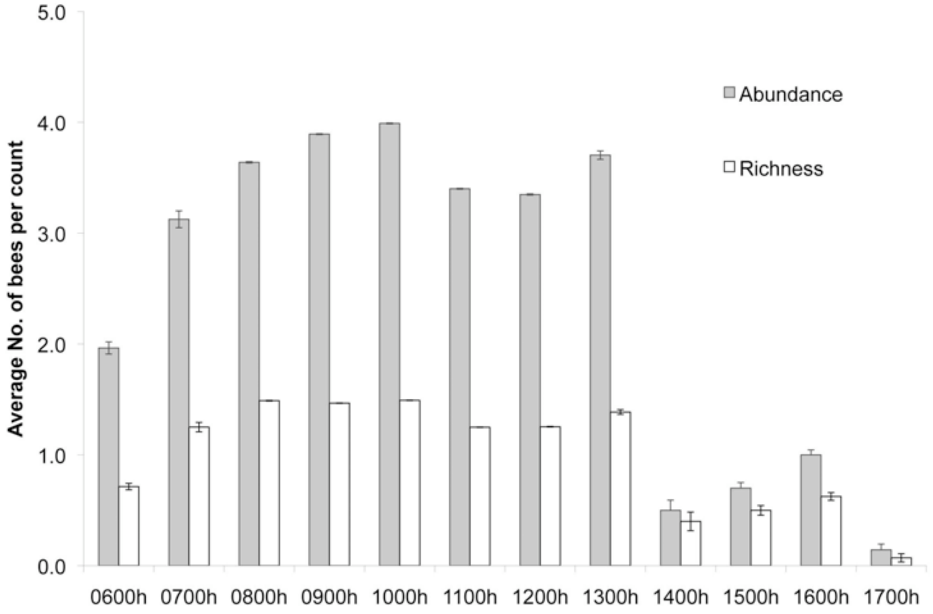

Figure 3.4: The daily patterns of forager abundance and richness on *T. stans* from all samples between the 0600h and 1700h, highlighting the significant decline in both after 1400h. Data are represented as the average number of bees recorded per 3 minute count across each one-hour time slot.

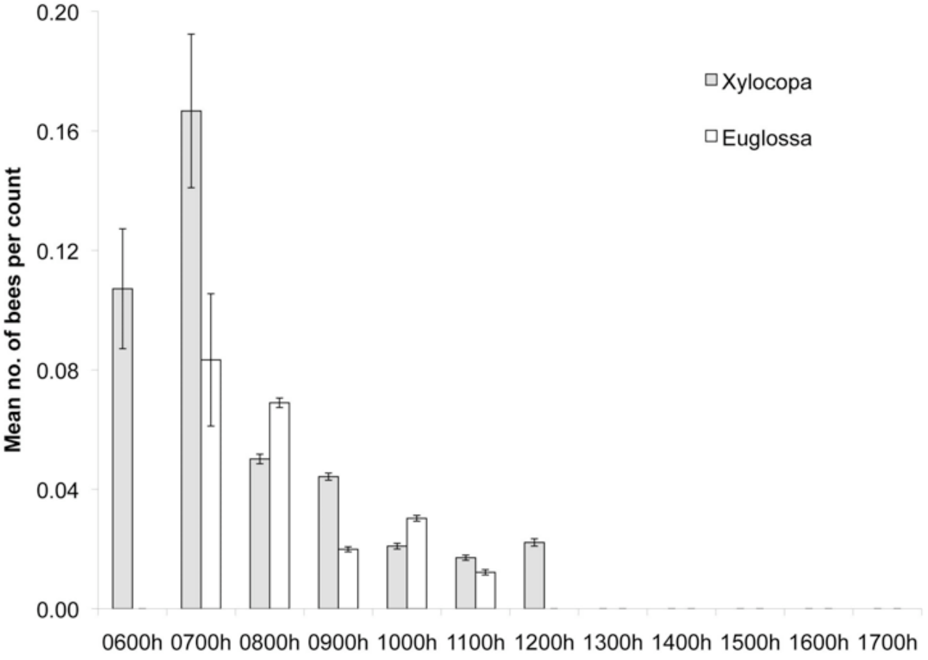

Figure 3.5: The representative patterns of typical early day foragers, *Euglossa* spp. (solid white) and *Xylocopa* spp. (solid grey). Early day foragers display a marked decline and are not present after 1200h.

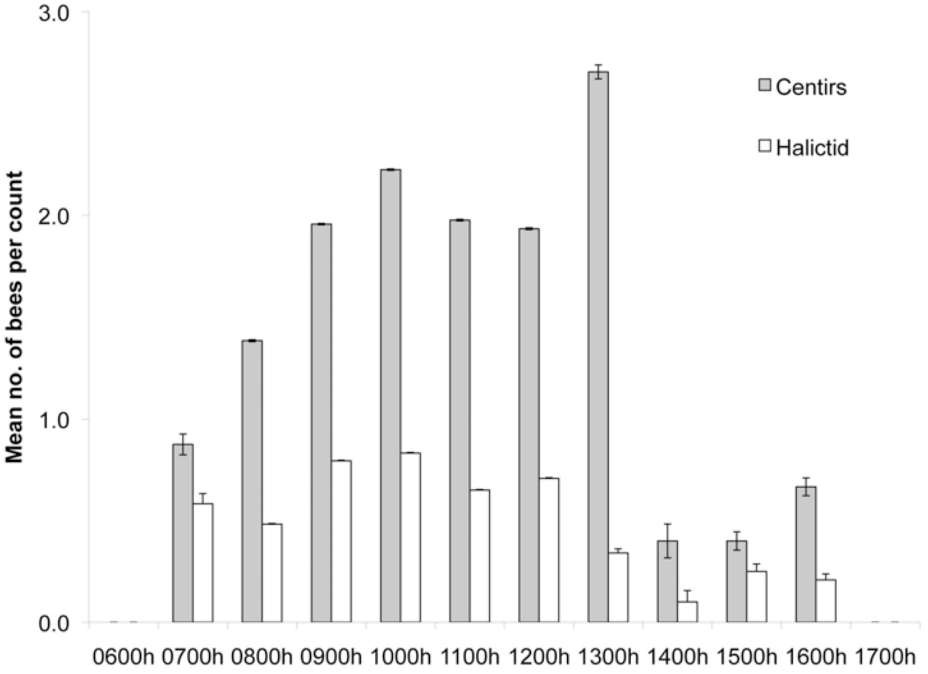

Figure 3.6: The representative patterns of typical full day foragers, *Centris* spp. (solid white) and members of the family Halictidea (solid grey). While the relative abundance of full-day foragers can vary, their patterns of visitation over time are congruent.

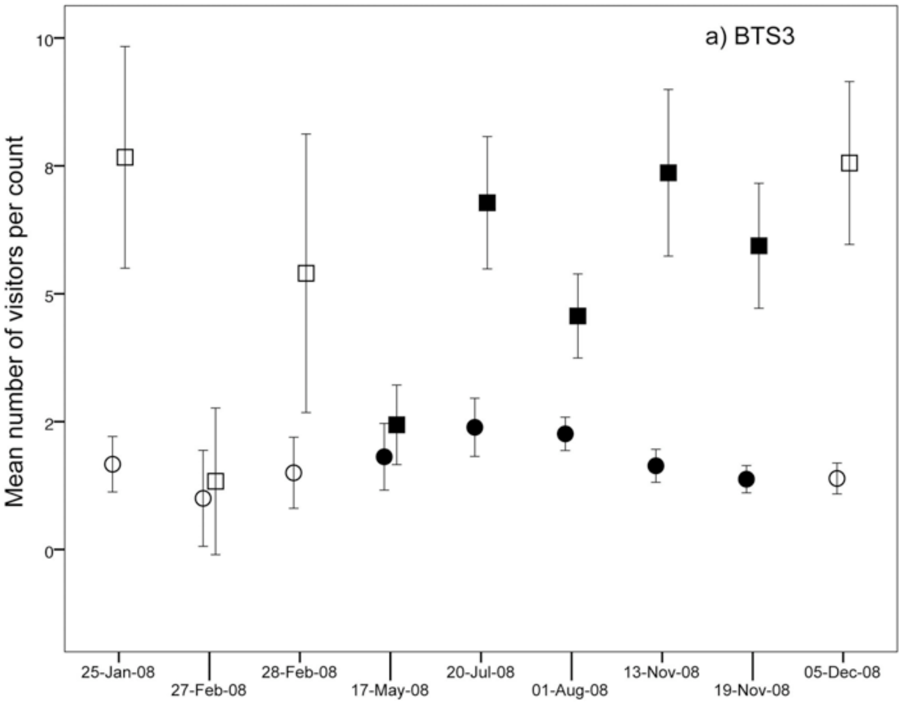

Figure 3.7a: The mean abundance (square) and richness (circle) of bees foraging on *T. stans* BTS3 that was sampled in Bagaces on nine occasions. The date of each sample is indicated on the categorical axis. Hollow white markers represent measurements collected during the wet season (May-November) and solid black markers represent measurements collected during the dry season (December-April). Bars represent the 95% confidence interval.

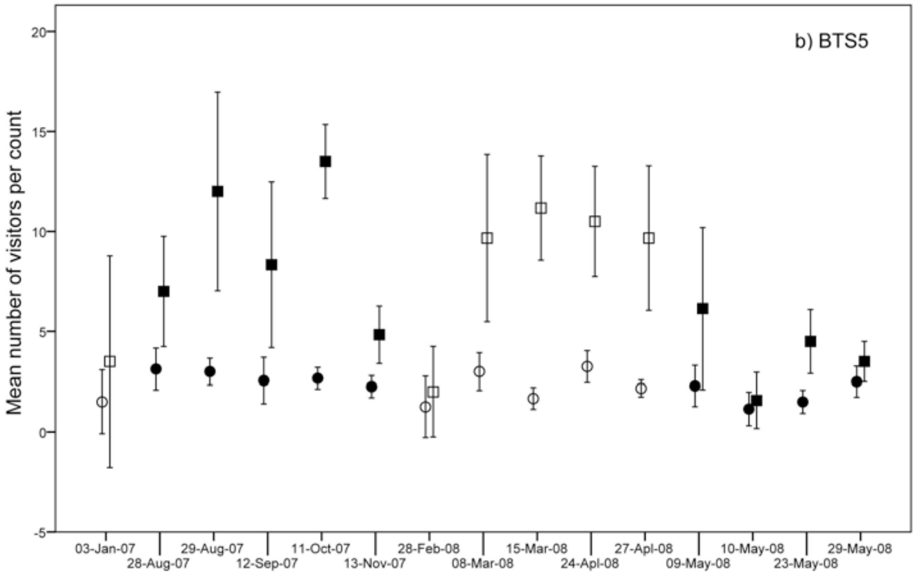

Figure 3.7b: The mean abundance (square) and richness (circle) of bees foraging on *T. stans* BTS5 that was sampled in Bagaces on 15 occasions. The date of each sample is indicated on the categorical axis. Hollow white markers represent measurements collected during the wet season (May-November) and solid black markers represent measurements collected during the dry season (December-April). Bars represent the 95% confidence interval.

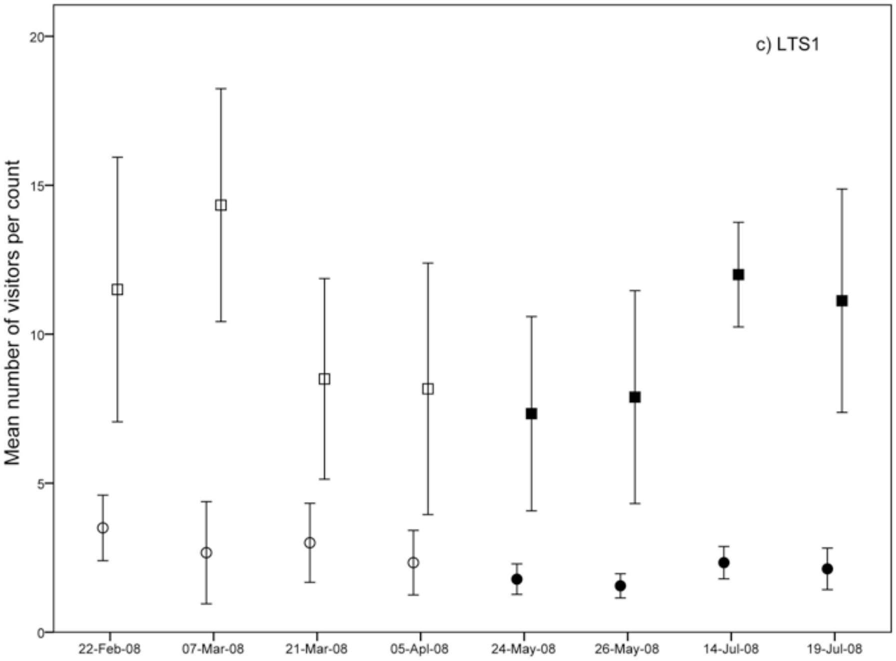

Figure 3.7c: The mean abundance (square) and richness (circle) of bees foraging on *T. stans* LTS1 that was sampled in Liberia on eight occasions. The date of each sample is indicated on the categorical axis. Hollow white markers represent measurements collected during the wet season (May-November) and solid black markers represent measurements collected during the dry season (December-April). Bars represent the 95% confidence interval.

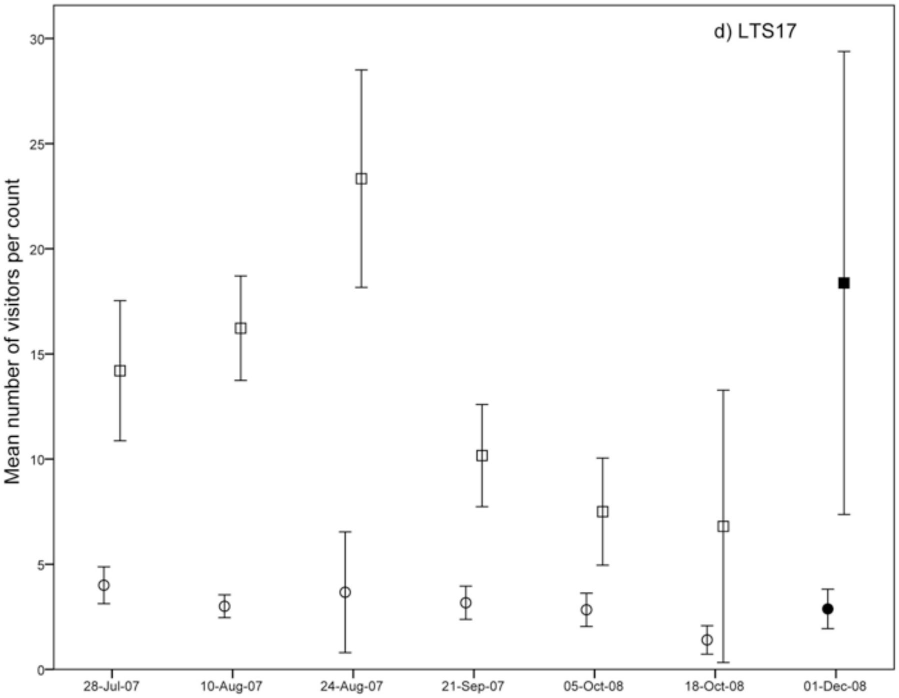

Figure 3.7d: The mean abundance (square) and richness (circle) of bees foraging on *T. stans* LTS17 that was sampled in Liberia on seven occasions. The date of each sample is indicated on the categorical axis. Hollow white markers represent measurements collected during the wet season (May-November) and solid black markers represent measurements collected during the dry season (December-April). Bars represent the 95% confidence interval.

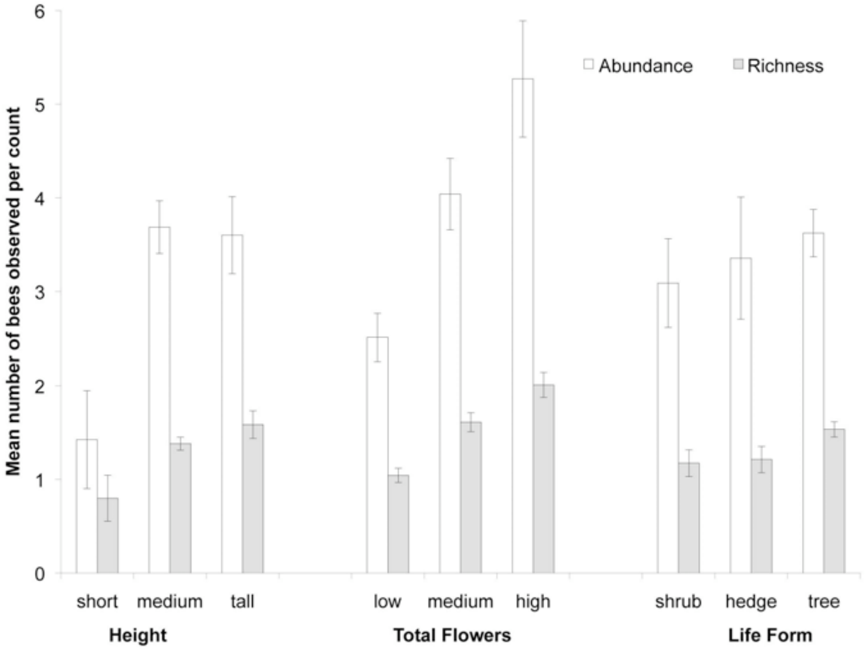

Figure 3.8: The mean abundance and richness of bees attracted per count to *T. stans* as a function of three different resource characteristics: height (short= less than 1 m; medium= between 1 m and 3 m; tall= taller than 3 m), life form (shrub, hedge, tree), and floral abundance (low= less than100 flowers; medium= 100 to 300 flowers; high= more than 300 flowers).

Table 3.1: Multivariate ANOVA assessing the variability in individual bee abundances, total bee abundance, and richness throughout the day from all counts recorded across the entire sample of *T. stans* resources (α=0.05, df=11,2074). Significant results, p>0.05, are indicated by the * symbol.

Bee Group	**MSE**	**F**	**p**
Centris*	39.682	5.903	0.000
Epicharis	0.016	0.448	0.934
Euglossa*	0.098	4.007	0.000
Eulema	0.112	1.548	0.108
Halictid*	5.863	2.789	0.001
Honeybee*	3.567	7.728	0.000
Melitoma	0.003	0.517	0.893
Mesoplea*	0.018	1.881	0.037
small bee	0.002	0.236	0.995
Trigona*	13.027	7.361	0.000
Xylocopa*	0.096	2.141	0.015
*Abundance**	73.291	5.91	0.000
*Richness**	8.958	9.638	0.000

Table 3.2: The range of attractiveness seen across all *Tecoma stans* resources, as well as within populations located in Bagaces, Cañas, and Liberia, presented as the minimum, maximum, and mean number of total bees (abundance) and bee types (richness) recorded per 3 minute count.

Location	**Min**	**Max**	**Mean**	**Standard Deviation**	**Coefficient of Variation**
All Cities					
Abundance	0	32	3.55	3.57	1.01
Richness	0	4	1.35	0.98	0.73
Bagaces					
Abundance	0	29	3.28	3.86	1.18
Richness	0	4	1.15	0.95	0.83
Cañas					
Abundance	0	27	3.89	3.64	0.94
Richness	0	4	1.37	0.86	0.63
Liberia					
Abundance	0	32	3.47	3.27	0.94
Richness	0	4	1.48	1.09	0.74

Table 3.3: The multivariate ANOVA testing for the main and interaction effects of resource characteristics on the mean rates of bee abundance and richness attracted.

Resource Characteristics	**Bee Group**	**Type III SS**	**df**	**MS**	**F**	**Sig.**
Corrected Model	Abundance	276.948	16	17.309	4.014	0.000
	Richness	26.775	16	1.673	4.836	0.000
Intercept	Abundance	493.635	1	493.635	114.465	0.000
	Richness	76.948	1	76.948	222.352	0.000
Life Form	Abundance	0.992	2	0.496	0.115	0.891
	Richness	1.094	2	0.547	1.580	0.211
Height	Abundance	11.263	2	5.631	1.306	0.275
	Richness	0.39	2	0.195	0.563	0.571
Total Flowers	Abundance	79.587	2	39.793	9.227	0.000
	Richness	10.918	2	5.459	15.774	0.000
Life Form * Height	Abundance	13.82	2	6.910	1.602	0.206
	Richness	0.815	2	0.407	1.178	0.312
Life Form * Total Flowers	Abundance	35.584	4	8.896	2.063	0.091
	Richness	0.773	4	0.193	0.558	0.693
Height * Total Flowers	Abundance	1.25	3	0.417	0.097	0.962
	Richness	1.838	3	0.613	1.770	0.157
Life Form * Height * Total Flowers	Abundance	0.554	1	0.554	0.128	0.721
	Richness	0.045	1	0.045	0.131	0.719
Error	Abundance	448.505	104	4.313		
	Richness	35.99	104	0.346		
Total	Abundance	2142.755	121			
	Richness	290.568	121			
Corrected Total	Abundance	725.454	120			
	Richness	62.766	120			

Abundance R^2=0.382; Adj. R^2=0.287
Richness R^2=0.472; Adj. R^2=0.338

Table 3.4: The multivariate ANOVA testing for the main and interaction effects of resource characteristics on the mean foraging rates of the four dominant bees groups: Centris, Halictid, AHB (African Honeybees), and STB (Stingless Bees).

Resource Characteristics	Bee Group	Type III SS	df	MS	F	Sig.
Corrected Model	Centirs	95.065	16	5.942	2.562	0.002
	Halictid	40.107	16	2.507	3.286	0.000
	AHB	7.226	16	0.452	5.649	0.000
	STB	8.886	16	0.555	1.112	0.354
Intercept	Centirs	103.453	1	103.453	44.609	0.000
	Halictid	25.17	1	25.17	32.995	0.000
	AHB	1.137	1	1.137	14.224	0.000
	STB	17.942	1	17.942	35.929	0.000
Life Form	Centirs	0.688	2	0.344	0.148	0.862
	Halictid	8.356	2	4.178	5.477	0.005
	AHB	0.3	2	0.15	1.878	0.158
	STB	1.703	2	0.851	1.705	0.187
Height	Centirs	3.022	2	1.511	0.651	0.523
	Halictid	5.512	2	2.756	3.613	0.030
	AHB	0.035	2	0.017	0.218	0.805
	STB	0.57	2	0.285	0.571	0.567
Total Flowers	Centirs	9.105	2	4.553	1.963	0.146
	Halictid	7.269	2	3.634	4.764	0.010
	AHB	1.366	2	0.683	8.54	0.000
	STB	1.654	2	0.827	1.657	0.196
Life Form * Height	Centirs	5.653	2	2.827	1.219	0.300
	Halictid	1.314	2	0.657	0.861	0.426
	AHB	0.663	2	0.331	4.144	0.019
	STB	1.575	2	0.788	1.577	0.211
Life Form * Total Flowers	Centirs	21.88	4	5.47	2.359	0.058
	Halictid	15.542	4	3.886	5.094	0.001
	AHB	0.062	4	0.015	0.193	0.942
	STB	2.284	4	0.571	1.144	0.340
Height * Total Flowers	Centirs	2.478	3	0.826	0.356	0.785
	Halictid	2.8	3	0.933	1.224	0.305
	AHB	0.637	3	0.212	2.658	0.052
	STB	1.326	3	0.442	0.885	0.451
Life Form * Height *Total Flowers	Centirs	0.011	1	0.011	0.005	0.944
	Halictid	2.099	1	2.099	2.751	0.100
	AHB	0.597	1	0.597	7.472	0.007
	STB	0.702	1	0.702	1.405	0.239
Error	Centirs	241.189	104	2.319		
	Halictid	79.335	104	0.763		
	AHB	8.314	104	0.08		
	STB	51.936	104	0.499		
Total	Centirs	704.485	121			
	Halictid	163.554	121			
	AHB	19.344	121			
	STB	103.938	121			
Corrected Total	Centirs	336.255	120			
	Halictid	119.442	120			
	AHB	15.54	120			
	STB	60.822	120			

Centirs R^2= 0.283; Adj. R^2= 0.172
Halictid R^2= 0.336; Adj. R^2= 0.234
AHB R^2= 0.465; Adj. R^2= 0.383
STB R^2= 0.146; Adj. R^2= 0.015

Appendix 3.i: Specie list of bees collected while foraging on *Tecoma stans* (Bignoniaceae) in the cities of the Bagaces, Cañas, and Liberia, Guanacaste, Costa Rica. Sociality (Eu=eusocial, S=solitary, S-ag= solitary but aggregate nester, CP=Celptoparasite), nesting habit (G=ground nester, G-v=ground nester preferring sloped/vertical sites T=twig nester, C=cavity nester, W=wood excavation), and feeding ranges (Poly=Polylectic, Oligo=Oligolectic, Meso=Mesolectic) are indicated. Classifications are adapted from Michener 2000.

Family	**Species**	**Nesting Habit**	**Sociality**	**Feeding Range**
Apidae:	*Ancyloscelis* sp.	G/G-v	S-ag	Oligo
	Apis mellifera scutellata Latreille	C	Eu	Poly
	Augochlora nigrocyanea Cockerell	G	S	Meso
	Centris aethyctera Snelling	G-v	S	Meso
	Centris eurypatana Snelling	G-v	S-ag	Meso
	Centris heithausi Snelling	G-v	S	Meso
	Centris sp.	G	S	Meso
	Ceratina sp.	T	S	Oligo
	Epicharis elegans Smith	G	S	Oligo
	Eufriesea sp.	C	S	Oligo
	Euglossa viridissima Friese	C	S	Oligo
	Eulema sp.	C	S/S-ag	Oligo
	Melitoma sp	G-v	S-ag	Oligo
	Mesoplia decorata	G	CP‡	Oligo
	Nannotrigona perilampoides (Cresson)	C	Eu	Poly
	Plebeia (Nogueirapis) sp.	C	Eu	Poly
	Plebeia frontais Friese	C	Eu	Poly
	Tetragonisca angustata (Lep.)	C	Eu	Poly
	Trigona fulviventris Guérin-Méneville	C	Eu	Poly
	Trigona sp.	C	Eu	Poly
	Xylocopa fimbriata Fabricius	W	S	Oligo
	Xylocopa subvirescens Cresson	W	S	Oligo
Halictidae:	*Agapostemon nasutus*	G	S	Oligo
	Halictus lutescens Friese	G/G-v	S-ag	Oligo
	Lasioglossum Dialictus sp.1	G/G-v	S-ag	Oligo
	Lasioglossum Dialictus sp.2	G/G-v	S-ag	Oligo

‡cleptoparastie on Centris and Epicharis species

Appendix 3.ii: The results of multivariate ANOVA comparing the relative occurrences of the 11 sampled bee groups across all samples taken between the three study cities; Bagaces (B), Cañas (C), and Liberia (L), as well as the relative differences in the average visitor abundance and taxon richness of the bees identified across all of the counts taken in each of the three cities. Significant differences (p>0.05) are indicated by the * symbol.

						95% Confidence Interval	
Bee Group	**City I**	**City J**	**Mean Difference Between Cities (I-J)**	**Std. Error**	**Sig.**	**Lower**	**Upper**
Honeybee	B	C	0.110*	0.039	0.004	0.035	0.186
	B	L	-0.191*	0.037	0.000	-0.263	-0.119
	C	L	-0.302*	0.035	0.000	-0.370	-0.233
Centris	B	C	-0.773*	0.148	0.000	-1.063	-0.482
	B	L	-0.047	0.141	0.741	-0.323	0.230
	C	L	0.726*	0.135	0.000	0.462	0.990
Epicharis	B	C	0.000	0.011	1.000	-0.021	0.021
	B	L	-0.039*	0.010	0.000	-0.059	-0.020
	C	L	-0.039*	0.010	0.000	-0.058	-0.020
Euglossa	B	C	0.015	0.009	0.100	-0.003	0.032
	B	L	0.001	0.009	0.899	-0.016	0.018
	C	L	-0.014	0.008	0.095	-0.030	0.002
Eulema	B	C	0.021	0.015	0.164	-0.009	0.051
	B	L	-0.059*	0.014	0.000	-0.088	-0.031
	C	L	-0.081*	0.014	0.000	-0.108	-0.053
Halictid	B	C	0.538*	0.082	0.000	0.377	0.698
	B	L	0.133	0.078	0.088	-0.020	0.286
	C	L	-0.405*	0.075	0.000	-0.551	-0.258
Mesoplea	B	C	0.000	0.006	1.000	-0.011	0.011
	B	L	-0.017*	0.005	0.002	-0.027	-0.006
	C	L	-0.017*	0.005	0.001	-0.027	-0.007
Melicta	B	C	0.016*	0.004	0.000	0.008	0.024
	B	L	0.013*	0.004	0.001	0.006	0.021
	C	L	-0.002	0.004	0.525	-0.010	0.005
small bee	B	C	0.005	0.006	0.370	-0.006	0.017
	B	L	-0.005	0.006	0.324	-0.016	0.005
	C	L	-0.011*	0.005	0.044	-0.021	0.000
Trigona	B	C	-0.521*	0.076	0.000	-0.670	-0.373
	B	L	0.012	0.072	0.870	-0.129	0.153
	C	L	0.533*	0.069	0.000	0.398	0.668
Xylcopa	B	C	-0.045*	0.012	0.000	-0.068	-0.021
	B	L	-0.017	0.011	0.140	-0.039	0.006
	C	L	0.028*	0.011	0.011	0.006	0.049
Abundance	B	C	-0.609*	0.202	0.003	-1.006	-0.212
	B	L	-0.184	0.193	0.339	-0.562	0.194
	C	L	0.425*	0.184	0.021	0.063	0.786
Richness	B	C	-0.218*	0.056	0.000	-0.327	-0.109
	B	L	-0.329*	0.053	0.000	-0.433	-0.226
	C	L	-0.111*	0.051	0.028	-0.210	-0.012

CHAPTER 4 – A MESO-SCALE ANALYSIS OF BEE FORAGING IN URBAN LANDSCAPES: RESOURCE QUANTITY AND DISTRIBUTION AS THE MAJOR DRIVERS OF BEE VISITATION IN THREE TROPICAL DRY FOREST CITIES.

Abstract

The influence of resource characteristics and landscape variables on the visitation rates of bees foraging on *T. stans* resources were examined in three tropical dry forest cities in Costa Rica. A three-year study monitored the occurrence bees at 120 resources. Visitation was catalogued as the number of individual bees (the total visitor abundance) and the number of different bee taxa (the overall taxon richness) using repeated standardized observations in a 1-meter by 1-meter count window for three minutes. Regression modeling was then used to determine the degree to which resource and landscape characteristics influenced bee occurrence at a site. In particular, the abundance of flowers possessed by a resource was significantly influential in structuring the overall patterns of bee visitation, with this variable occurring in the majority (30 of 32) of the visitation models developed. Individual bee groups displayed differential responses to the tested variables, with some responding exclusively to resource characteristics and other responding to landscape variables. The size of the city influenced the complexity of the visitation model that described the taxon richness patterns, with increasing complexity correlating with decreasing city size. With respect to uniquely urban variables, residential land use stood out, with a significant positive influence on bee foraging rates, especially generalist species such as African honeybees and native Stingless bees.

Introduction

The heterogeneous landscape of urban systems creates a patchwork of potential habitats. Remnant and constructed ecological features are present throughout the city. The biotic and abiotic portions of the urban biome are dynamic and subject to intensive human management. Gardens change from year-to-year, vacant land develops, parks are manicured, and derelict sites are rehabilitated. Each city block occupies a unique point in the urban ecosystem, with adjacent blocks often providing different resources to organisms. Within all of this, urban landscapes have been shown to be ecologically functional at many levels, providing homes for flora and fauna (Angold et al. 2006, Smith et al. 2006).

Early twentieth century taxonomic surveys verify that bees have been a fixture in urban landscapes for some time (Robertson 1929; Graenicher, 1930). Diverse communities of bees have been documented in cities across the globe in North America (Frankie et al. 2002; Tommasi et al., 2004; Matteson et al., 2008), Central America (Frankie et al. 2009), South America (Taura and Laroca 2001; Loyola and Martins 2006; Nates-Parra 2006), Europe (Banaszak 1982; Berezin 1995; Saure 1996), and Asia (Sakagami and Fukuda 1973; Hisamatsu and Yamane 2006). In addition to these recently published accounts, many naturalists have documented "back-yard" bee faunas (Owen 1991). The existence of rich floral resources within cities provides food resources to which bees are preferentially attracted (Tommasi et al. 2004; Hisamatsu and Yamane 2006; Fetridge et al. 2008). Studies that have examined the ecology of urban bees in more detail reveal patterns and trends in occurrence and behavior within the city limits.

A change in the bee community structure (Lui and Koptur 2003) as well s in absolute bee numbers have been observed along wildland-to-urban gradients, often with urban landscapes having increased diversity patterns. A comparison of bee richness between multiple landscapes in the northeaster United States revealed a more diverse bee community within the suburbs when compared to the adjacent forested landscape (Winfree et al. 2007). This general trend in increase species numbers within certain urban landscapes has been suggested to be driven by the increased floral resource diversity present in private residential gardens (Smith et al. 2006; Loram et al. 2008). Not all urban landscapes that possess diverse flora attract measurable numbers of visiting bees; instead, the composition of the urban flora and the local garden management culture are influential (Frankie et al. 2009). Temporal foraging shifts between wild and urban landscapes have been observed, suggesting that urban resources that persist through time are able to sustain the foraging of bees when wildland resources are diminished or out of bloom (Cane et al. 2006). Although it is clear that bees are present and abundant in some urban landscapes, observations, and published works demonstrate their distribution within the urban landscape to vary.

The successful acquisition of food resources is essential to the reproduction and survival of bees that actively provision pollen and nectar for their developing brood (Michener 2000). The costs and benefits of foraging are therefore carefully calculated and optimized. Flight direction and duration, as well as the time spent foraging on a resource patch by wildland bumblebees are influenced by a resource quality, and this is particularly evident in larger bodied species with increased energy requirements, such as bumblebees (Heinrich 1979). The spatial distribution of resource patches also structures the flight patterns and stay-times displayed by bumblebee foragers (Cartar and real 1997). The size of the resource patch has been shown to correlate with bee visitation, with larger patches receiving more visits (Cresswell and Osborne 2004). Many bee species also forage along trap-lines, following the same route from day-to-day reducing the energy losses associated with searching for new food sites (Roubik 1989; Williams and Thomson 1998). It is, however, unclear how urban land use the impacts foraging strategies of bees, and if these impacts are consistent across all urban bee species.

At the landscape level, contrasting results exist for the interplay between patch dynamics and landscape context. Steffan-Dewenter and Kuhn (2003) found that the local landscape context had more of an impact on honeybee foraging than the characteristics of the foraging site. A similar pattern was reported by Heard et al. (2007) when the bumblebee density in agro-environments was examined. In contrast, Collevatti et al. (2000) showed that the quality and quantity of resources at constructed patches determined the foraging patterns in seven bee species, irrespective of the local landscape. In a study of the tropical dry forest in Costa Rica, nearness to undisturbed forests increased the number of bees visiting a site and the local land management had little to no effect (Brosi et al. 2007). Further differential responses at multiple landscape scales have been documented between individual bee guilds in complex landscape systems (Steffan-Dewenter et al. 2002). These differential responses to resource characteristics and landscape context that are exhibited by individual bee species and bee groups may be driven by different variables in different ecosystems. These trends remain to be determined, especially in urban landscapes.

The goal of this study is to achieve a better understanding of how site specific, neighborhood-scale, and more regional landscape-level characteristics interact and impact bee visitation and the composition of foraging bees within urban ecosystems. The following study aims to: (1) describe and model the factors that are influencing bee food resource usage in the tropical dry forest urban system; (2) further examine these factors at the community level and in terms of individual bee guilds to see if congruent or contrasting patterns emerge; and (3) assess the influences of the regional landscape context and city size on bee resource usage. Distance to wildland habitats, proximity to other landscape features (riparian areas and open space), land use type (residential versus commercial), local resource characteristics (quality, character, and density), and resource distribution are examined for their effect on the abundance and richness of bees foraging on *Tecoma stans* in tropical urban landscapes in Costa Rica. Within the mix of variables that might be influencing resource usage by bees in cities are those that are unique to urban landscapes, such as residential and commercial land use and the separation of a site from the wild land habitat by the urban matrix. A parallel focus of this analysis is to determine to what extent these '*urban'* factors impact bee resource usage.

Materials and Methods

The study was conducted from July 2007 to March 2009, during which time the visitation of bees to 120 *T. stans* resources in three tropical dry forest cities (Bagaces, Cañas, and Liberia, Costa Rica) was recorded and monitored.

Site description

The cities of Liberia (10°37'47.19"N, 85°26'17.75"W), Bagaces (10°31'34.29"N, 85°15'17.73"W), and Cañas (10°25'35.95"N, 85°05'28.02"W) lie in a row along Central America Highway 1 in the Guanacaste province of Costa Rica. These three cities are characteristic of developing cities in Costa Rica, with increasing peripheral growth due to increased commercial and residential development. The three cities range in size and population but are characterized by similar patterns of urbanization and municipal land use. The size of each city was calculated using ArcMap 9.3 (© ESRI Inc. 2009, Chicago IL). Liberia is approximately 7.97 $km^{2,}$ Bagaces is approximately 0.76 km^2, and Cañas is approximately 2.98 km^2. The most recently available census data puts the urban population of Liberia, the provincial capital, at 34,469, Bagaces at 3,645, Cañas at 16,512, and (INEC 2000).

Regional Landscape Classification

A combination of satellite imagery, local zoning records, and site visits were used to assess and quantify the surrounding regional land use. The natural surrounding landscape is tropical dry forest; an ecosystem dominated by mass-flowering angiosperms constituting savanna and mesic habitats. The natural habitat has been fragmented to varying degrees by cattle ranching, agriculture, and commercial development. Cattle ranching and large scale hay and feed growing dominate the landscape surrounding both Bagaces and Liberia. These two cities also lie in closer proximity of a network of biological reserves and conservation areas, as well as private ranches. Cañas is surrounded by more intensive irrigated agriculture.

Urban Land Classification

The landscape characteristics and classifications of urban land use were coded from satellite images and from ground observations, where appropriate. Appendix 4.i lists the set of landscape and resource characteristic variables used in this study, along with the variable name abbreviations used in the statistical analysis. The distance of each tree to the urban-wildland (d wui) interface and the distance of each tree to the nearest riparian (d rip) area was calculated in ArcGIS using the Near Feature tool (ArcMap 9.3 © ESRI Inc. 2009, Chicago IL). Nearest Neighbor was used to find the closest conspecific individual. The number of *T. stans* individuals within radii of 10 m, 50 m, and 100 m were calculated in ArcGIS by first creating buffers polygons of the corresponding distances and then using Points in Polygon tool in the Hawth's Tools package.

Proximity to open space (open space) and urban land classification as either commercial (com) or residential (res) was coded categorically from a combination of satellite imagery and ground observations. Proximity to open space was coded as present (1) when the *T. stans* individual was on, or adjacent to, a city block that contained unmanaged open spaces (e.g., large yards, vacant lots) and public parks or fields. The variable was coded as absent (0) when there was no adjacent open space. Land use was classified as residential if the dominant usage on the block was either single or multifamily housing and the variable was coded as (1). Land use was classified as commercial if the dominant use consistent of either public or private business, shopping, government offices, banks, and parking lots, and this variable was coded as (0).

Resource Characterization

The yellow trumpet tree, *Tecoma stans* Kunth (Bignoinaceae) is a common mass-flowering woody perennial found across Costa Rica, and much of the tropics. Its native range in the Americas extends from the south central and southeastern United States (Arizona to Florida) to the Antilles, down into Argentina (Hammel 2005; Zuchowski 2007). In urban environments *T. stans* is prominent in home gardens, city squares, and lining city streets. In the three urban landscapes studied here, *T. stans* is ubiquitous and well distributed. The series of photographs displayed in Figures 4.1 through 4.4 present the variation in resource characteristics and the surrounding urban landscape within which *T. stans* is found. Individuals can reach a height of 10 meters (Zuchowski 2007), but are commonly shorter in urban landscapes. Multiple morphologies are displayed by urban *T. stans* resulting form pruning and management. As a result individuals can be a low shrub, a taller hedge, or a tree with a range of trunk branching patterns. Although *T. stans* flowers year-round, the most intense flowering occurs between November and March. Previous work has indicated that *T. stans* attracts a wide range of bee species, representing multiple feeding, social, and size guilds, and accounting for approximately 10% of the local wildland bee species diversity (see Chapter 3).

A survey of each city was conducted to catalogue all visible *T. stans* individuals. A combination of local knowledge and street canvassing was used to complete the resource survey over the study period. Each individual *T. stans* was mapped using a hand-held GARMIN Vista C *e*trex GPS unit. The GPS coordinates were downloaded using DNRGarmin (Minnesota Department of Natural Resources, v 5.4.1, 2008, St. Paul, MN) and were then uploaded into ArcGIS. In total, 147 individuals were catalogued, of which 120 that were easily accessible from public land, and were used in the study. The catalogued individuals were given unique alphanumeric identifies as mentioned in the previous chapter (see Chapter 3). Figures 4.5 through 4.7 show the distribution of all of the catalogued *T. stans* resources in the three cities. Each *T. stans* individual was also photographed digitally for visual reference, character coding, and resource metric estimation. Resource height and crown width at the widest part of the crown were estimated from the referenced photographs to the nearest 25 cm. Each individual was also field-coded into three classes of life form (shrub, hedge, or tree) depending on its shape (see Chapter 3 for a more thorough explanation of the life form coding).

The number of flowers that an individual *T. stans* possessed was estimated using a stratified sub-sample of the inflorescences in the canopy. The canopy of each resource was fractioned into a manageable sector based on the overall size (either 2, 4, 8, or 10 sectors). The number of fractioned sectors was then used as an expansion factor (k) to calculate the estimated number of inflorescences (i) and the subsequent total flowers per resource (flw). The total number of inflorescences in one randomly selected sector was counted (i). A random subsample of the enumerated inflorescences was then selected and the total number of flowers contained in each inflorescence was counted, and averaged over the total sample (f). The calculated average number of flowers per inflorescence was then multiplied by the number of inflorescences and the expansion factor as follows:

$$\text{flw} = f \times i \times k\,,$$

where i is equal to the number of enumerated inflorescences in a random sector; k is the expansion factor that is equal to the number of sectors; and f is the estimate of mean floral abundance per inflorescence. All calculations were performed in Microsoft Excel 2008. In the case of some individual resources that possessed very few flowers (BTS12, BTS45, CTS5, CTS7, CTS36, LTS39, LTS42, LTS49, LTS58, and LTS65) the total number of flowers was enumerated using a census.

Bee Monitoring and Identification

The bee visitor abundance and richness was measured at each resource within a standardized 1-meter by 1-meter square observation frame that was visually projected onto an easily observable and unobstructed area of the floral resource. The visitation rates of bees to all of the flowers within this visual frame were recorded for the duration of three minutes that were timed with an electronic stopwatch. Bee visitation counts were taken approximately every 45 minutes between the daylight hours of 0600h and 1800h. Efforts were made to randomize the observation frames over repeated visits to each resource to achieve a more representative account of bee foraging at each sample. Samples were repeated at three temporal scales: throughout the day, across multiple days, and across the wet and dry seasons. Bee visits were counted at eight evenly spaced times throughout the day between the hours of 0800h and 1400h, corresponding to the peak visiting hours of *T. stans,* in an effort to catalogue the total community using this species which is known to be temporally variable. To acquire a measure of coarse taxon richness, bee taxa were identified on-the-wing to one of eleven taxonomic categories: Africanized honeybees (AHB: *Apis mellifera scutellata*), Stingless bees (STB: *Trigona* spp.), Centris (members of the tribe Centrini), Eulema (*Eulema* spp.), Epicharis (*Epicharis* spp.), Euglossa (*Euglossa* spp.), Halictid (members of the tribe Halictini), Mesoplea (*Mesoplea* spp.), Melitoma (*Melitoma* spp.), and Xylocopa (*Xylocopa fimbriata* and *X. subvirescens*). These groups were later sorted into guild specific categories that were used in the additional regression models including: non-native eusocial (AHB), native eusocial (Trigona), and native solitary (Centris, Eulema, Epicharis, Euglossa, Halictid, Mesoplea, Melitoma, and Xylocopa species). Native solitary bees were further subdivided into small bees (Halictids) and large bees (Centris, Eulema, Epicharis, Euglossa, Mesoplea, Melitoma, and Xylocopa).

Aerial netting was used to collect representative individuals for further taxonomic identification. Collected bees were identified to the lowest operational taxonomic unit (OUT) using the reference collection held at the University of California Essig Museum and with assistance from Dr. Laurence Packer and Jason Gibbs of York University, Toronto, Canada and Dr. Ricardo Ayala of UNAM, Mexico.

Statistical Analysis

The average number of total bees and the average number of different bee groups recorded per three-minute count was calculated for each resource from all of the counts taken during the entirety of the study period. Thirteen variables were tested for their significant influence on bee visitation rates including: the number of flowers a resource had (flw), how tall the resource was (height), the distance to the wildland-urban interface (d wui), the distance to the nearest riparian area (d rip), the characteristic life form of the resource (tree, hedge, or shrub), the number of conspecific resources within the neighborhood (con-sp in 10 m, 50 m, and 100 m), the presence of adjacent open space (open space), and the land use at the site of the resource (residential, res; or commercial, com).

Regional and city specific models were then generated for the abundance of bees, the number of bee types, and for each the individual bee group (large bees, small bees, solitary bees, eusocial bees, native eusocial bees, and non-native eusocial bees) using backward stepwise regression with $p=0.10$ as the entrance criterion and $p=0.05$ as significant. A comparison of the overall bee visitation numbers for abundance, richness, and the individual bee groups and guilds between the three study cities was also tested using ANOVA, $\alpha=0.05$, followed by Tukey's HSD for multiple comparison to determine if there were any association between visitation rates and city size or the surrounding landscape. All of the statistical analyses were performed in SPSS 16.0 (© Chicago IL 2007).

Results

The landscape and resource characteristics that had significant correlations with bee visitation to *T. stans* varied between the individual cities. A summary of the multivariate regression models constructed for the resource visitation patterns for the community (the total abundance and the overall taxon richness), and the other taxonomic categories are displayed Table 4.1. More detailed models are presented for each taxonomic category in Appendances 4.ii-ix. The trends seen in bee abundance and in the number of different taxon groups attracted to a resource were similar in the global (all city) model (see appendix 4.ii and 4.iii, respectively) and were positively influenced by increasing resource abundance and an increasing number of nearby conspecific resources. The number of flowers that a resource possessed (flw; p=0.000) and the number of other *T. stans* resources within a 10 meter radius (con-sp 10; p=0.049) were the globally significant drivers of bee abundance at site (Appendix 4.ii). The overall taxon richness was influence by the total number of flowers that a resource had (flw; p=0.000) (Appendix 4.iii).

A site-specific analysis of the drivers of bee visitor abundance and the overall bee taxon richness revealed further variability between the study sites. Abundance patterns were driven by a mix of resource characteristics and land use variables in each of the three study cities, however, in each case, the number of flowers that a resource possessed remained a significant variables (flw; p<0.010, see Appendix 4.ii). In the smallest city, Bagaces, residential land use (res; p=0.032) correlated strongly with bee visitor abundance; on average 2.643 (± 1.164 S.E.) more bees were attracted per count to resources that were on residential land compared to commercial land (Appendix 4.ii). In Cañas, in addition to an increasing number of flowers per resource (flw; p=0.000), the proximity to open space (open space; p=0.054), and an increasing distance from the wildland-urban interface (d wui; p=0.054) were positively correlated with increased bee abundance. On average, resources that were near open space had 1.288 (± 0.644) more bee visitors per count than those not near open space, while an increase of 0.6 (± 0.3) bees could be expected per count for each 100 meters further away a resource was from the wildland urban interface. In Liberia, the number of flowers that a resource (flw; p=0.000) had and if that resource was a shrub (shrub; p=0.028) were positively associated with increasing bee visitation, while open space was negatively associated (open space; p=0.037).

A trend of decreasing model complexity with increasing city size was evident in the case of taxon richness. In the smallest city, Bagaces, the number of flowers that a resource had, if the resource was a shrub, the residential land use, the number of conspecific resources within 10 meters, and the distance to the wildland-urban interface were all significant drivers of bee taxon richness observed per count (p<0.032, see Appendix 4.iii). In Cañas and Liberia, only the number of flowers that a resource had was retained as a significant driver of the taxon richness observed per count (flw; p=0.001). Model fit also improved when each individual city was examined, especially in the case of the two smaller cities, Bagaces and Cañas.

Guild Specific Resource Usage

Models of the resource usage patterns of the individual taxon groups revealed contrasting trends between social guilds, size guilds, and between native and non-native eusocial bees. All of the pooled city models and the vast majority of the individual city models (15/18=83.33%) presented in Table 4.1 indicated the significant positive correlation between the number of flowers that a resource possessed (flw) and the abundance of individual bee taxa recorded per three-minute observation made. The effect of each additional flower that a resource possessed corresponded to an increase of approximately 0.004 (± 0.002) bees per observation (ranging form a low of 0.001 to a high of 0.007). Although this effect is low on a per flower basis, the sampled resources varied from 2 to1200 flowers. The cumulative effect of this trend indicates that for an increase in 100 flowers 0.4 additional bees could be expected per observation.

Solitary bees

In the pooled city model, only the number of flowers that a resource possessed significantly influenced the foraging rates of solitary bees (p=0.000, Appendix 4.iv). The number of flowers was consistently significantly positively correlated to increased the solitary bee visitation in each city but was not the only factor driving visitation patterns. In Bagaces, residential land use also significantly increased the number of solitary bees foraging per observation by 2.364 (± 0.917) individuals per count compared to commercial land use (res; p=0.016). In Cañas an increasing distance from the wildland-urban interface (d wui; p=0.001) and if the resource was a tree (tree; p=0.012) also significantly positively increased solitary bee numbers. In addition to the positive influence of flowers on bee numbers in Liberia, there was a negative correlation with solitary bee foraging rates and proximity to open space (open space; p=0.041), but a positive correlation with resources that were considered shrubs (shrub; p=0.018). Solitary bees include both large bodied species (e.g., *Centris* spp., *Xylocopa* spp., *Euglossa* spp., *Eulema* spp.) and smaller bodied species (e.g., *Halictid* spp.).

Large bees

Across all of the study sites, the occurrence of large bees was significantly positively correlated with the number of flowers that a resource had (flw; p=0.000, Appendix 4.v) and with the number of con-specific resources within 10 meters (con-sp 10; p=0.015). As city size increased the model complexity decreased. In Bagaces, the foraging rates of large bees are significantly positively influenced by the total number of flowers (flw; p=0.018) and residential land use (res; p=0.002) and are significantly influenced by a decreasing distance to riparian areas (d rip; p=0.000). In Cañas, large bee foraging rates are significantly positively correlated with the resource characteristics (flw; p=0.002 and tree; p=0.018), as well as the distance to the wildland (d wui; p=0.000). In Liberia, only the number of flowers that a resource had (flw; p=0.050) was a significant driver of large bee visitation, with amore large bees visiting resource that has greater floral abundance.

Small bees

In the pooled city model (see Table 4.1 and Appendix 4.vi), the visitation rates of small bees were significantly positively correlated with the number of flowers a resource possessed (flw; p=0.003) and with the resource characteristics, with shrubs being preferentially visited (shrub; p=0.003). The proximity to open space was significantly negatively correlated to small bee visitation (open space; p=0.010). The influence of floral abundance was not consistent across the three cities. Cañas was the only city in which floral abundance on small bee visitation rates was significantly correlated with increased small bee visitation (flw; p=0.000), along with decreasing resource height (height; p=0.010). In Liberia, only the resource characteristics, specifically the resource being a shrub (shrub; p=0.003), significantly positively correlated with small bee visitation. In Bagaces only an increasing distance from riparian areas (p=0.000) impacted small bee visitation.

Eusocial Bees: Stingless bees (STB) and African honeybees(AHB)

The foraging rates of the community of eusocial bees (see Appendix 4.vii) that visited *T. stans* within the urban landscape studied were influenced globally by the number of flowers that a resource possessed (flw; p=0.000) and by the distribution of conspecific resources within a 10 meter radius (con-sp 10; p=0.009). The number of flowers possessed by a resource remained an important influence on the visitation rates of euscoial bees in all of the study cities (flw; p<0.010). In Bagaces the life form of the resource is significant with hedges attracting significantly more visitors than shrubs or trees (hedge; p=0.075), while in Cañas and Liberia the distribution (con-sp 10; p=0.062) and the location of the resource within the urban landscape is important (d wui; p=0.015).

The foraging of the local native eusocial bees (STB, predominantly *Trigona* spp. see Appendix 4.viii) was correlated exclusively with resource characteristics (flw, p=0.00) and distribution (con-specifics in 10 meters, p=0.049) across the pooled city sample, and this is similar to the overall eusoical foraging patterns. Floral abundance remained significantly positively influential in Bagaces and Liberia (flw; p=0.000 and p=0.055, respectively), but not in Cañas where proximity to open space (open space; p=0.004) and resource characteristics (hedge; p=0.052) were the significant drivers of foraging rates.

The foraging of non-native social bees (AHB), on the other hand, was correlated with both resource characteristics and landscape variables (see Appendix 4.ix). Globally, residential land use increased the foraging rate of AHB (p=0.021), as did an increasing distance away from the wild land (p=0.000). Increasing floral abundance remained a significant positive driver of AHB foraging rates in all three cities. The most complex model is seen in Liberia, were floral abundance, residential land use, an increasing number of *T. stans* within 10 meters, and an increasing distance from the wildland-urban interface were all significantly positively correlated with increased AHB foraging (p<0.013).

City size and landscape context

The size of the city had a significant impact on the number of bee taxa that were observed on average per count. Figure 4.8 displays the number of bee types attracted per count in each of the three cities. The cities are arranged on the categorical axis in order of increasing size, from

Bagaces to Liberia. The number of bee types per count increases significantly in the order Bagaces<Cañas <Liberia, which is consistent with an increase in size from the smallest to the largest urban landscape. The increase in richness between each city is significant (p>0.040). Figure 4.9 displays the mean numbers of individuals in the taxonomic categories of Centirs, Halictid, STB, and AHB observed per count in each city; three of the four common bee groups display patterns associated with the regional landscape context of the city (Table 4.2). The mean visitation rates of the Centris, Halictid, and STB groups do not differ statistically between Bagaces and Liberia, with p=0.741, p=0.088, and p=0.870, respectively. The mean visitation of these same groups in Cañas was significantly different when compared to both Bagaces and Liberia (p>0.000). More Centris and STB were recorded per count in Cañas than in both Bagaces and Liberia, while Halictids were more abundant per count in Cañas. The mean visitation of AHB in the three cities did not show any pattern of variability with landscape context, but was significantly different between all of the city pairings (p>0.04), with Liberia having the highest per count numbers, followed by Bagaces and then Cañas.

Discussion

The populations of bees using *T. stans* resources in the urban landscapes of northwestern Costa Rica preferentially visit resources that possess abundant flowers, irrespective of the situation of the resource in the urban landscape. Across all cities at the regional scale, the visitation patterns of bees to *T. stans* were driven by the quality and quantity of resources found at a site. Floral abundance consistently appears as factor that positively influences bee visitation to a site. The importance of characteristically urban landscape variables generally decreased as city size increased in this study, suggesting that bees foraging in larger urban areas are not influenced by the urban matrix to the same degree at those foraging in smaller cities. The richness of bee visitors to *T. stans* in the larger cities, Cañas and Liberia, were influenced only by the number of flowers. In Bagaces, the smallest of the three cities, characteristically urban variables, such as the distance to the wildland, nearby patches of open space, and residential land use, became more and more influential. In smaller cities, the foraging bees may not be exclusive urban residents, but rather a mix of species that nest both within and at the periphery of the city. Their foraging ranges may include both wildland and urban resources, and the influence of the urban landscape might be more significant for these bees.

The differential responses of individual guilds

When the community of bees foraging on *T. stans* is analyzed in terms of functionally and ecologically similar guilds, more distinct trends appear. Some groups, such as large bees, display visitation patterns that parallel the trends seen in overall taxon richness. Large bees of the genus *Centris* are the dominant forages on *T. stans*, representing 52% of the recorded visitors constituted by four species. These four species (*C. aethyctera, C. eurpatana, C. heithausi*, and *C.* sp 1) also represent 15% of the species diversity known to visit this resource in urban landscapes (see Chapter 3). Large bees, as a group, account for 51% (14/27) of all of the species that visit *T. stans* (see Chapter 3). The overall trend in abundance is likely driven by the response of large bees, and in particular *Centris* species, to the urban landscape.

Large versus small bees

The large and small bee species that are common to the tropical dry forest are generally known to forage on different resources, with larger bees preferentially selecting mass flowering trees and smaller bodied bee species preferring herbs (Frankie and Vinson 2004). In addition, large bodied bees have been suggested to stratify their foraging in systems that display vertical resource structure (Roubik 1993). In this study, large bees responded with increased foraging to resources that possessed more flowers and to those that were clustered with more conspecifics. In the smaller cities, there was also a very significant positive response to residential land use. The foraging patterns of large bees in these systems may be influenced by underlying principals of foraging energetics and optimal foraging. Foraging bees have been shown to pattern their resource visitation to favor nearby patches of flowers, optimizing the energy lost in flight with that acquired from nectar (Heinrich 1979). As the energy requirements of larger bees are greater than those of smaller ones, it would follow that their foraging patterns would respond more substantially to resource quality and spatial distribution.

Small bees were more likely to visit on *T. stans* resources that possessed more flowers, but were influenced by the life form of the resource, foraging in larger numbers on shorter resources that were shrubs. These life form and size categories resemble the lower-growing herbaceous species that are more common forage for small species. Small bees also foraged more preferentially on resources that were closer to areas of open space, which are likely the locations of their nests. The nest-to-resource foraging range of smaller bodied species is assumed to be approximately 250 meters or less (Greenleaf et al. 2007). Much of the open space in the three study sites is characterized by exposed ground or by the presence of remnant wildland grasses. Both materials are ideal nesting substrates for species such as *Agapostemon nasutus* Smith and *Halictus lutescens* Friese that commonly nest in the ground, or *Ceratina* sp. that build nest within dried grasses and twigs (Michener 2000).

Solitary bees versus Eusocial bees

As a group, solitary bees responded to resource quantity, defined by the number of flowers that a resource had. They visited *T. stans* in increasing numbers when the resource had more in all three of the cities studied but within each city, unique patterns emerged. Solitary bees are the dominant and most diverse assemblage of the approximately 250 species that constitute the local community in the tropical dry forest. Their life history characteristics vary greatly in terms of feeding range and nesting style. Similar proportions of bees in higher taxonomic groupings were seen between some cities, especially between Bagaces and Liberia, but the species make-up of these taxon groups varies. Unique species of bees have been noted to fill functionally similar niches in complex landscapes (Cane et al. 2006, Cane et al. 2005). The lack of a consistent response to resource characteristics and landscape variables is likely due to the autecology of each species in the local community.

As a group, social bees forage in response to landscape variables, including the distance to the wildland, proximity to open space, and the distribution of resources. Social bees forage at the colony level, sending out scouts that communicate the location to subsequent foragers. The capacity that social bees have to access food is increased, as is their range from nest to resource.

Native versus non-native eusocial bees

The social bees identified in this study are both native stingless bees (e.g., *Nannotrigona* spp., *Plebeia* spp., *Tetragonica* spp., and *Trigona* spp.) and the non-native African honeybees (AHB), *Apis mellifera scutellata* Larteille. The foraging of these two groups was modeled by different sets of variables. Locally native species responded with increased visitation to floral abundance, but also responded to the spatial distribution of resources, favoring to forage on clusters of conspecifics. Non-native AHB, on the other hand, responded strongly to the land use within the urban landscape, favoring resources that were located in residential areas. The increased occurrence of bees in residential areas has been noted by many authors as being driven by the overall increased diversity of the floral resource base located at these sites (Tommasi et al. 2004; Frankie et al. 2005; Winfree et al. 2009). Honeybees in particular are the epitome of generalist foragers, feeding broadly on all resources. The foraging activity of many generalist species has been suggested to increase when the diversity of the food resource increases. Explanations include the so-called "shopping mall effect" where bees are considered to preferentially forage at localities with more diverse resources (Frankie et al. 2005), even if their feeding ranges are narrow, or the assumed attraction of bees to sites frequented by other bees.

The importance of uniquely urban variables

Certain landscape and habitat characteristics, such as the degree of human land modification, the extent of the urban matrix, and the specific qualities of the urban matrix (a large proportion of impermeable surface, tall buildings increased rooftop areas, commercial and residential land use, etc.) are unique to cities. Urban organisms must interact with features that wildland species do not experience, which leads urban ecologists to question if these uniquely urban habitat elements have a significant or correspondingly unique affect on urban fauna. In this study, the proximity to open space and the proximity to the wildland-urban interface had a small impact on some bees that forage on *T. stans*. The largest affect was seen between residential and commercial land use. Residential gardens have long been noted as sites of diverse floral resource that in turn attract ample anthophile species (Smith et al. 2006). In this particular study, the magnitude of difference between some of these urban variables (i.e., the distance from the wildland, the degree of commercialization, and the extent of the city) is not that great. Parallel work has been conducted in the cities of Berkeley, Emeryville, and Oakland in California, USA examining similar trends in bee visitation where the degree of urbanization is greater. In the following chapter, a greater range in variables (such as the distance to the wildland and the degree of urbanization) will allow for a more detailed understanding of some of the finer trends exhibited by bees in response to urban land use and the urban matrix.

Urban-wildland interaction

Commonalities exist between the visitation rates of bees in Bagaces and Liberia, and these cities are both located within the same regional land use: rangeland with nearby conservation areas. Cañas displays unique patterns, and is located in a different landscape. A more refined species-specific analysis of the bee communities would reveal if there are more substantial trends in taxon presence and absence in urban areas located within different landscapes. An initial study of urban landscapes across California conducted by Frankie et al. (2009) indicated that species numbers attracted to a set of targeted ornamental plants differ between the individual cities, and even between those located within similar eco-regions. The community of bees at a locality is determined by history, context, and the current management practices. Historical presence/absence records are not always available for a site, and this is the case for the cities of Bagaces, Cañas, and Liberia. The species that occur in urban landscapes can be a mix of local natives migrating in from the wildland, generalists that are successful in novel landscapes, or introduced exotics (a common species group due to the influence of active and passive human introductions). A worthwhile study of the impact of urban land development on bee species diversity would include a pre- and post-development analysis to better outline and understand the trends.

Conclusions and implications for conservation and management

Although landscape variables do impact the rates at which certain bee groups and certain species visit a resource, bee visitors were present at almost all of the available *T. stans* resources present in the urban landscapes. Abundant floral resources and the characteristics of these resources drive site-specific patterns of bee foraging, regardless of where it is situated within the city. The generally consistent correlation between increased floral resource abundance and increased bee visitor abundance facilitates the conservation and management of bee within cities. Landscape management that aims to promote the visitation of beneficial pollinators, such as bees, can focus on developing rich and abundant habitat patches, irrespective of their location. Any land that becomes opportunistically available for management can be used with a reasonable probability of success, for at least a part of the bee community.

Ideas and perceptions about cities and urban land use are changing, and the integration of traditionally external land use practices, such as conservation and agriculture, are becoming more common within the city limits. Urban agriculture is a reality and is being practiced in cities across the globe, especially in developing regions such as the tropics and Central America. The successful production of fruit relies on functional pollination systems, regardless of the landscape context. In larger cities, especially at the center or further away from the perimeter, wild land bees cannot be relied on to provide pollination services. Resident species that cycle through their entire reproductive phase within the city limits will be the main pollinators. If healthy and diverse populations of bees can be promoted within cities through a network of food resources, their pollination services can be used for private, community, and commercial agricultural efforts. Proximity to intact habitat has been correlated to increased agricultural productivity due to both increased pollinator abundance and richness (Kremen et al. 2002; Kremen et al. 2004). Both the conservation of bee habitat (Klein et al. 2003; Morandin and Winston, 2006) and the instillation of habitat areas near sites that require pollination services have been shown to improve pollinator diversity and resultant seed set. Similarly, an improved urban crop production could be expected with increased habitat contained within the city limits and next to urban agricultural sites.

Acknowledgements

Thanks to Meaghan Jastrebski and Laura Fine for their assistance with data collection in the field. Financial support for this work was provided by the Schwabacher Memorial Scholarship in Forestry, and made trips into the field possible. The staff of the GIF at UC Berkeley provided technical support and advice for GIS analysis. Thanks to G. S. Biging for continued advice on statistically modeling. Special thanks to J. R. McBride for supporting this work and pushing to see it complete.

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Figures, Tables, and Appendices

Figure 4.1: A common street view in Liberia, Costa Rica with *T. stans* growing in the foreground (front left, two resources growing in a ditch near the road) and in the background (back right, three resources planted along the sidewalk). Photo credit: Victoria Wojcik.

Figure 4.2: An urban *T. stans* resource representing a 'tree' life form, Cañas, Costa Rica. Photo credit: Victoria Wojcik.

Figure 4.3: An urban *T. stans* resource representing a 'shrub' life form, Liberia, Costa Rica. Photo credit: Victoria Wojcik.

Figure 4.4: An urban *T. stans* resource representing a ‘hedge’ life form, Bagaces, Costa Rica. Photo credit: Victoria Wojcik.

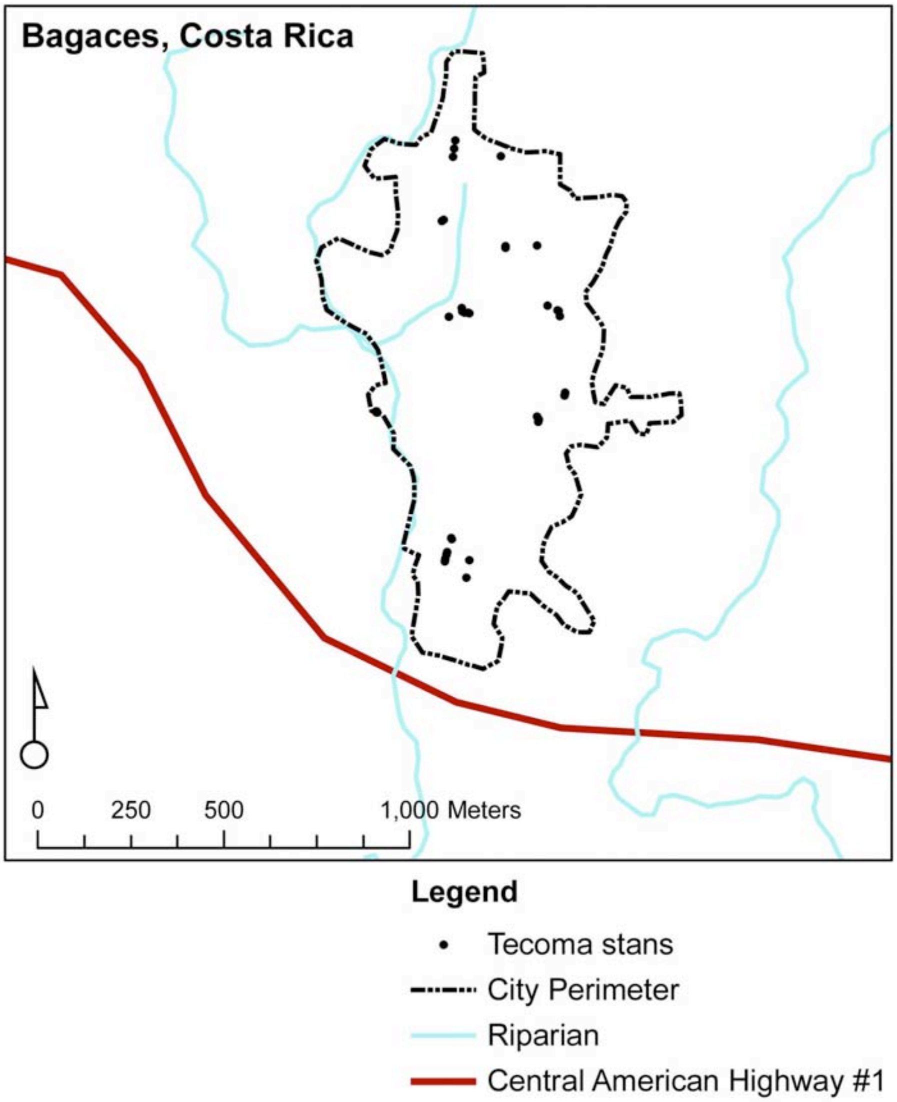

Figure 4.5: A map showing the locations of the individual *T. stans* resources distributed throughout the landscape of Bagaces, Costa Rica.

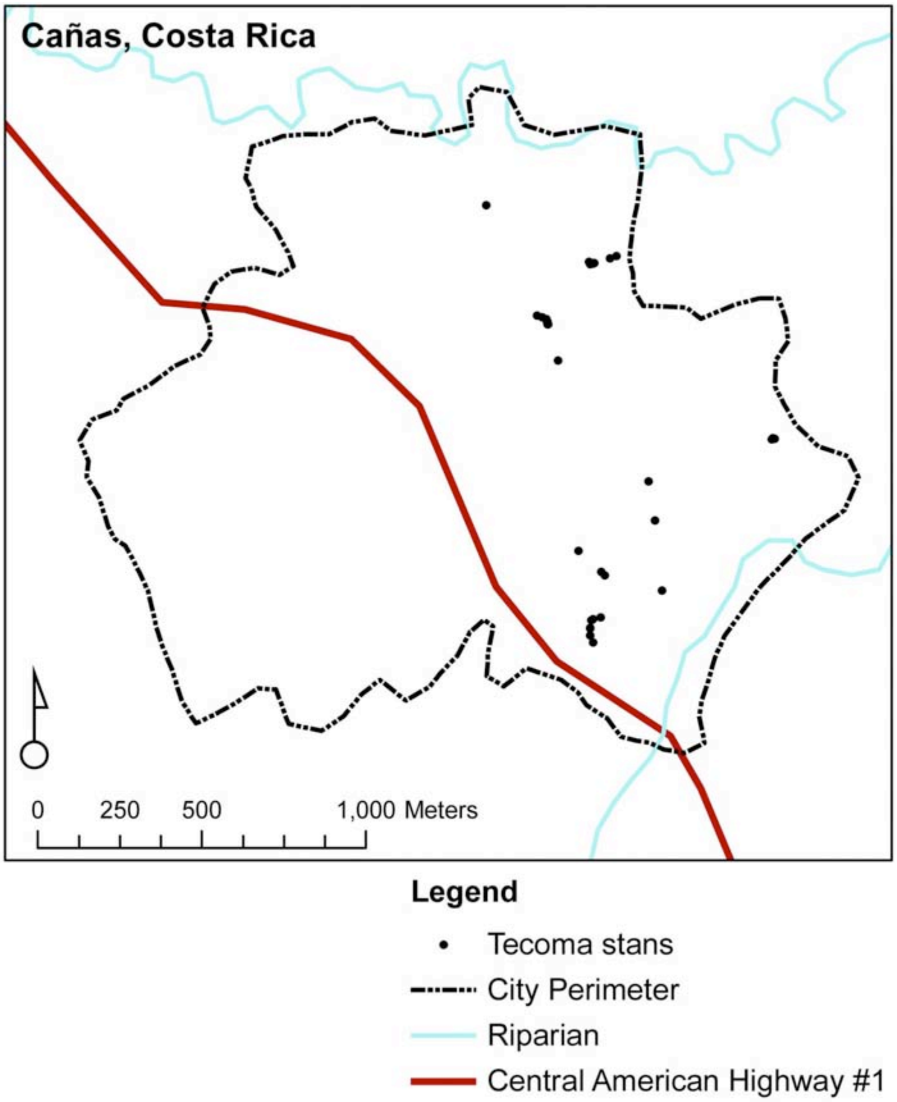

Figure 4.6: A map showing the locations of the individual *T. stans* resources distributed throughout the landscape of Cañas, Costa Rica.

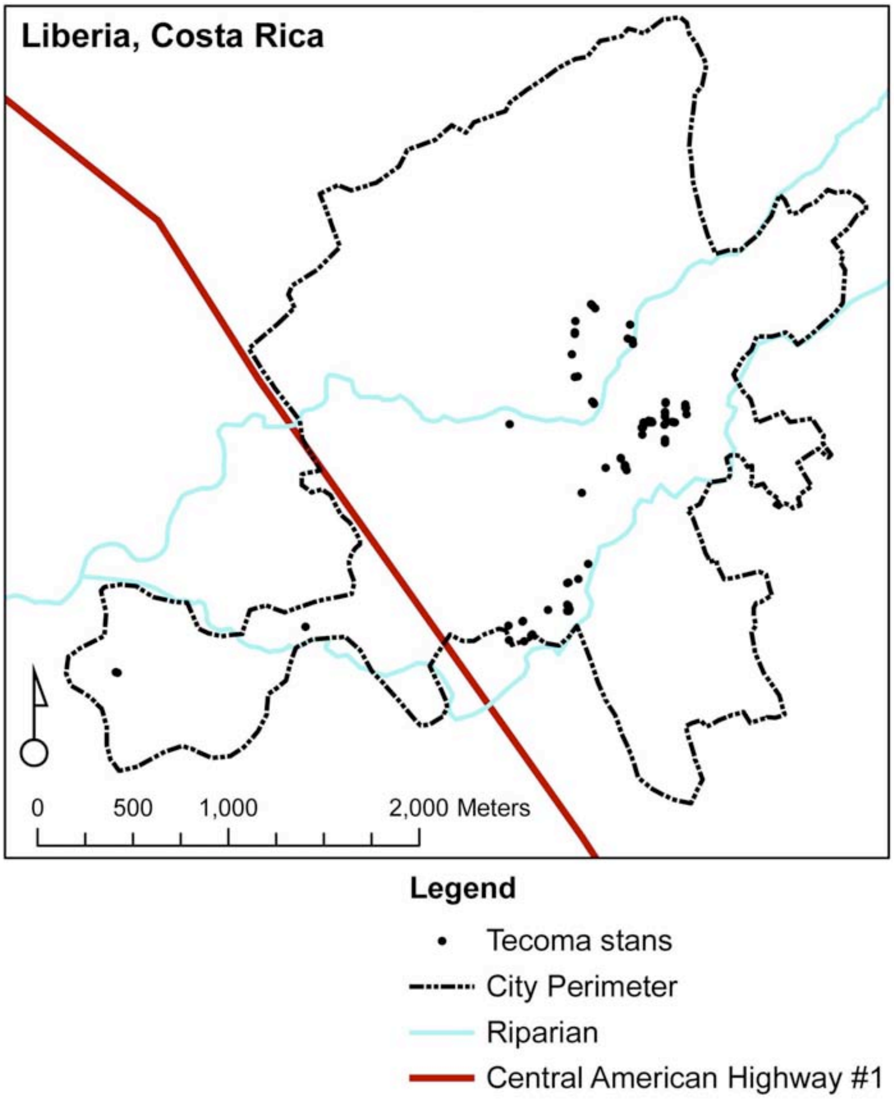

Figure 4.7: A map showing the locations of the individual *T. stans* resources distributed throughout the landscape of Liberia, Costa Rica.

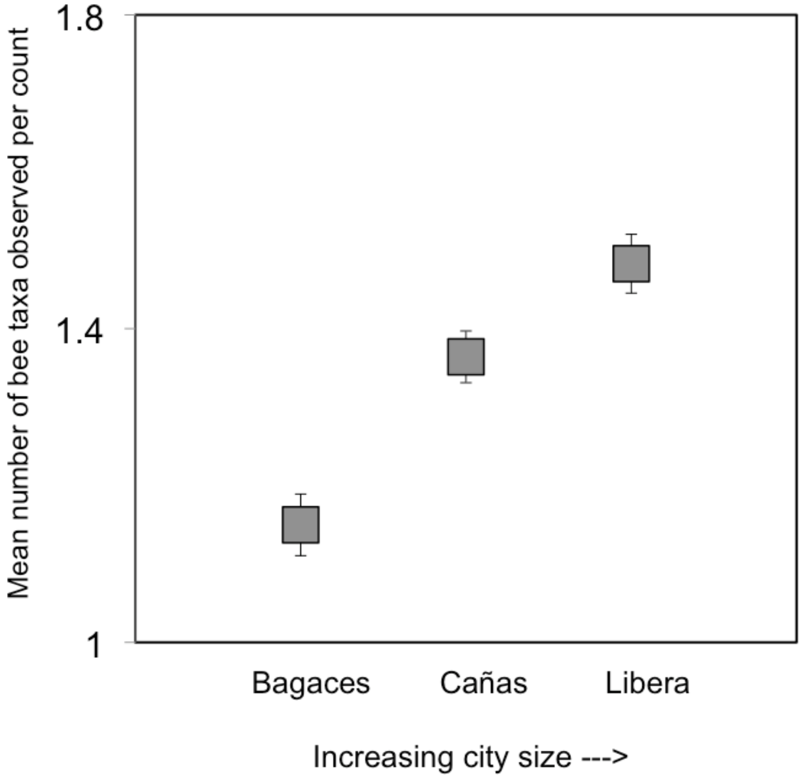

Figure 4.8: The mean number of different bee taxa observed per three-minute count across all counts taken in the three study cities, Bagaces, Cañas, and Liberia. The cities are arranged on the categorical axis in order of increasing size. The populations of *T. stans* within each of the cities attract different numbers of bee taxa per count, and in each case there are on average significantly more bee types per count as the city size increase increases (p=0.000). Error bars represent the 95% confidence intervals for each measure.

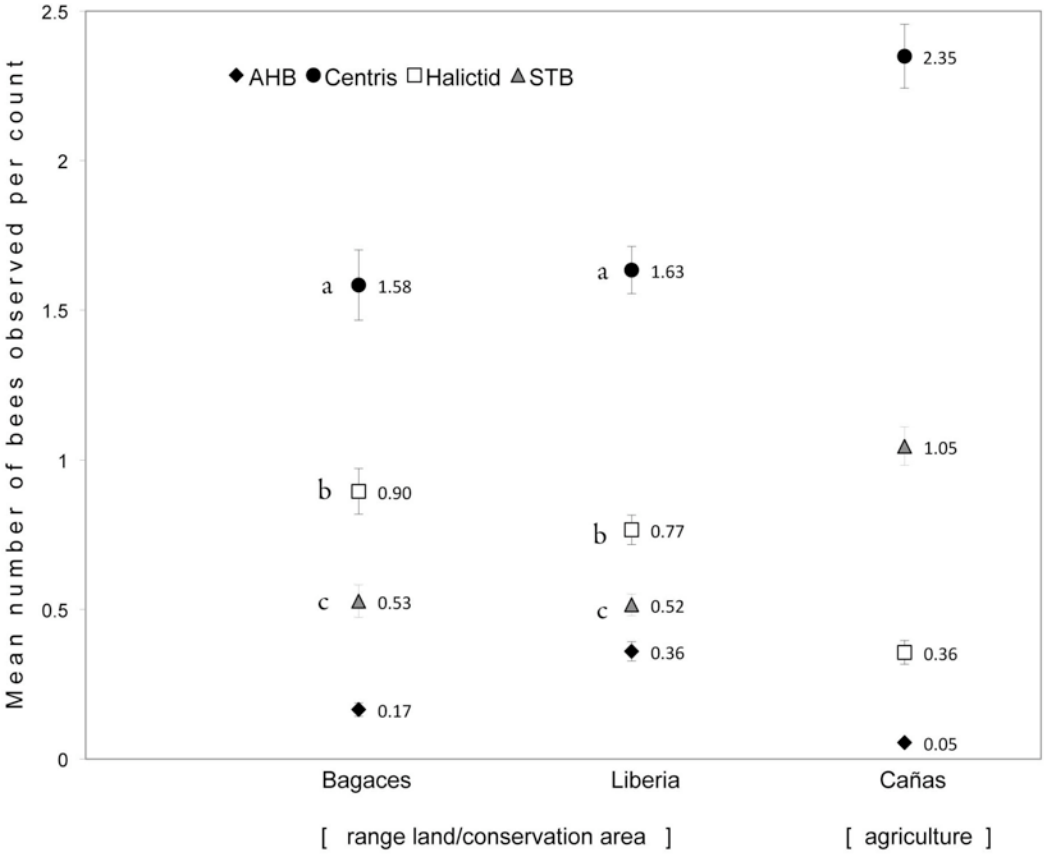

Figure 4.9: The mean observed bee visitation rates for the four most commonly observed bee groups (Centris, Halictid, STB, and AHB) that visit *T. stans* in the three study cities. The cities are grouped based on their regional landscape situation. The means for each group are indicated on the graph. Mean visitation rates that do not differ statistically are indicated for each bee group with corresponding lower case letters (a=Centris, b=Halictid, c=STB). Error bars represent the 95% confidence intervals for each measure.

Table 4.1: Summary of the pooled and individual city bee visitation models for the total community (abundance and taxon richness) as well as individual guilds that are using *T. stans* as a pollen and nectar resource in the small and developing urban landscapes of Guanacaste, Costa Rica. All of the variables shown are significant at the α=0.05 level unless indicated by (‡) where they are significant at α=0.08. Variable abbreviations are as follows: flw=total flowers, con-sp 10=the number of other *T. stans* within a 10 meter radius of the sampled resource, res=residential land use, open space=proximity to open space, d wui=distance to the wildland-urban interface, and d rip=distance to riparian areas. The life form of the resource is indicated as a tree, shrub, or hedge. The + or – sign next to the variable in parenthesis indicates the direction of correlation. The explicit models for each taxon group are presented in Appendices 4.ii through 4.xi

			Increasing city size →	
	All cities	**Bagaces**	**Cañas**	**Liberia**
Community				
abundance	(+) flw (+) con-sp 10	(+) flw (+) res	(+) flw (+) open space‡ (+) d wui‡	(+) flw (-) open space (+) shrub
richness	(+) flw	(+) flw (+) res (-) con-sp 10 (-) d wui (-) shrub	(+) flw	(+) flw
Guilds				
solitary bees	(+) flw	(+) flw (+) res	(+) flw (+) d wui (+) tree	(+) flw (-) open space (+) shrub
large bees	(+) flw (+) con-sp 10	(+) flw (+) res (-) d wui (-) d rip	(+) flw (+) d wui (+) tree	(+) flw (-) open space
small bees	(+) flw (-) open space (+) shrub	(-) d rip	(+) flw (-) height	(+) shrub
social bees	(+) flw (+) con-sp 10	(+) flw (+) hedge‡	(+) flw (+) con-sp 10‡	(+) flw (+) d wui
native social	(+) flw (+) con-sp	(+) flw	(+) open space (+) hedge‡	(+) flw‡ (-) res
non-native social	(+) flw (+) res (+) d wui	(+) flw (+) d rip	(+) flw‡	(+) flw (+) res (+) con-sp 10 (+) d wui

Appendix 4.i: The resource characteristics of *T. stans* and the landscape variables used in the backward stepwise regression model development (n=120). The continuous variables are listed with their minimum, maximum, and mean values, along with the standard error. Categorical variables are presented in binary form with the number of *T. stans* in each category indicated.

Continuous	***Description***	**Min**	**Max**	**Mean**	**Std. Error**
d rip	distance to the nearest riparian area, measured in meters	39.753	535.901	235.340	12.523
d wui	distance to the wildland-urban interface, measured in meters	0.535	830.858	261.350	18.271
height	height of the resource, measured in meters to the nearest 25 cm	0.000	6.000	2.670	0.113
flw	the total number of flowers that a resource possessed, estimated through a sub sample of the canopy	2.000	1200.000	148.178	15.979
con-sp 10	the number of other *T. stans* within a 10 m radius	0.000	9.000	1.680	0.180
con-sp 50	the number of other *T. stans* within a 10 m radius	0.000	11.000	4.100	0.295
con-sp 100	the number of other *T. stans* within a 10 m radius	0.000	19.000	6.130	0.403

Categorical	***Description***		**no. of cases**		**no. of cases**
open space	the presence of open or green space adjacent to the *T. stans* resource	no=0	98	yes=1	22
land use	the dominant land use at the site	commercial (com)=0	32	residential (res)=1	88
shrub	lower growing *T. stans* individuals without a trunk	no=0	86	yes=1	34
hedge	taller *T. stans* individuals with foliage extending the length of the form	no=0	97	yes=1	23
tree	taller *T. stans* individuals with an obvious trunk	no=0	57	yes=1	63

Appendix 4.ii: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean bee visitor abundance observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

						95% CI	
All Cities	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	2.129	0.327		6.507	0.000	1.481	2.777
flw	0.006	0.001	0.451	5.483	0.000	0.004	0.009
con-sp 10	0.205	0.103	0.164	1.992	0.049	0.001	0.409

$F_{2,118}$=15.959; p=0.000; R^2=0213; Adj. R^2=0.200

						95% CI	
Bagaces	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.044	1.091		0.041	0.968	-2.208	2.297
flw	0.008	0.003	0.456	2.815	0.010	0.002	0.014
res	2.643	1.164	0.368	2.271	0.032	0.241	5.046

$F_{2,24}$=7.189; p=0.004; R^2=0.375; Adj. R^2=0.323

						95% CI	
Cañas	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.856	0.745		1.148	0.260	-0.664	2.376
flw	0.009	0.002	0.520	4.031	0.000	0.004	0.013
open space	1.288	0.644	0.260	2.001	0.054	-0.024	2.601
d wui	0.006	0.003	0.258	2.002	0.054	0.000	0.013

$F_{3,31}$=10.521; p=0.000; R^2=0.504; Adj. R^2=0.457

						95% CI	
Liberia	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	2.111	0.415		5.083	0.000	1.279	2.944
flw	0.006	0.002	0.533	4.102	0.000	0.003	0.009
open space	-1.922	0.899	-0.271	-2.138	0.037	-3.723	-0.121
shrub	1.525	0.674	0.275	2.264	0.028	0.175	2.876

$F_{3,55}$=6.1688; p=0.001; R^2=0.252; Adj. R^2=0.211

Appendix 4.iii: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean bee taxon richness observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

							95% CI	
All Cities		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	1.041	0.073		14.169	0.000	0.896	1.186
	flw	0.002	0.000	0.536	6.920	0.000	0.002	0.003

$F_{1,119}$=47.892; p=0.000; R^2=0.287; Adj. R^2= 0.281

							95% CI	
Bagaces		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.883	0.265		3.330	0.003	0.331	1.434
	flw	0.003	0.001	0.631	4.599	0.000	0.001	0.004
	res	0.898	0.239	0.514	3.761	0.001	0.402	1.395
	d wui	-0.003	0.001	-0.302	-2.328	0.030	-0.006	0.000
	con-sp 10	-0.235	0.102	-0.365	-2.302	0.032	-0.447	-0.023
	shrub	-0.478	0.189	-0.340	-2.526	0.020	-0.871	-0.084

$F_{5,21}$=8.765; p=0.000; R^2=0.676; Adj. R^2= 0.599

							95% CI	
Cañas		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	1.100	0.102		10.783	0.000	0.893	1.308
	flw	0.002	0.001	0.535	3.637	0.001	0.001	0.003

$F_{1,33}$=13.226; p=0.001; R^2=0.286; Adj. R^2=0.264

							95% CI	
Liberia		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	1.107	0.124		8.933	0.000	0.859	1.355
	flw	0.002	0.000	0.511	4.485	0.000	0.001	0.003

$F_{1,57}$=20.117; p=0.008; R^2=0.261; Adj. R^2=0.248

Appendix 4.iv: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean solitary bee visitation observed per three-minute count on T. *stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

						95% CI	
All Cities	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	2.047	0.223		9.189	0.000	1.606	2.488
flw	0.004	0.001	0.354	4.128	0.000	0.002	0.006

$F_{1,119}$=17.042; p=0.000; R^2=0.125; Adj. R^2=0.118

						95% CI	
Bagaces	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.036	0.859		0.041	0.967	-1.738	1.809
flw	0.005	0.002	0.392	2.397	0.025	0.001	0.01
res	2.364	0.917	0.422	2.579	0.016	0.472	4.256

$F_{2,24}$=6.825; p=0.005; R^2=0.363; Adj. R^2=0.309

						95% CI	
Cañas	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	-0.294	0.530		-0.554	0.584	-1.375	0.788
flw	0.006	0.001	0.528	4.685	0.000	0.004	0.009
tree	1.061	0.396	0.303	2.682	0.012	0.254	1.868
d wui	0.008	0.002	0.424	3.797	0.001	0.003	0.012

$F_{3,31}$=17.410; p=0.000; R^2=0.628; Adj. R^2=0.591

						95% CI	
Liberia	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	1.767	0.378		4.673	0.000	1.009	2.525
flw	0.004	0.001	0.403	2.969	0.004	0.001	0.007
open space	-1.714	0.818	-0.277	-2.096	0.041	-3.354	-0.075
shrub	1.497	0.613	0.310	2.440	0.018	0.268	2.726

$F_{3,55}$=4.180; p=0.010; R^2=0.186; Adj. R^2=0.141

Appendix 4.v: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean large bee visitation observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

							95% CI	
All Cities		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	1.129	0.241		4.679	0.000	0.651	1.607
	flw	0.003	0.001	0.332	3.843	0.000	0.002	0.005
	con-sp 10	0.170	0.076	0.193	2.234	0.027	0.019	0.320

$F_{2,118}$=9.003; p=0.000; R^2=0.132; Adj. R^2=0.118

							95% CI	
Bagaces		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.703	0.713		0.985	0.335	-0.773	2.178
	flw	0.005	0.002	0.396	2.616	0.015	0.001	0.008
	res	2.095	0.724	0.438	2.893	0.008	0.597	3.593
	d rip	-0.007	0.002	-0.528	-3.438	0.002	-0.011	-0.003

$F_{2,23}$=7.464; p=0.001; R^2=0.493, Adj.R^2=0.427

							95% CI	
Cañas		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	-0.669	0.563		-1.189	0.243	-1.816	0.478
	flw	0.005	0.001	0.406	3.316	0.002	0.002	0.008
	tree	1.053	0.420	0.308	2.509	0.018	0.197	1.908
	d wui	0.009	0.002	0.498	4.101	0.000	0.004	0.013

$F_{5,31}$=13.168; p=0.000; R^2=0.560; Adj. R^2=0.518

							95% CI	
Liberia		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	1.386	0.281		4.940	0.000	0.824	1.948
	flw	0.002	0.001	0.256	2.003	0.050	0.000	0.004

$F_{2,54}$=5.255; p=0.008; R^2=0.163; Adj. R^2=0.132

Appendix 4.vi: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean small bee visitation observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

						95% CI	
All Cities	**B**	**Std. Error**		**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.433	0.141		3.080	0.003	0.154	0.711
flw	0.002	0.001	0.281	3.061	0.003	0.001	0.003
open space	-0.606	0.231	-0.234	-2.630	0.010	-1.063	-0.15
shrub	0.632	0.206	0.280	3.067	0.003	0.224	1.04

$F_{3,116}$=5.825; p=0.001; R^2=0.120; Adj. R^2=0.108

						95% CI	
Bagaces	**B**	**Std. Error**		**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.006	0.386		0.015	0.988	-0.789	0.801
d rip	0.005	0.002	0.540	3.211	0.004	0.002	0.009

$F_{1,25}$=10.314; p=0.004; R^2=0.292; Adj. R^2=0.264

						95% CI	
Cañas	**B**	**Std. Error**		**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.535	0.162		3.309	0.002	0.206	0.864
flw	0.002	0.001	0.763	4.267	0.000	0.001	0.004
height	-0.188	0.069	-0.490	-2.738	0.010	-0.327	-0.048

$F_{2,32}$=9.113; p=0.001; R^2=0.363; Adj. R^2=0.323

						95% CI	
Liberia	**B**	**Std. Error**		**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.654	0.140		4.681	0.000	0.374	0.934
shrub	0.923	0.298	0.380	3.099	0.003	0.326	1.519

$F_{1,57}$=9.802; p=0.003; R^2=0.144; Adj. R^2=0.129

Appendix 4.vii: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean eusocial bee visitation observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

	B	Std. Error	Std. B	t	Sig.	95% CI	
All Cities	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.296	0.105		2.826	0.006	0.089	0.504
flw	0.002	0.000	0.479	5.973	0.000	0.001	0.003
con-sp 10	0.087	0.033	0.212	2.648	0.009	0.022	0.153

$F_{2,118}=19.768$; P=0.000; $R^2=0.251$; Adj. $R^2=0.238$

	B	Std. Error	Std. B	t	Sig.	95% CI	
Bagaces	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.027	0.180		0.152	0.880	-0.345	0.400
flw	0.003	0.001	0.536	3.412	0.002	0.001	0.004
hedge	0.447	0.240	0.292	1.860	0.075	-0.049	0.942

$F_{3,24}=8.837$; p=0.001;$R^2=0.424$; Adj. $R^2= 0.376$

	B	Std. Error	Std. B	t	Sig.	95% CI	
Cañas	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.481	0.234		2.057	0.048	0.005	0.957
flw	0.003	0.001	0.434	2.719	0.010	0.001	0.005
con-sp 10	0.091	0.047	0.309	1.937	0.062	-0.005	0.187

$F_{2,32}=4.630$; p=0.017; $R^2=0.224$; Adj. $R^2=0.176$

	B	Std. Error	Std. B	t	Sig.	95% CI	
Liberia	**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
(Constant)	0.046	0.159		0.287	0.775	-0.273	0.364
flw	0.002	0.000	0.559	5.277	0.000	0.001	0.003
d wui	0.001	0.000	0.265	2.503	0.015	0.000	0.001

$F_{2,56}=16.592$; p=0.000; $R^2=0.372$; Adj. $R^2=0.350$

Appendix 4.viii: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean native eusocial bee (STB) visitation observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

							95% CI	
All Cities		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.253	0.099		2.555	0.012	0.057	0.449
	flw	0.001	0.000	0.279	3.247	0.002	0.000	0.002
	con-sp 10	0.103	0.031	0.285	3.317	0.001	0.042	0.165

$F_{2,118}$=9.647; p=0.000; R^2=0.141; Adj. R^2=0.126

							95% CI	
Bagaces		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.140	0.158		0.883	0.386	-0.186	0.466
	flw	0.002	0.001	0.425	2.346	0.027	0.000	0.003

$F_{1,25}$=5.504; p=0.027; R^2=0.180; Adj. R^2=0.148

Cañas		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.581	0.164		3.536	0.001	0.246	0.916
	hedge	0.77	0.385	0.320	2.020	0.052	-0.007	1.563
	open space	0.789	0.254	0.493	3.110	0.004	0.272	1.306

$F_{3,32}$=5.566; p=0.008; R^2=0.258; Adj. R^2=0.212

							95% CI	
Liberia		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.516	0.134		3.850	0.000	0.247	0.784
	flw	0.001	0.000	0.244	1.958	0.055	0.000	0.002
	res	-0.307	0.152	-0.253	-2.024	0.048	-0.610	-0.003

$F_{2.56}$=4.151; p=0.021; R^2=0.129; Adj. R^2=0.098

Appendix 4.ix: The backward stepwise regression models that describe the correlation the corresponding resource characteristics and landscape variables to the mean non-native eusocial bee (AHB) visitation observed per three-minute count on *T. stans* resources and across all of the cities (n=120) and at each individual study site; Bagaces (n=27), Cañas (n=35), and Liberia (n=58). Cities are arranges from top to bottom in order of increasing city size.

							95% CI	
All Cities		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	-0.226	0.076		-2.991	0.003	-0.376	-0.076
	flw	0.001	0.000	0.533	7.217	0.000	0.001	0.001
	res	0.146	0.063	0.180	2.333	0.021	0.022	0.270
	d wui	0.001	0.000	0.279	3.623	0.000	0.000	0.001

$F_{3,117}$=22.456; p=0.000; R^2=0.365; Adj. R^2=0.349

							95% CI	
Bagaces		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	-0.149	0.090		-1.661	0.110	-0.335	0.036
	d rip	0.001	0.000	0.499	3.325	0.003	0.000	0.002
	flw	0.001	0.000	0.395	2.632	0.015	0.000	0.001

$F_{2,24}$=11.059; p=0.000; R^2=0.480; Adj. R^2=0.436

							95% CI	
Cañas		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	0.001	0.000		0.211	0.834	-0.098	0.121
	flw	0.011	0.054	0.303	1.824	0.072	0.000	0.001

$F_{1,33}$=3.326; p=0.077; R^2=0.092; R^2 Adj.=0.069

							95% CI	
Liberia		**B**	**Std. Error**	**Std. B**	**t**	**Sig.**	**Lower**	**Upper**
	(Constant)	-0.233	0.107		-2.184	0.033	-0.447	-0.019
	flw	0.001	0.000	0.585	6.765	0.000	0.001	0.002
	d wui	0.001	0.000	0.384	4.394	0.000	0.000	0.001
	res	0.227	0.071	0.278	3.207	0.002	0.085	0.369
	con-sp 10	-0.089	0.035	-0.223	-2.567	0.013	-0.158	-0.019

$F_{4,54}$=20.971; p=0.000; R^2=0.608; Adj. R^2=0.579

CHAPTER 5 – DRIVERS OF BEE VISITATION TO PATCHES OF URBAN AND WILDLAND CALIFORNIA POPPIES, *ESCHSCHOLZIA CALIFORNICA*: THE INTERPLAY BETWEEN RESOURCE CHARACTERISTICS AND LANDSCAPE CONTEXT.

Abstract

An early-season survey assessed the visitation rates of bees to patches of California poppies, *Eschscholzia californica,* in both wildland and urbanized ecosystems in the East Bay cities of Berkeley, Emeryville, and Oakland, California. Floral resource characteristics (patch size and floral density), the landscape characteristics (distance to wildland, distance to riparian areas, distance to green space, land use, and traffic disturbance), and the regional landscape context (urban versus wildland) were examined for their impact on the visitation rates of eight taxonomic groups of bees that are common visitors to the California poppy. Although the mean observed visitor abundance and taxon richness between urban and wildland poppy patches did not differ significantly, the individual taxa did show divergent dominance patterns between the two landscapes. Generally, larger bodied species were significantly more abundant at wildland patches while smaller bodied species were more abundant at urban patches. At the community level, floral visitation was modeled by the size and density of the resource, and this trend was consistent between both landscapes. At the guild level, the visitation rates of larger bodied bees (*Megachile* spp.) and social bees (*A. mellifera* and *B. vosensenskii*) were modeled by resource patch size and floral density, while smaller bodied bees (members of the Family Halicitidea and *Andrena* spp.) were influenced by landscape characteristics such as distance to the wildland urban interface and distance to riparian areas.

Introduction

Urban landscapes have been identified as sites of diverse flora and fauna. The taxonomically rich urban floral community (Thompson et al. 2003) attracts a correspondingly rich assortment of anthophilic species (Smith et al. 2006a; Smith et al. 2006b). Invertebrates, and in particular arthropods, constitute a significant proportion of the urban fauna (Owen 1991; Bolger et al. 2000). Many of these species provide important ecological services that can benefit urban ecosystems and the urbanites that inhabit them. Notable among the beneficial insects are the bees (Hymneoptera: Apoidea); an abundant taxon group that provides the essential ecological service of the pollination.

Abundant and diverse populations of bees have been recorded foraging and nesting within cities. The continued study of urban bees has reveled some general trends of occurrence and ecology. Broadly, species patterns have been are associated with preferred forage resources (Tommasi et al. 2004; Hisamatsu and Yamane 2006), as well as with increasing resource diversity (Frankie et al. 2005, Smith et al. 2006a; Smith et al. 2006b). Patterns of bee diversity have been shown to increase from the adjacent wildland into the urban landscape (Winfree et al. 2007). Within the urban landscape, suburban residential areas have a tendency towards higher bee diversity, which has been attributed to both the increased floral diversity the results form individual gardening practices (Frankie et al. 2005) and to the proximity of the suburbs to wildland populations of bees (Winfree et al. 2007). Seasonal patterns of plant and bee phenology are conserved in many urban landscapes (Wojcik et al. 2008; Frankie et al. 2009). Changes in taxon richness patterns between the urban and wildland landscape also occur when wildland resources diminish and urban resources continue to be in bloom (Cane et al. 2005). In this manner, cities have the potential to serve as habitat reserves, and might even possess conservation value for certain species (McFrederick and LeBuhn 2006).

Landscape scale and context can influence the bee community composition as well as the behavior of individual foraging bees. In wildland and agricultural systems, the structure of the landscape impacts both the diversity and the function of pollinating species (Kremen et al. 2004). In modified landscapes, social bees have been shown to respond to complexity at the landscape level with changes in their dance language communication and subsequent foraging strategy modifications (Steffan-Dewenter and Kuhn 2003). The landscape scale becomes important, especially for smaller species such as bees, as the distribution of local habitat elements, such as the arrangement and spacing of flowers in a meadow, influences their daily activities. The maximum flight dispersal range from a nest to a floral resource is limited by body size and an optimization of foraging energetics (Heinrich 1979; Greenleaf et al. 2007). Resulting unique responses are seen across the different size guilds in the bee community within the same landscape (Steffan-Dewenter et al. 2002).

Practical, proactive, and successful management of the resources present in the urban ecosystem depends on a deeper understanding of the factors that drive species occurrence. Some general trends appear to be emerging regarding the degree to which resource quantity and landscape context impact bee species occurrences. More detailed examinations of the factors that influence the foraging patterns of bees within urban landscapes, however, are limited in the literature. Finer scale assessments of bee forging in the wildland suggest that the quantity (Heinrich

1979; Goulson et al. 1999; Collevatti et al. 2000) and structure (Heinrich 1979; Roubik et al. 1982; Cartar and Real 1997) of the resource at a site are the primary drivers of foraging – this also appears to be the case for some urban landscapes (see Chapters 3 and 4).

Habitat complexity within the urban matrix and the influence of the adjacent landscape likely work synergistically to structure the bee community within a city. The question that remains is to what extent do the characteristics of resources or the characteristics of the urban landscape influence bee foraging. In the previous study of bee foraging in three tropical urban landscapes in Costa Rica, both the degree of urbanization and the range of variation in the landscape variables under investigation were not characteristic of larger, heavily urbanized landscapes such as those that are common in temperate developed regions (i.e., megalopolis areas such as the Greater Chicago Area, the Greater Toronto Area and the Golden Horseshoe, the Eastern Seaboard, and the SF Bay Area). Furthermore, the ability to compare the relative influence of resource and landscape characteristics between wildland and urban systems was lacking, as the target plant, *Tecoma stans*, was only common in the wildland adjacent to one of the three study sites. In the present study of bee visitation to the California poppy (*Eschscholzia californica*), a larger scale comparative sample of urban and wildland resources is conducted in a temperate, highly urbanized ecosystem – the eastern region of the San Francisco Bay. The project aims to further the study of bee ecology and visitation within the urban landscape, and to better define the influence of characteristically urban variables (i.e., residential and commercial land use) on bee visitation rates. The goals of this study are to:

1) Outline the daily and monthly patterns of bee visitation to the California poppy growing in both urban and wildland landscapes.
2) Compare visitation rates between urban and wildland resources to determine if there are any changes in the bee community composition across the two landscapes.
3) Determine if the influence of resource characteristics (total patch size, percentage of poppies in the patch, total poppy area, poppy density, and floral resource species richness) and situation near roadways (traffic class) is paralleled between California poppy patches in adjacent but different landscapes (urban versus wildland).
4) Further investigate the drivers of bee visitation within an urban landscape, and to better understand the degree to which landscape variables (distance to the wild land, distance to riparian areas, and distance to open and/or green space), disturbances (nearness to roads and the class of traffic patterns), resource characteristics (total resource patch size, poppy coverage, total poppy area, poppy density, and floral species richness), and uniquely urban variables (residential and commercial land use) impact bee visitation rates.

Materials and Methods

Site descriptions

The cities of Berkeley (37°52'18"N 122°16'22"W), Emeryville (37°49'53"N 122°17'07"W), and Oakland (37°48'16"N 122°16'15"W) are located in the eastern portion of the San Francisco Bay. The east side of Berkeley and the northeast side of Oakland abut the foot of the Tilden East-Bay Regional Park system. Emeryville is nested between South Berkeley and West Oakland; the western portion of Emeryville extends along the shore of the San Francisco Bay. The native vegetation prior to urbanization in this region primarily included grasslands that were later ranched and transformed into residential, commercial, and industrial land use. The area has been urbanized in part since the late 1800s. Presently, urban land use extends continuously from the shores of the San Francisco Bay to the foot of, and partially up, the western hill sides of the East Bay Tilden range. Continuous urbanization extends to the north and south of the study sites. The most recently available census data puts the population of Berkeley at 102,743; Emeryville at 9,727; and Oakland at 420,183 (United States Census Bureau 2007). The population densities in Berkeley, Emeryville, and Oakland are 3,792/km^2, 2,180/km^2, and 2,751.4/km^2, respectively. The immediate landscape within the study region is characterized by a mix of single and multi-family homes, as well as multi-family low-rise units. Commercial avenues bisect many of the residential neighborhoods, and each city center has a more commercialized downtown. In the areas closer to the San Francisco Bay, industrial land use is also present.

Floral resource characteristics

The Berkeley-Emeryville-Oakland region possesses a mix of green spaces and floral resources. Open space is present in the form of parks, playing fields, and in some cases smaller tracts of conservation land. Gardens are common in the front and back yards of homes and apartment buildings. In addition, medians, traffic calming roundabouts, and planters provide floral resources. The floral resources within this region have been documented to contain more than 170 bee-attractive elements (species, hybrids, cultivars, varieties) that attract over 80 know native bee species from 5 families (Frankie et al. 2005). Of these 170 plant elements, approximately 10 are more significantly attractive to a broad range of species (Frankie et al. 2009). The California poppy is one of these broadly attractive plant elements that is visited by bees representing different functional feeding, size, and nesting guilds, again making it an appropriate floral species for comparative analysis at the community level.

The California poppy, *Eschscholzia californica,* is a pervasive component of the urban flora within the East San Francisco Bay region. Private and municipal gardening practices favor local native species that are drought tolerant. Being the official state flower and having an aesthetic orange bloom period in the early spring (that can last late into the summer with irrigation in urban landscapes), *E. californica* is preferentially planted in many gardens and community spaces and also occurs as an opportunist (Figure 5.1a-d). In addition, *E. californica* is an aggressive seed disperser that frequently populates and repopulates parts of the urban landscape.

A representative subset of the *E. califronica* resources within the three cities were catalogued and then monitored for their bee visitation. In total, 124 sites were sampled, of which 103 were located within the urban matrix and 21 were located in the Tilden East Bay Regional Park.

Each individual poppy patch was catalogued using a hand-held GARMIN Vista C *e*trex GPS unit. The GPS coordinates were downloaded using DNRGarmin (Minnesota Department of Natural Resources, v 5.4.1, 2008, St. Paul, MN). Figure 5.2 shows the locations of each catalogued patch within the urban and wildland areas of Berkeley, Oakland, and Emeryville. Table 5.1 displays the characteristics and the summary statistics for the set of resource and landscape variables used in the analysis. The total size of each patch (patch size) was measured using a tape measure. The proportion of each patch that was covered in *E. californica* (percentage poppy) was then visually estimated. The estimated poppy cover was then multiplied by the total size of each patch to achieve measure of total poppy area (poppy area). The average density (flw density) of poppy flowers at each sampling site was also determined for each visitation count taken by counting the number of individual poppy flower heads in a 30 cm^2 area within the 1 m by 1 m observation window. The number of additional known bee-attractive flowering species (see Frankie et al. 2005) within or in the immediate vicinity of the resource patch was noted and used as a measure of floral richness (floral richness).

Bee visitation counts

The visitation rates of bees foraging on *E. californica* patches in both urban and wildland landscapes were monitored from March to June in 2009. A randomly selected 1-meter by 1-meter observation window was used as the standard counting frame. The numbers (visitor abundance) and types (taxon richness) of the bees that visited this counting frame over three minutes were recorded. The observation window was visually projected onto a representative portion of the total poppy patching to create the sample frame. Visual identification was used to catalogoue the individual bees that landed on a flower within the counting frame. Bee visitors were identified to the lowest distinguishable taxonomic category, including three taxa that were identified to species; *Apis mellifera*, *Bombus californicus*, *B. vosnesenskii*; two that were identified to genus *Andrena* spp., *Megachile* spp., and three sub categories of the family Halictidea representing large Halictids (Halictus species measuring approximately 1 cm or larger, generally *Halicuts ligatus* and *H. rubicundus,* but also *Agapostemon texanus*), medium Halictids (Halictids between 5mm and 1 cm, generally *H. tripartitus*), and small Halictids (Halictid bees smaller than 5 mm, generally *Lassioglossum* spp.).

Visitation data was collected from the hours of 0900h to 1400h, which correspond to the natural opening of the flowers and to the subsequent early afternoon cooling due to the regional climate, respectively. The rates of bee visitation to a patch of poppies were recorded on multiple days throughout the four-month study period, and at multiple times during each data collection day.

Landscape Variables

The locations of riparian areas and open space were identified using a series of satellite images, the Creek and Watershed Map of Berkeley and Oakland (Oakland Museum of California 2000), and through ground-based observations. The distances of each study patch to the urban-wildland interface, riparian areas, and sites of open space (parkland and remnant green/open space) was calculated in ArcGIS v 9.3 (© ESRI Inc 2009) using the Near function (see Table 5.1). The situation of each poppy patch within commercial or residential land use was determined using the respective city land use classes provided by the municipalities of Berkeley (City of Berkeley, California 2009: http://www.ci.berkeley.ca.us/SubUnitHome.aspx?id=32594), Emeryville (City of Emeryville, California 2009: http://www.ci.emeryville.ca.us/index.aspx?nid=545), and Oakland (City of Oakland, California 2009: http://oaklandnet.com/government/ceda/).

To examine the effect of traffic on bee foraging rates, the number of cars per 15 minutes was recorded at various locations representative of the general road classes next to which the poppy patches were located. Traffice counts were taken each hour from the hours of 900h to 1400h, corresponding to the bee monitoring times used. The mean traffic intensity common to each road class was then calculated by taking an average of all vehicles observed across all measures for each site. Five traffic categories were then determined based on the mean number of cars observed in 15 minutes and the road type. Poppy patches that were more than 3 meters away from the edge of a road were classified as having little to no traffic disturbance (road class of 1). The subsequent traffic categories included: quiet residential (less than 40 cars in 15 minutes, road class 2), busy residential (between 41 and 80 cars in 15 minutes, road class 3), commercial (between 81 and 170 cars in 15 minutes, road class 4), and busy thru-fare (more than 171 cars in 15 minutes, road class 5).

Statistical analysis

In order to determine if there were any differences in the total visitor abundance, overall taxon richness, and in the visitation rates of the individual taxnomic groups between the urban and wildland poppy patches, a series of student's t-tests were conducted, followed by Levene's test for detecting equal variances. Subsequent adjustments in degrees of freedom were made as needed. In order to determine if any significant temporal and seasonal patterns in visitation were present, the visitation rates of all of the bee taxa were compared using ANOVA, with an α of 0.05 that was Bonferroni-adjusted accordingly for time of day (urban, 0.05/6=0.0083; wildland, 0.05/4=0.0125) and for the month of bee occurrence (0.05/4=0.0125). The multivariate comparison analyses were conducted in SPSS (SPSS Inc, Chicago, IL 2007).

To determine the influence of the combination of landscape variables and resource patch characteristics on bee visitation within and between the wildland and the urban landscapes, a series of backwards stepwise regression models were generated. The probability of removal was set to $\alpha>0.05$. The covariance matrices of each model were examined for variable association and these values were minimal. All of the regression-based models were run in STATA 10.0 (STATA Corp, College Station, TX 2008).

For the urban poppy patches, the influence of urban landscape variables (land use class, distance to green space, and distance to the wildland-urban interface), disturbance variables (road class), and resource characteristics (total patch area, percentage poppies, total poppy area, poppy flower density, and floral richness) were modeled for correlation with the visitor abundance and mean taxon richness of bee foragers. A further investigation of the correlation between honeybees (*Apis mellifera*), *Bombus vosensenskii*, *Megachile* spp. *Andrean* spp., and both medium and small Halictids were tested. There was not sufficient data to generate significant models for *B. californicus* and large Halictids within the urban landscape.

In the wildland landscape, the influence of the distance to riparian areas, road class, and resource characteristics (total patch area, proportion of patch represented by poppies, total poppy area, poppy density, and floral richness) were modeled for their correlation with the total visitor abundance and mean taxon richness of bees foraging on wildland poppy patches. A set of models was generated for honeybees (*A. mellifera*), *B. vosensenskii*, and both medium and small Halictids. There was insufficient visitation data to generate significant models for *B. californicus, Megachile* spp., *Andrena* spp., and large Halictids within the wildland landscape.

The influence of the greater regional land use on bee visitation rates was then tested by modeling the resource characteristics (patch area, percentage of patch covered in poppies, total poppy area, poppy density, and floral richness) and landscape variables (distance to riparian areas and road class) that were common to both the urban landscape and the wildland sites. In this manner, models were generated for total visitor abundance, mean taxon richness, and for *B. vosensenskii*, *Andrean* spp., *Megachile* spp., medium Halictids, and small Halictids. The specific goal of this analysis was to determine if, in addition to resource characteristics and local land use, the regional land use (wildland or urban) was significantly corrected with the visitation rates of bees. Significant models could not be generated for *B. californicus* and large Halictids.

Behavioral observations

Throughout the course of the study, behavioral observations were noted regarding the occurrence of territorial males and nesting. These observations are presented in the results and discusses briefly thereafter.

Results

In this study of bee visitation to *E. californicus*, 1,848 individual observations recorded the visitation of 2,563 bees. The most abundant visitor across both urban and wild landscapes was *B. vosnesenskii* (n=579 in urban and n=306 in wildland). Non-native honeybees, *A. mellifera*, were the second most commonly recorded taxon in both landscapes. Halictids were the third most common group, but varied in their relative representation by size class between the two sites; medium sized Halictids were the most common type at urban sites, while small Halictids were the most common in the wildland of Tilden Park. The rarest visitors present in both landscapes were *Megachile* species. *Andrena* species were recorded only in the urban landscape and showed very low numbers with a restricted seasonal occurrence (n=6).

Landscape occurrence patterns

Distinct patterns of visitation were evident between the two landscape types. Figure 5.3 graphs the comparative mean number of bees recorded per visitation count across all counts between the two study regions. Table 5.2 displays the results of the statistical comparison of the mean visitation rates between urban and wildland poppy patches. The overall mean visitor abundance recorded per count in the urban sites was 1.53 (± 0.056 SE) and at the wildland sites was 1.35(± 0.125); these two means did not differ significantly (p=0.199). The mean richness of the bee taxa recorded per count in the urban sites was 0.76 (± 0.023) and in the wildland sites it was 0.74 (± 0.047), and these two measures also did not differ significantly (p=0.727). There were, however, significant differences in the mean visitation rates between the two landscapes for five of the eight taxonmic groups examined (*B. vosensenskii*, honeybees, and small, medium, and large Halictids; see Table 5.2 and Figure 5.3). In addition, there is a general trend of more larger-bodied bees visiting wildland sites, while smaller bodied species are comparatively more common at urban sites. For example, large bodied, social *Bombus* species were more commonly observed at the wildland sites than at the urban sites. *B. vosnesenskii* was significantly more abundant per observation in the wildland (p=0.000), with an average of 1.1 (± 0.102) individuals per count observed on Tilden Park poppy patches compared to an average of 0.34 (± 0.021) individuals per count at the urban poppy patches. There were also more *B. californicus,* on average, per count in Tilden compared to the urban landscape, but this difference was not significant. Both the large and medium size classes of the generally smaller bodied Halictids where significantly more abundant per observation at the urban sites ($p>0.031$). Halictids in the small size class were also more abundant at urban sites, but this difference was not significant. *Megachile* species were more abundant per count at the urban sites, but this difference was also not significant ($p=0.030$). *Andrena* species were only recorded in the urban landscape.

Temporal patterns of bee occurrence

The daily temporal patterns of visitation include a general increase in visitation from 0900h, with peak visitation between 1100h and 1300h, followed by a decline towards 1400h that is common to both wildland and urban systems (Figure 5.4). A statistical analysis (ANOVA) of the mean visitor abundance and taxon richness in urban landscapes over time indicated that there is significant variability in urban landscapes ($p<0.0083$). A taxon specific analysis (Table 5.3), however, shows that significant temporal variability in foraging is only exhibited by three groups: honeybees and small and medium Halictids. Figure 5.5 displays the daily visitation patterns exhibited by Halictids in both urban and wildland landscapes. The hours of 1100h and 1200h show increased visitation rates for small and medium sized individuals, and these increases are significant ($p<0.0083$). No general pattern is evident in the foraging of Halictids of any size at wildland poppy patches (see Figure 5.5). Honeybees forage in significantly higher numbers during the morning hours in urban landscapes, while in the wildland landscapes their visitation is more truncated between the hours of 1000h and 1300h.

The remaining bee taxa have consistent visitation rates throughout the day ($p>0.010$). In the urban landscape in particular there is a rush of early morning activity just as the flowers open, and likely when pollen and nectar amounts are the highest. Prior to 0900h the poppies were generally closed; later into the afternoon the local climatic conditions cause a cooling that reduced bee activity, and was often also associated with petal closing. These patterns are paralleled across both landscapes, however, foraging begins later in the day at the wildland sites.

Only the visitor abundance varied significantly over time in wildlands (Table 5.4). The significant peak in visitation is shifted later into the day. No significant trends were seen in the overall taxon richness patterns throughout the day; however, social bees (*A. mellifera*, *B. californicus*, and *B. vosnesenskii*) exhibited increased foraging after 1200h compared to the morning hours. This trend is exemplified by *B. vosensenskii*, the dominant forager in wildland systems (Figure 5.6). The late morning the early afternoon had significantly higher numbers of *B. vosensenskii* at poppy patches than the hours prior to 1100h (Figure 5.6). There is no significant trend in *B. vosensenskii* foraging numbers over time at urban poppy patches. The first visitors to most sites in both the urban and wildland landscapes are larger bodied and social foraging species. The local solitary native species being to forage more substantially after 1000h.

A seasonal analysis of the patterns of the visitor abundance and taxon richness showed a general increase from March through to June, and these patterns were paralleled between both the urban and wildland sites (Figures 5.7 and 5.8). At urban poppy patches the monthly increases in bee visitor numbers were significant through the season form month to month ($p>0.002$), while at wildland patches only the later season increase (from April to May, and then from May to June) were significant ($p>0.042$). Individual taxonomic groups display distinct seasonal occurrence patterns that were are not always paralleled between the two landscape types. The occurrence of the most abundant taxon, *B. vosnesenskii*, increased gradually from March to June at urban sites, while at wildland sites foraging was delayed until April, and then the numbers of visitors increased significantly from month to month until June ($p>0.012$, Figure 5.9). *A. mellifera* numbers at urban sites increased through the season, with a significant peak in June ($p=0.000$), while at wildland sites their occurrence was patchy and without a distinct seasonal trend (Figure 5.10).

As a group, Halictids visiting urban sites have significantly higher occurrence rates between April and June, while their occurrence at wildland sites does not present a clear trend (Figure 5.11). Examining the individual size classes shows that small and large Halictids also have a generally higher visitor abundance pattern later in the season at urban sites and a patchy occurrence at wildland sites (Figure 5.12 and 5.14). Medium-sized Halictid taxa, generally *H. tripartitus*, on the other hand, have a latent but significantly high and consistent occurrence rate at urban sites from April to June compared with the numbers observed in March ($p>0.000$). At the wildland sites, the numbers of Halictids gradually build from April to June, but this increase is not significant (Figure 5.13). In every month, however, urban medium-sized Halictid numbers are significantly higher than wildland numbers ($p>0.000$).

Megachile species are predominantly summer species, and had a significant occurrence peak in the urban landscape in June ($p=0.025$), with consistent but lower numbers in the wildland (Figure 5.15). As mentioned previously, *Andrena* spp. were only present at urban poppy patches in low numbers ($n=6$) and their occurrence was restricted to later April and early May.

Visitation models

The models generated for bee visitation at urban and wildland poppy patches showed some parallels. In particular, resource characteristics were a common driving factor, irrespective of land use. Urban models were generally more complex than wildland models. Table 5.5 summarizes the results of these models. More elaborate models can be found in Appendices 5.i through 5.vii.

In urban landscapes, a mix of resource characteristics and landscape variables structured the visitation rates of bees. The local land use (either commercial or residential), distance to open and/or green space, and the class of road did not have any significant correlation with visitation rates at the community level, or in individual taxon groups. Visitor abundance was correlated exclusively with resource characteristics ($F_{2,100}=9.64$, $p=0.000$, see Appendix 5.i), while taxon richness and the visitation rates of the specific taxon groups were correlated with both resource characteristics and landscape variables ($F_{4,98}=7.57$, $p=0.000$, see Appendix 5.ii). The patterns of overall bee visitor abundance at *E. californicus* were correlated positively with an increasing total poppy patch area ($p=0.029$) and an increased density of poppies ($p=0.001$) (Table 5.5, and Appendix 5.i). On average, larger patches of poppies that were denser attracted more bees, irrespective of their land use context (i.e., residential vs. commercial). The taxon richness for visitors at urban poppy patches was also positively correlated to the total poppy area and the density of the poppies ($p=0.016$ and $p=0.004$, respectively), and was also correlated with two landscape variables: distance to the wildland-urban interface ($p=0.035$) and the distance to riparian areas ($p=0.001$) (Table 5.5, and Appendix 5.ii). Taxon richness was higher at large, dense poppy patches that were closer to the wildland, but further from riparian areas.

Within the urban landscape, social species (*A. mellifera* and *B. vosnesenskii*) and larger bodied species (*Megachile* spp.) had visitation rates that correlated with poppy patch resource characteristics. Bumblebees of the species *B. vosensenskii* foraged with increasing numbers on patches that were denser in poppies (p=0.040) as well as those that had an overall larger poppy area (p=0.011) (see Table 5.5 and Appendix 5.iii). The visitation rates of *B. vosensenskii* were also correlated positively to increasing distance from riparian areas (p=0.033). Honeybees, *A. mellifera*, foraged with increasing numbers on denser patches (p=0.002), and those with more floral richness (p=0.019) (see Table 5.5 and Appendix 5.iv). *Megachile* spp. foraged in higher numbers on denser patches of poppies (p=0.045, see Table 5.5 and Appendix 5.v).

The visitation rates of smaller-bodied taxa (*Andrena* spp. and the various Halictid taxa) in the urban landscape were correlated exclusively with landscape variables. In particular, an increasing distance to the wildland-urban interface correlated with a reduction in small and medium sized Halictid visitation (p=0.022 and p=0.004, respectively; see Table 5.5 and Appendix 5.vi). The foraging rates of *Andrena* species were positively associated with an increasing distance from riparian areas (p=0.010, see Table 5.5 and Appendix 5.vii), and this was also the case for small Halictids (p=0.000). Floral resource characteristics did not have any significant correlation with small bee visitation rates in urban landscapes, neither did land use class or patterns of traffic.

Wildland landscapes

In the wildlands, the density of the poppy resources and the richness of other bee-attractive species in the vicinity were significant correlated with the total visitor abundance ($F_{2,18}$=16.23, p=0.000, see Appendix 5.i). The richness of bee taxa was exclusively positively correlated with floral density ($F_{2,18}$=16.23, p=0.000, see appendix 5.ii) . On average, an increase of one additional floral resource species corresponded to an increase of 0.500 (± 0.153 S.E.) bees observed at that site per count. Similarly, and increase of one additional flower per 30 cm^2 corresponded to an increase of 0.156 (± 0.037 S.E.) bee taxa per observation. This significant positive correlation between resource richness and density was maintained for the dominant taxon foraging in this landscape, *B. vosensenskii* ($F_{2,18}$=11.12, p=0.000, see Appendix 5.iii). Small Halictids foraging in wildland landscapes also had their visitation rates positively correlated to increasing patch density ($F_{1,19}$=7.79, p=0.012, see Appendix 5.vii). The visitation rates of medium and large-sized Halictids, on the other hand, were negatively correlated to increasing road class (p=0.028 and p=0.084, respectively). Medium sized Halictids also responded to both the total size of the resource patch (p=0.033) and the size of the poppy area within the total patch (p=0.034). The visitation rates of honeybees, *A. mellifera*, in wildland landscapes correlated with resource patch structure ($F_{2,18}$=11.12, p=0.000, see Appendix 5.vi). Patches that were smaller and that had more poppy coverage, on average had more honeybee visitation per count (p=0.008 and p=0.007, respectively).

The influence of the regional landscape context

When the floral visitation rates of both the urban and wildland landscapes were pooled to determine if there was any influence of regional land use on the visitation models, only two models retained regional land use as a significant variable: *B. vosensenskii* and medium Halictids. The visitation rates of *B. vosensenskii* were found to be positively correlated with poppy patch area (p=0.000), and poppy density (0.004) in both landscapes (see Table 5.6). An increasing distance from riparian areas corresponded to more visitation form *B. vosensenskii* as well (p=0.03). In this model, urban land use was negatively correlated with visitation rates (p=0.000), corroborating the previous comparison of the mean visitation rates between urban and wildland sites (see Table 5.6). On average, there were 0.618 (± 0.123 S.E.) *B. vosensenskii* foragers at the poppy patches in urban landscapes when compared to the equivalently characterized patches in wildland landscapes. The pooled model for medium sized Halictids indicated the same significant correlation with nearness to the urban wildland interface and increasing visitation (p=0.002), as well as an increasing rate of visitor occurrence when the poppy patch was located within the urban landscape (p=0.002; Table 5.6). On average, there were 0.301 (± 0.094 S.E.) medium Halictid foragers at the poppy patches in urban landscapes when compared to the equivalently characterized patches in wildland landscapes.

Behavioral observations

Over the course of data collecting, nesting was observed in both landscapes. The nesting of *Halictus tripartitus* was observed in the ground near the base of planted floral resources. An aggregation of nests was observed in a planted area on the northern side of Ashby Avenue east of the intersection with Ellsworth Street between the concrete sidewalk and the road. Evidence of *Megachile* spp. using the petals of California poppies to create and line their nests was observed in both urban and wildland landscape. Nest of *Megachile* species were also recorded in many of the planted medians in the Tilden Park wildland area.

Male bees holding territory around patches of poppies were observed in urban landscapes. Medium sized and small sized Halictids were seen holding territory around some urban poppy patches. Successive data collection visits to these sites recorded the same male to be present from 0900h to 1300h. The territorial male also chased other conspecific males and pursued conspecific females. Large *Megachile* spp. males were observed actively holding territory around abundant poppy patches located within traffic-calming roundabouts.

Discussion

When a resource was available and abundant in either in the wildland or in urban landscapes it was frequently visited by foragers. The interplay of landscape context and resource characteristics influenced the relative dominance of taxa visiting *E. californicus* and the characteristics of the resource impacted the degree to which the patch was visited. Neither the regional landscape context nor the local land use patterns impacted the site-level visitation rates of bees. The primary drivers of visitation patterns were the characteristics of the resource patch, in particular the size and density of the patch, suggesting that bee visitation to a site is structure by an optimization of foraging at a local level and not by regional factors. Regional factors structure the overall bee communities that exist at a site, but the behavior of bees within landscapes is structured by micro-scale site-level characteristics.

Patterns of overall visitation

The visitors to *E. californica* included large and small, native and exotic, and social and solitary species. The occurrence patterns of foraging bees on urban and wildland poppy patches displayed generally parallel trends in daily and seasonal abundance and richness patterns, although both daily and seasonal foraging occurred at later times in the wildland. The delayed daily foraging in the hills of the Tilden Park wildland poppy patches are likely linked to local fog patterns. Poppies were often still closed on visits to the wildland sites prior to 1000h. Mid-afternoon fog also impacted the wildland sites much earlier in the day due to their higher elevation.

Rather than seasonal wildland foraging being delayed, urban foraging is likely advanced. Urban floral resources are known to have phenologies that extend earlier and later than wildland resources due to urban garden management (early planting, planting green-house reared plants, and increased irrigation) and, in the case of early blooming, increased temperatures due to the heat island effect (Lu et al.2006; Neil and Wu 2006; Chung et al. 2009). Populations of urban bees are thought to emerge sooner and to outlast wildland population that can be limited by the natural cycles of wildland resources. Wildland to urban migration by bees has also been reported in landscapes when the natural season of the wildland species is over and urban resources become the dominant or only available food source (Cane et al. 2006).

Although absolute visitor abundance and taxon richness numbers did not differ between the two landscapes, the composition of the visitors did. Larger bodied bees, specifically *B. vosnesenskii*, were significantly more common as visitors at wildland poppy patches. At urban floral resources, smaller bodied taxa, in particular *Halictus* and *Lassiglossum* species, were the dominant visitors. Both the foraging flight ranges and the energy requirements of large and small bees differ (Steffan-Dewenter et al. 2002; Greenleaf et al. 2007; Araujo et al. 2004), causing each group to respond to a different set of landscape level and sites specific characteristics.

Larger bodied bees have longer forage flight ranges and greater dispersal abilities compared to smaller bodied bees. Large social bumblebees are capable of a foraging radius of more than 1 kilometer from the nest (Steffan-Dewenter and Kuhn 2003), while smaller solitary bees generally are through to only fly about 250 meters from their nest to their foraging sites (Greenleaf et al. 2007). The floral resource patches in the wildland of Tilden Park are spatially separated compared to those in the urban landscape. Smaller bees foraging in this system therefore might not have the same patch-to-patch dispersal abilities that larger bees do, accounting the generally lower observed numbers. In urban landscapes, especially in residential neighborhoods, gardens occur at nearly every home – well within the 250-meter foraging range of small bees.

Life history characteristics might be another factor that increase bumblebee numbers in the wildland, compared to those seen in the urban landscape. Smaller bodied solitary bees nest by digging into the ground or within twigs and small pre-existing holes. Bumblebees, on the other hand, require larger cavities and usually make use of vacant rodent burrows. Ahrne et al. (2009) found that as urbanization increased, the number of *Bombus* species and their abundance decreased, even in the presence of appropriate foraging habitat, and linked this trend to a lack of nest site occurrence. Conversely, Osborne et al. (2007) recorded higher bumblebee nest density in English gardens compared to woodland and grassland habitats. Similarly, Pawlikowski and Pokorniecka (1990) observed higher numbers of *Bombus* species in residential and agricultural areas when compared to the native wildland in Poland.

In the urban landscape, the occurrence of appropriate nesting substrate for bumblebees can be limited by pest management practices that reduce rodent populations. There is also the likelihood of the elimination of bumblebee nests if they are viewed as a pest or a nuisance species. A further investigation is needed to determine if nesting sites or resource dynamics drive large bee occurrence as this aspect of urban bee ecology is generally poorly understood.

Drivers of landscape and local-level foraging

The local land use (residential versus commercial) in the urban landscape did not have any significant correlation with forager occurrence. Corresponding resource patches in commercial and residential areas received the same numbers of visitors. Diverse gardens have been touted as sites of increased bee diversity within the urban landscape (Tommasi et al. 2004; Frankie et al. 2005; Frankie et al. 2009). These diverse gardens occur predominantly in residential areas (Thompson et al. 2003; Thompson et al. 2004; Loram et al. 2008). These studies however, focus on community composition and overall species occurrence rather than the behavior and visitation patterns of individual species or guilds. Bees are known to exhibit patterns of floral usage and preference (Michener 2000; Frankie et al. 2005; Wojcik et al. 2008; Frankie et al. 2009) and their occurrence may not necessarily be influenced by an increase in floral richness per say.

Honeybees were the only group in this study that responded positively to increased floral richness within the urban landscape. Honeybees are an example of an extreme generalist polylectic forager – a trait that, in addition to their colonial life style, has accounted for their integration into commercial agriculture. The other taxa under study have narrower, oligolectic, and mesoletic feeding preferences. The particular floral resources recorded in the richness assessment included some native floral species (wild California lilacs, *Ceanothus* spp.; fleabane, *Erigeron karvinskianus*; and black sage, *Salvia mellifera*), but were predominantly decorative ornamental species including many that are not locally native: North American lilac (*Ceanothus* spp.), other sage species (*Salvia greggii*, *S. uliginosa*, *S.* spp.), rosemary (*Rosmarinus officinalis*), red hot poker (*Kniphofia uvaria*), dandelion (*Taraxacum* spp.), and other lavenders (*Lavandula* spp.). The native bee specie that are foraging on *E. californica* might, therefore, not be influenced by these floral species.

In the wildland there was a mix of native (*Lupinus* spp., *Ranunculus califronicus*) and non-native species (Queen Anne's Lace, *Daucus carota*; Thistile, *Centarea* spp. and *Silybum* spp.) associated with patches of *E. californica*. Patch floral richness was a significant driver for bee visitation in this particular wildland system. The overall bee taxon richness was higher at patches with more floral species and the larger bodied species were more common at these more floristically diverse patches. The overall landscape level diversity of floral species in the Tilden Park wildland was lower than in the urban landscape, as is often the trend when wildland and urban floral are compared (Thompson et al. 2003; Loram et al. 2007; Loram et al. 2008). In such a case, areas of higher floral diversity stand out in fields of native grasses that do not possess blooms that attract pollinators.

Roads and traffic patterns were not found to impact forager visitation in the urban landscape. In the wildland the smaller bodied taxa displayed decreasing numbers at a site as the traffic intensified. Previous studies have suggested that roadways and other traffic corridors are barriers to bee movement through a landscape (Bhattacharya et al. 2003). In this particular study, bees readily visited sites that were in high-traffic areas. A subset of the study sites were located along road-way medians and in traffic-calming roundabouts. Unless the foragers were nesting in the ground at these sites, they were obliged to cross roadways to reach the resource. Observations of bees (both large and small bodied) flying across roadways were common in this study.

The observations of nesting, nest substrate collection, and male territoriality within the urban landscape imply that bee species are in fact completing their entire lifecycle within the boundaries of the city; highlighting the importance of considering both feeding and nesting habitats to the management of successful urban bee populations. Published accounts of bee species nesting in urban landscape are, however, limited (Barthell et al. 1998; Osborne et al. 2007;

Loyola and Martins 2006). Winged species have the ability to disperse from their home or nest site to acquire food and water, but the availability of acceptable and accessible nesting substrates will ultimately limit the ability of bees to efficiently access food and provision for their young.

Urban landscapes possess the potential to become thriving and diverse ecosystems. Classical planning and management practices aimed at satisfying the aesthetic needs of urbanites have created floral diversity hot spots that are attractive to many fauna. Many of the faunal species that have taken advantage of urban habitat resources are involved in the provision of important ecosystem services that can benefit both urban and adjacent wildland systems. In particular, bees, the premier pollinators of nearly 80% of all flowers species (Kevan 1999; Kevan 2001), being responsible for fruiting and the creation of two out of every three bites of food consumed by humans (Buchmann and Nabhan 1996), are present in urban landscapes across the globe (Saure 1996; McIntyre and Hostetler 2001; Tommasi et al. 2004; Frankie et al. 2005; Cane et al. 2006; Antonini et al. 2006; Nates-Parra et al. 2006; Hismatsu and Yamane 2006; McFrederick and LeBuhn 2006; Fetridge et al. 2008; Matteson et al. 2008). It is also clear in this work, and from the previous chapter, that urbanization or urban land use does not preclude active foraging by bees. Bee occurrence patterns are driven by bee-plant associations that have developed over millennia. No portion of the urban landscape appears to be inappropriate for bee habitat development. If the appropriate resources are present, bees will visit the site. The natural occurrence of bees within the urban landscape and their explorative foraging biology could be used to provide pollination services for urban agricultural projects.

Acknowledgements

Many thanks are due to Joe McBride, who provided academic support and guidance throughout the project. I would like to extend special thanks and appreciation to Steven La, who worked extensively on this project with both data collection and data management. I would also like to thank Sean Fine, Melisa Lin, Jessica Dugan, and Yenny Martin for their assistance with data collection through the 2009 season. The staff at the GIF, in particular Jeremy Freund and Kevin Koy, were very helpful and provided assistance with spatial data management. Funding was provided for this work through the College of Natural Resources SPUR (Sponsored Undergraduate Research) Program and made the extensive travel required for this project possible.

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Figures, Tables, and Appendices

Figure 5.1a: An example of an urban poppy patch growing in a traffic round-about at the intersection of Russell Street and Fulton Street in Berkeley, California. Photo credit: Victoria A. Wojcik.

Figure 5.1b: An example of a strip of poppies growing along the sidewalk on Russell Street, Berkeley, California. Photo credit: Victoria A. Wojcik.

Figure 5.1c: California poppies growing in a planter box at the site of a house at 64th Street and Shattuck Avenue in Oakland, California. Photo credit: Victoria A. Wojcik.

Figure 5.1d: A *Bombus vosensenskii* visiting a poppy at Telegraph Avenue and 62nd Street, Oakland, California. Photo credit: Victoria A. Wojcik.

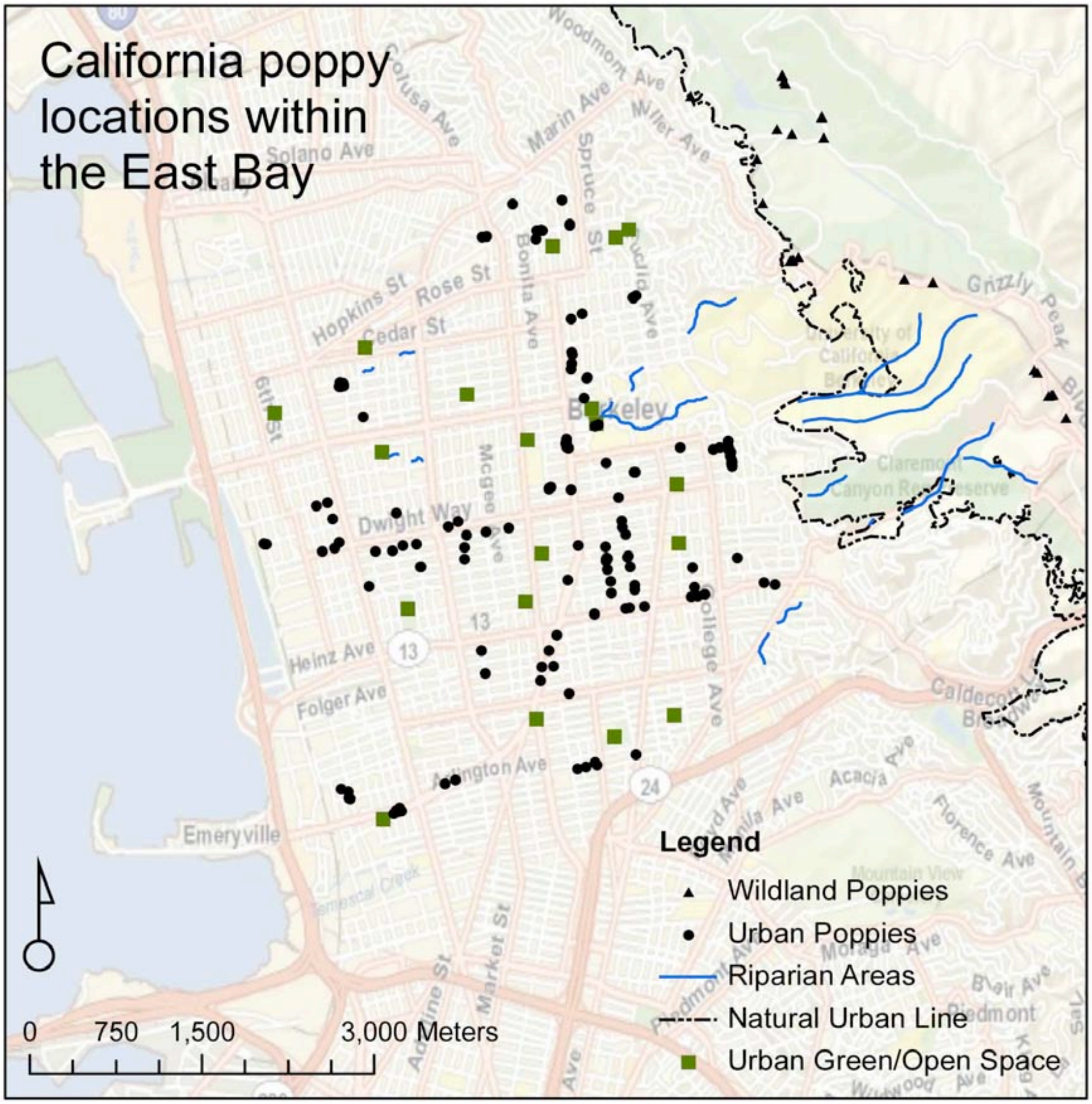

Figure 5.2: A map showing the sampled patches of California poppy (*Eschscholzia californica*) in both urban and wildland habitats. Riparian areas and day-lighted creeks are indicated, as well as areas of open space (green space, parks, etc.). The wildland-urban interface between Tilden East Bay Regional Park is also indicated as the natural urban line.

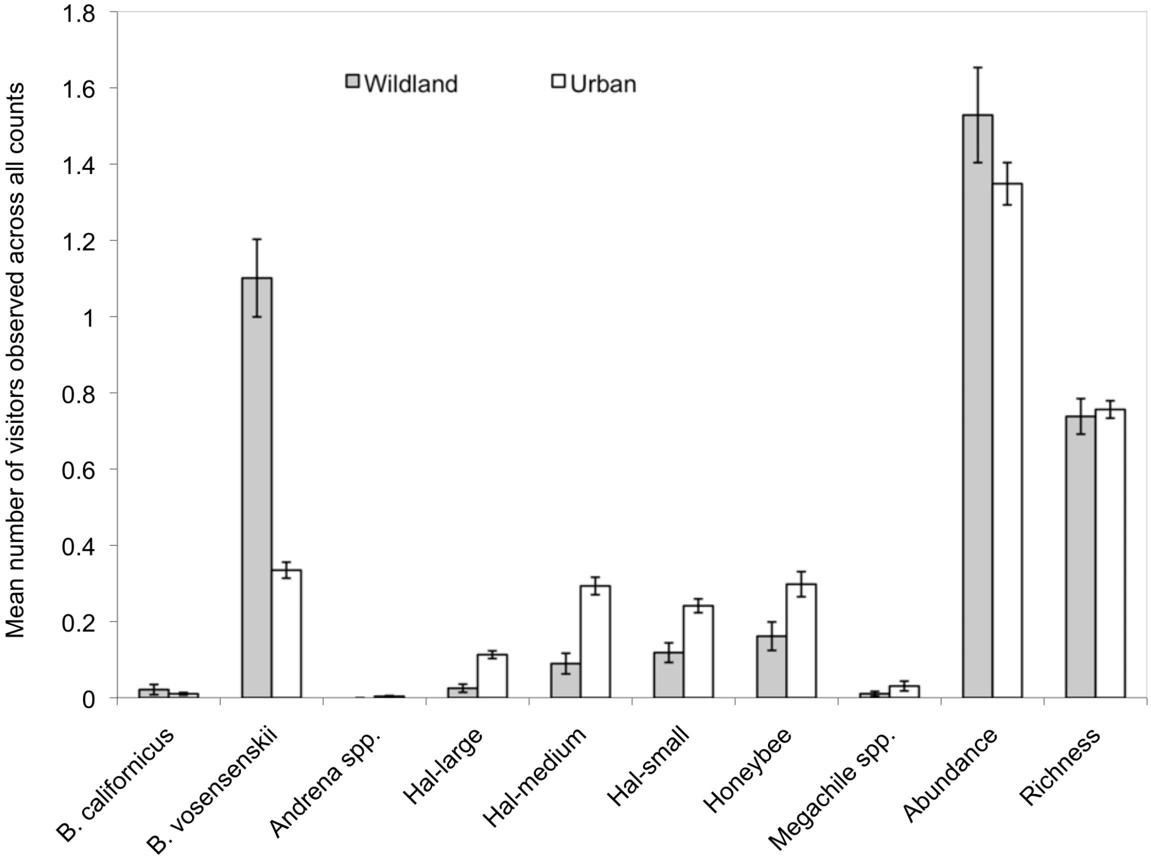

Figure 5.3: The mean number of bees observed per three-minute count, including the total visitor abundance, bee taxon richness, and the occurrence of eight other groups at poppy patches between the wildland and urban landscapes.

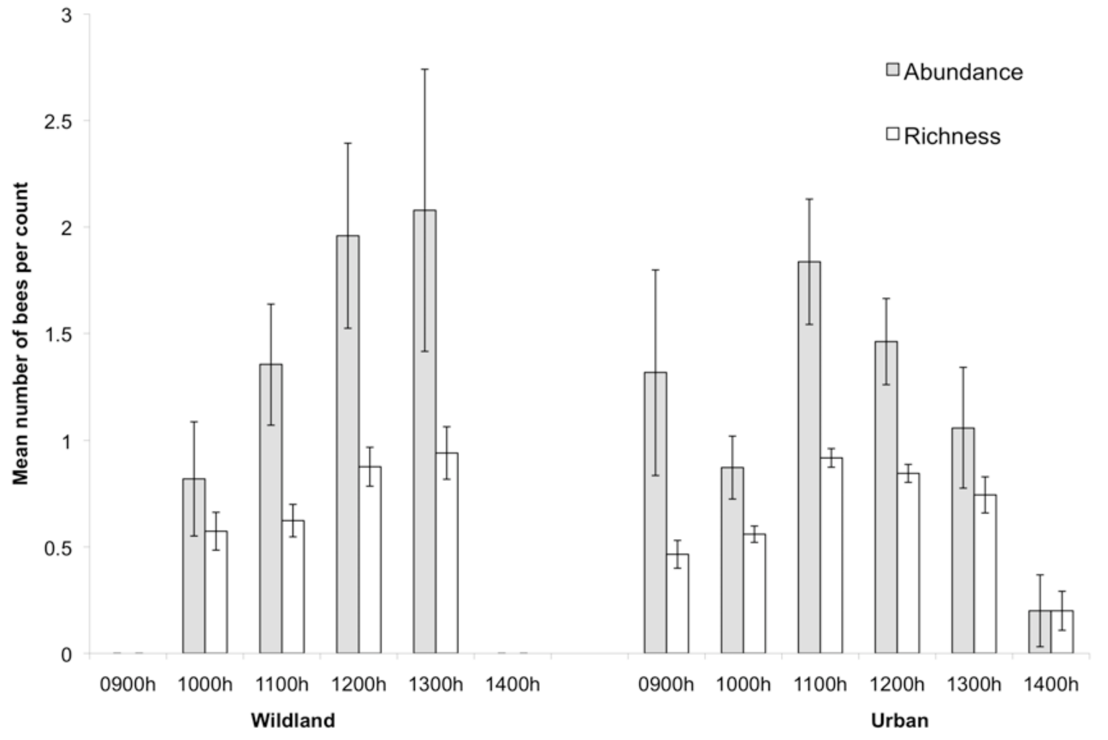

Figure 5.4: The mean patterns of visitor abundance and taxon richness of the bee visitors to poppy patches in both urban and wildland landscapes over time.

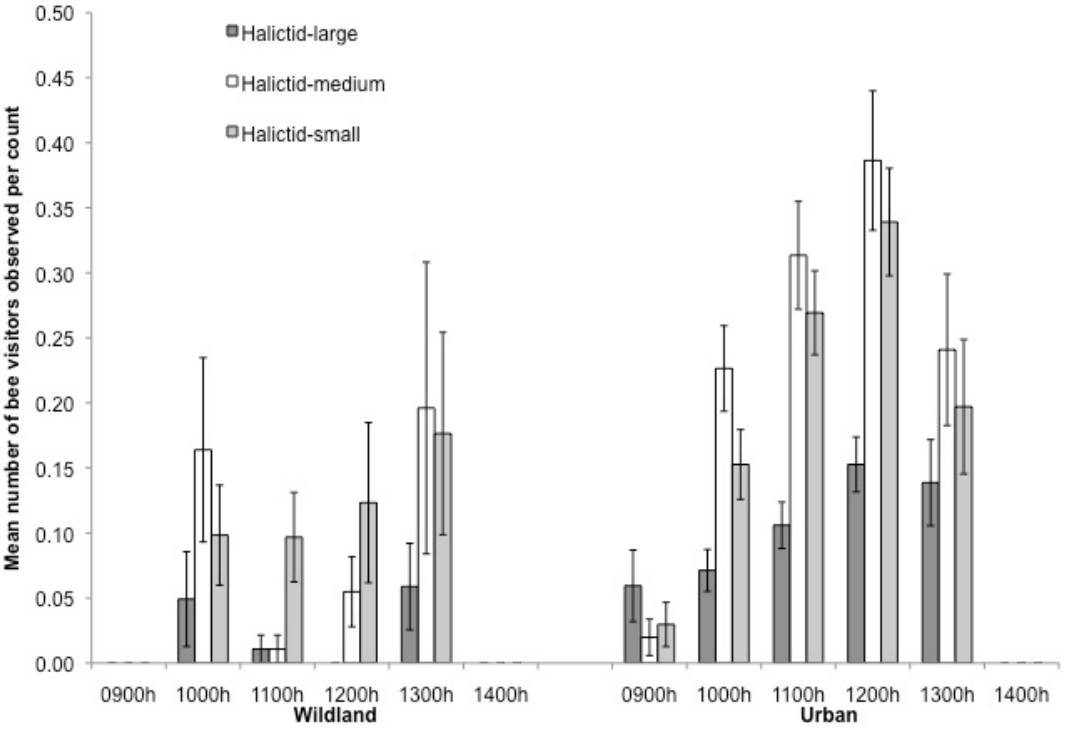

Figure 5.5: The daily foraging patterns of small, medium, and larger Halictids (abbreviated Hal) at poppy patches in both wildland and urban landscapes. The mean number of foragers observed per count across all counts taken during each hour of study are presented.

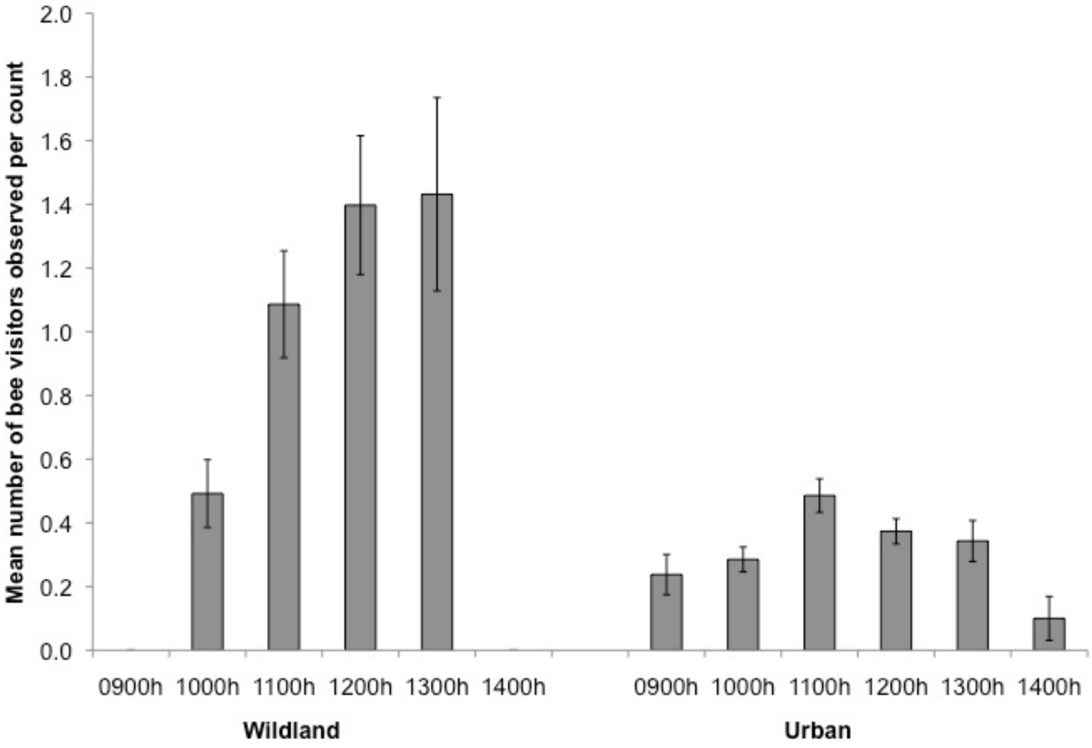

Figure 5.6: The daily foraging patterns of *B. vosensenskii* at poppy patches in both wildland and urban landscapes. The mean number of foragers observed per count across all counts taken during each hour of study are presented.

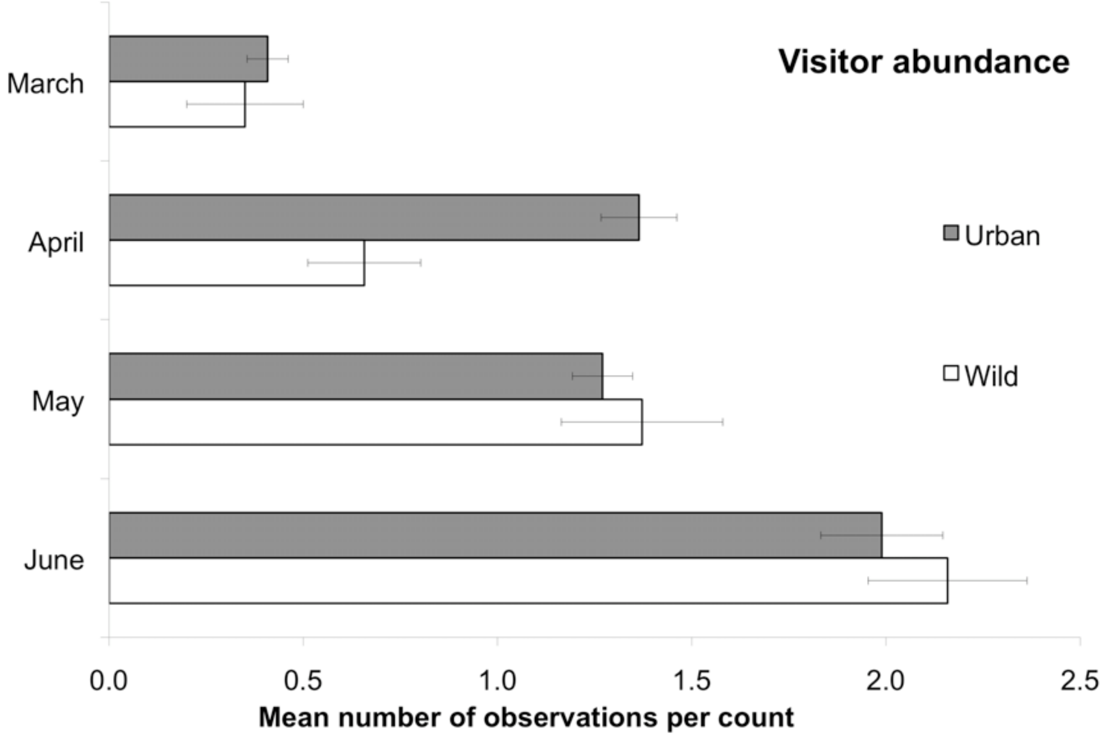

Figure 5.7: The mean visitor abundance recorded per observation at both the wildland and urban poppy patches.

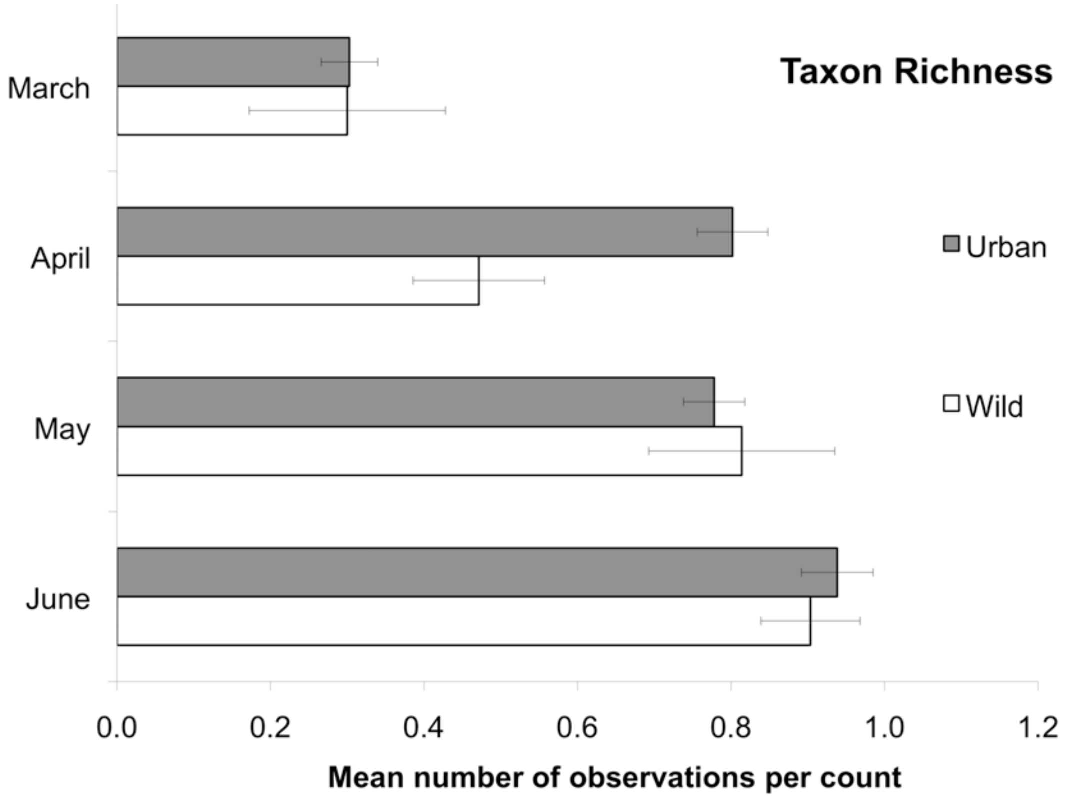

Figure 5.8: The mean number of taxon richness recorded per observation at both the wildland and urban poppy patches.

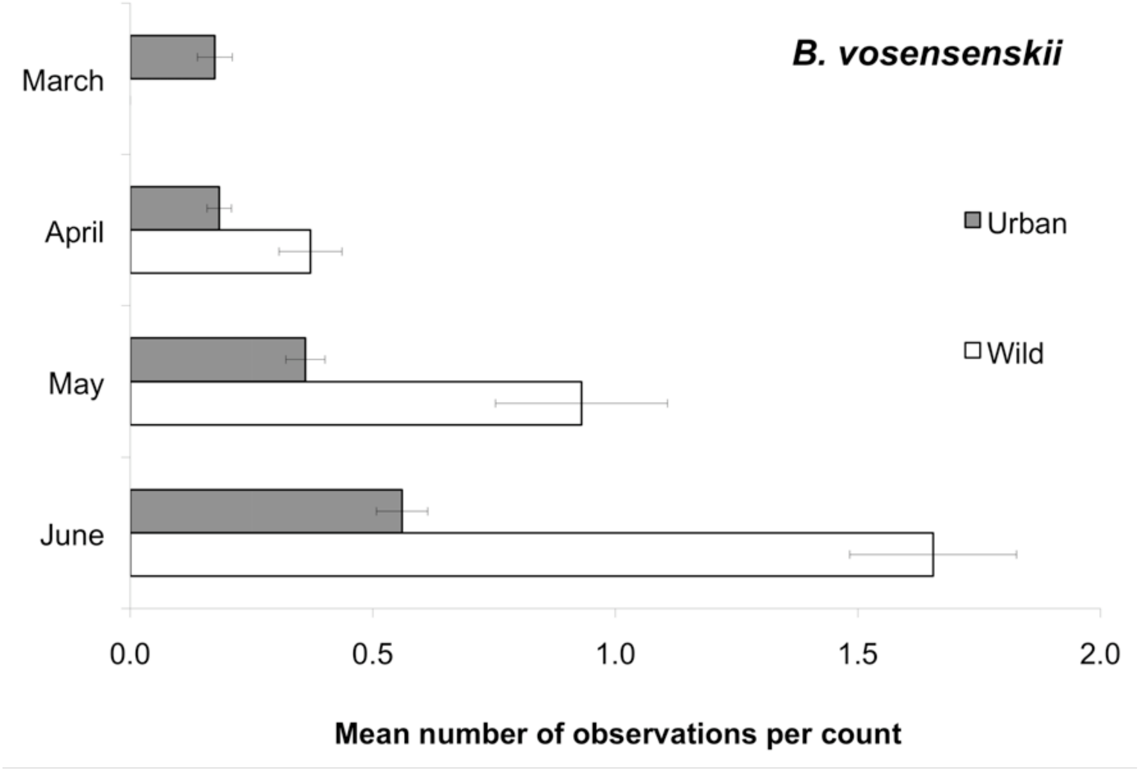

Figure 5.9: The mean number of *B. vosensenskii* recorded per observation foraging at both the wildland and urban poppy patches.

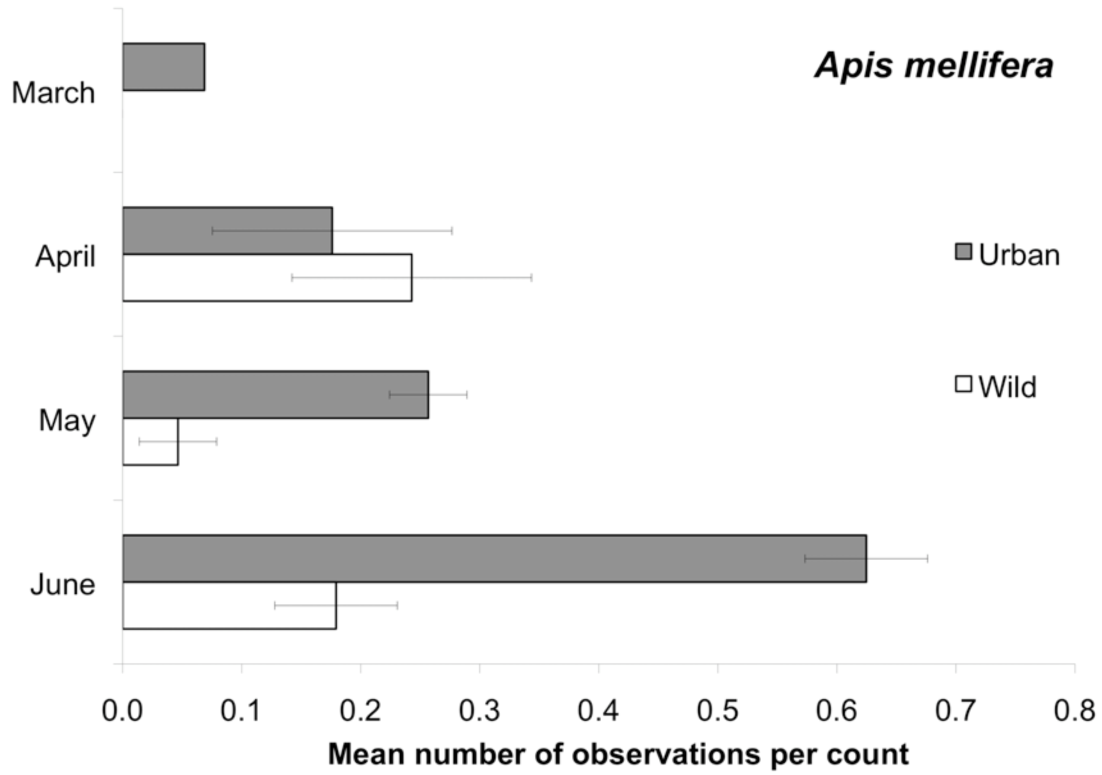

Figure 5.10: The mean number of *A. mellifera* recorded per observation foraging at both the wildland and urban poppy patches.

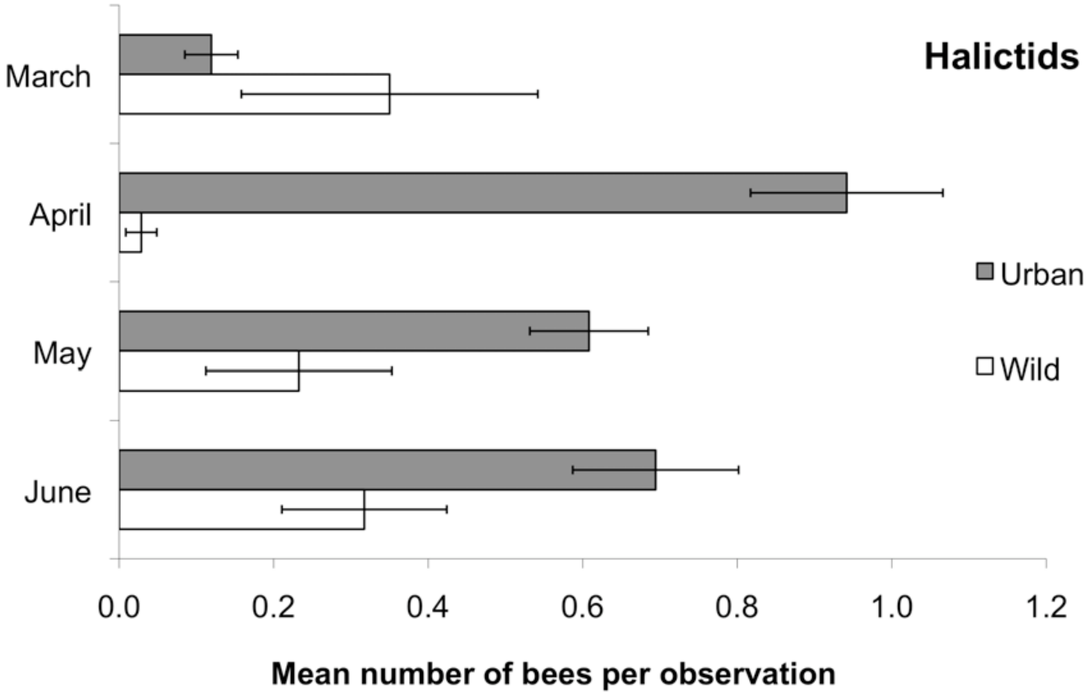

Figure 5.11: The mean number of all Halictid individuals recorded per observation foraging at both the wildland and urban poppy patches.

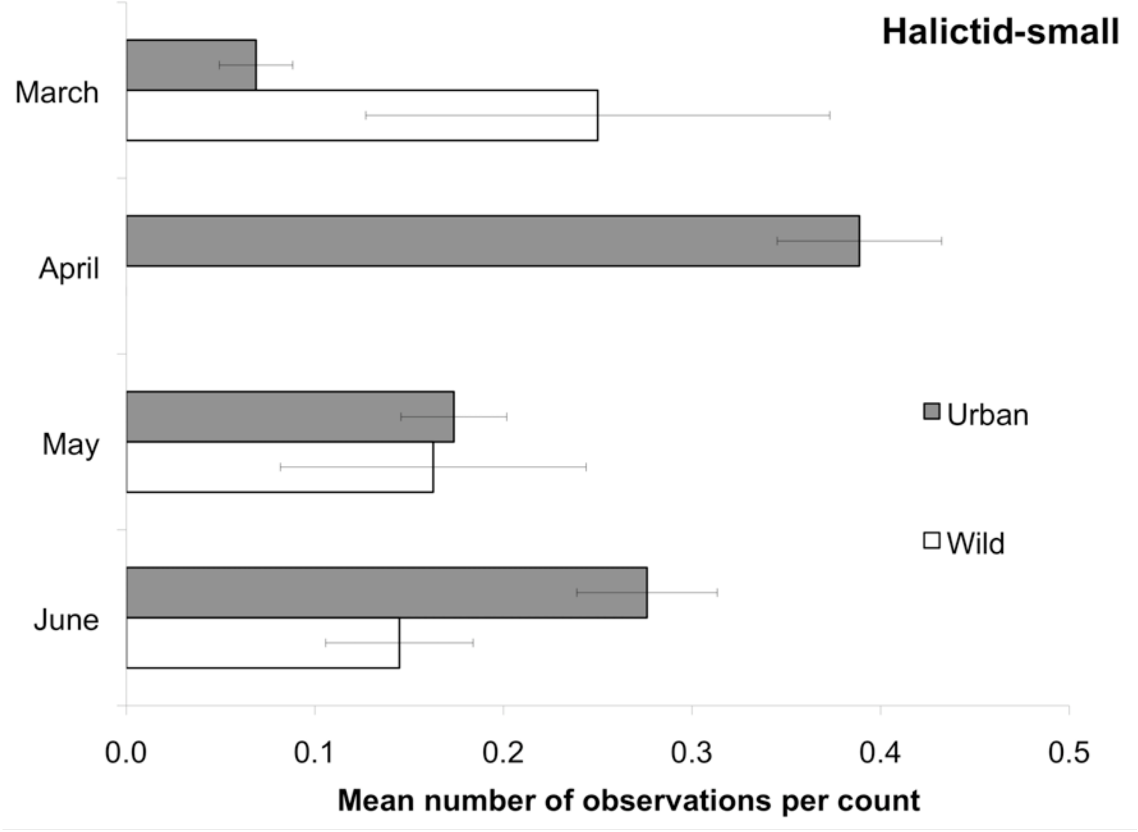

Figure 5.12: The mean number of small Halictids recorded per observation foraging at both the wildland and urban poppy patches.

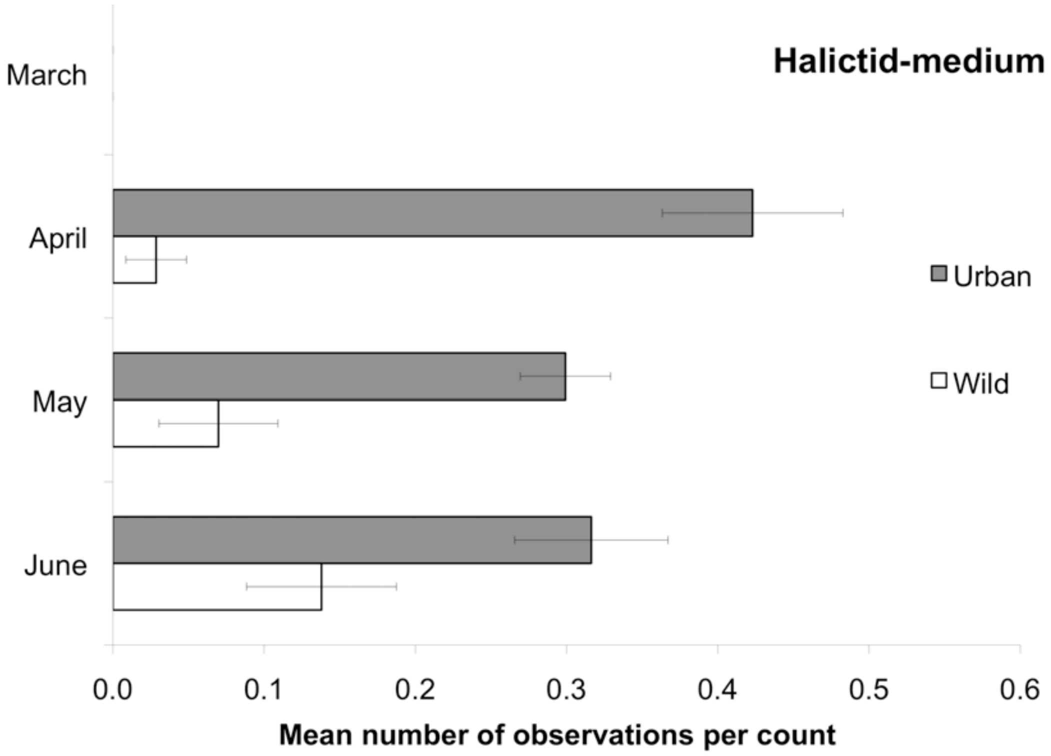

Figure 5.13: The mean number of medium Halictids recorded per observation foraging at both the wildland and urban poppy patches.

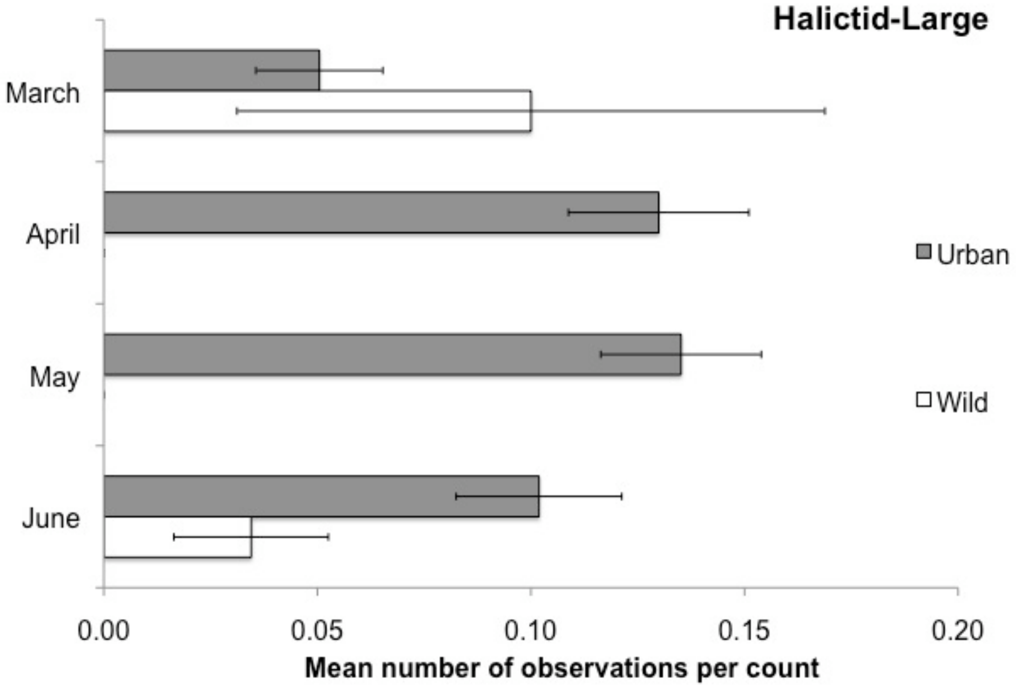

Figure 5.14: The mean number of large Halictids recorded per observation foraging at both the wildland and urban poppy patches.

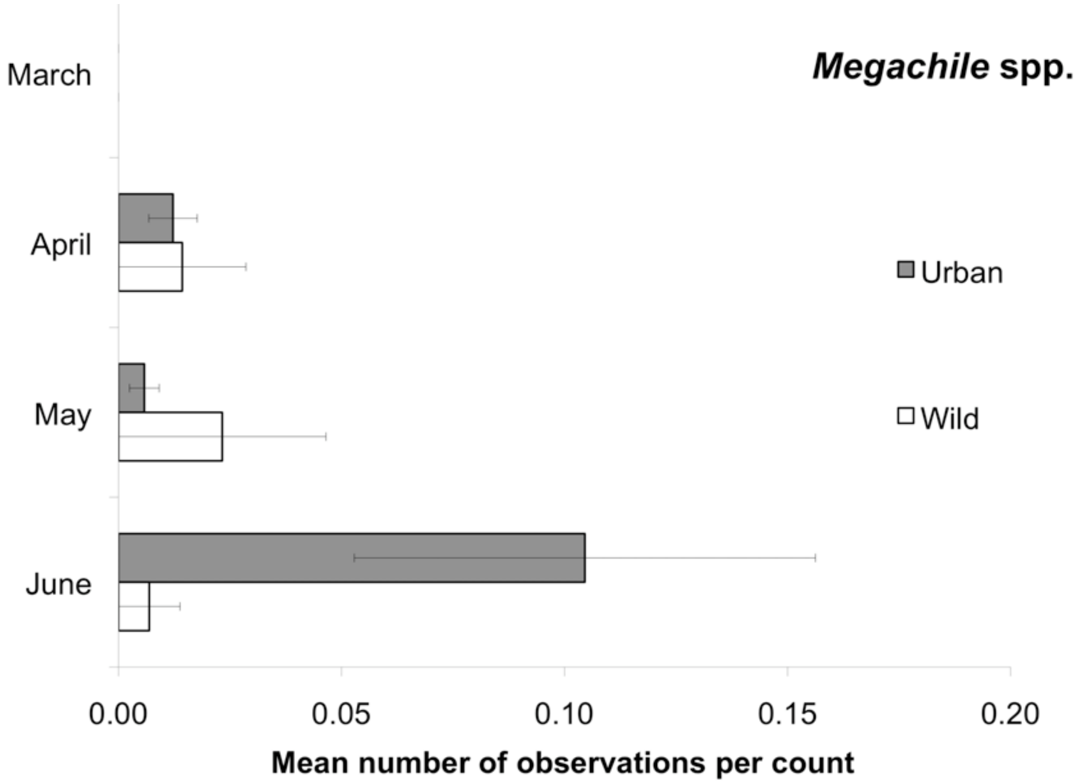

Figure 5.15: The mean number of *Megachile* spp. individuals recorded per observation foraging at both the wildland and urban poppy patches.

Table 5.1 A description of the variables used in the model building and analysis, along with the descriptive statistics for each variable (n=124 sites: urban=103, wildland =21).

Variable Name	Description	Measure	Obs	Mean	Std. Dev.	Min	Max
d wui	Distance to the urban wildland interface, increasing values mean that a site is further away from the wildland	meters	124	1858.207	1260.958	0.937441	4615.057
d rip	Distance to the to riparian areas, increasing values mean that a site is further away from the riparian area	meters	124	1046.134	727.0953	12.00017	3075.944
d green	Distance to the to green space, increasing values mean that a site is further away from the green space	meters	124	400.281	270.4944	1	1145.214
patch area	The total size (area in meters square) of the resource patch	square meters	124	15.21019	39.60339	0.09	300
% poppy	The proportion of the resource that is made up of California Poppy	percentage	124	0.6951613	0.2693276	0.05	1
poppy area	The total area (in meters square) of California Poppy	square meters	124	10.16567	27.60803	0.07432	157.3945
floral rich	The number of other bee-attractive flowers within or adjacent to the resource patch	number of flowers	124	1.443548	1.231711	0	6
flw den	The density of blooms, calculated as the number of individual poppy flowers in a 30 cm2 area.	flowers per 30 cm2	124	7.729188	3.399417	2	20
urban	regional landscape type	categorical	124	0.8306452	0.3765866	0	1
wild	regional landscape type	categorical	124	0.1693548	0.3765866	0	1
res	local land use	categorical	124	0.5080645	0.5019631	0	1
com	local land use	categorical	124	0.3225806	0.4693602	0	1
road class	traffic intensity per 15 minutes	categorical	124	2.467742	1.05488	1	5

Table 5.2: The results of the student's t-test comparison between the mean number of bees in each of the eight taxonomic category observed per three-minute count between the wildland (Tilden, n=278) and the urban (Berkeley-Emeryville-Oakland, n=1,518) California poppy patches. The mean total visitor abundance and taxon richness per count were also compared. Levene's test for equal variances was conducted as the sample sizes between the two localities differed. The degrees of freedom were adjusted accordingly and the † symbol denotes when equal variances are not assumed, Levene's test for equality of variance is significant ($p>0.05$). The * symbol indicated a significant result at $\alpha=0.05$.

Taxon	**t**	**df**	**Sig. (2-tailed)**	**Mean Dif**	**SE Dif**	**95% CI Lower**	**95% CI Upper**
A. mellifera†	-2.738	788.473	*0.006	-0.137	0.050	-0.234	-0.039
B. californicus†	0.796	315.160	0.426	0.011	0.014	-0.016	0.038
B. vosensenskii†	7.349	301.092	*0.000	0.765	0.104	0.560	0.970
Halictid Small†	-3.908	592.641	*0.000	-0.123	0.031	-0.185	-0.061
Halictid Medium†	-5.731	746.594	*0.000	-0.204	0.036	-0.274	-0.134
Halictid Large†	-6.006	859.201	*0.000	-0.088	0.015	-0.117	-0.059
Megachilea spp.	-0.668	1794.000	0.504	-0.020	0.030	-0.079	0.039
Andrena spp.	-0.907	1793.000	0.818	-0.004	-0.002	-0.008	-0.003
Abundance	1.285	1794.000	0.199	0.180	0.140	-0.095	0.456
Richness†	-0.350	421.713	0.727	-0.018	0.052	-0.120	0.084

Table 5.3: ANOVA testing for temporal variation between the hours of 900h and 1400h in bee visitation to patches of California Poppies in urban landscapes, using a Bonferroni adjusted α of 0.0083. The * symbol indicates significance at the adjusted α.

	Bee Taxa	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	And	0.01	5	0.002	0.457	0.808
	B. Cal	0.15	5	0.030	1.709	0.129
	B. Vos	12.26	5	2.451	3.053	0.010
	Hal-large	2.06	5	0.412	2.814	0.015
	Hal-medium	15.44	5	3.088	4.005	*0.001
	Hal-small	13.94	5	2.787	5.834	*0.000
	HB	81.81	5	16.362	10.348	*0.000
	Meg	2.78	5	0.555	2.286	0.044
	Abundance	241.67	5	48.334	10.651	*0.000
	Richness	45.65	5	9.130	12.033	*0.000
Intercept	And	0.01	1	0.009	1.774	0.183
	B. Cal	0.05	1	0.049	2.768	0.096
	B. Vos	44.92	1	44.918	55.938	0.000
	Hal-large	3.76	1	3.755	25.618	0.000
	Hal-medium	18.95	1	18.950	24.573	0.000
	Hal-small	13.18	1	13.178	27.580	0.000
	HB	42.47	1	42.466	26.857	0.000
	Meg	0.72	1	0.723	2.976	0.085
	Abundance	613.89	1	613.888	135.281	0.000
	Richness	187.83	1	187.831	247.560	0.000
Hour	And	0.01	5	0.002	0.457	0.808
	B. Cal	0.15	5	0.030	1.709	0.129
	B. Vos	12.26	5	2.451	3.053	0.010
	Hal-large	2.06	5	0.412	2.814	0.015
	Hal-medium	15.44	5	3.088	4.005	*0.001
	Hal-small	13.94	5	2.787	5.834	*0.000
	HB	81.81	5	16.362	10.348	*0.000
	Meg	2.78	5	0.555	2.286	0.044
	Abundance	241.67	5	48.334	10.651	*0.000
	Richness	45.65	5	9.130	12.033	*0.000
Error	And	7.97	1563	0.005		
	B. Cal	27.69	1563	0.018		
	B. Vos	1255.08	1563	0.803		
	Hal-large	229.08	1563	0.147		
	Hal-medium	1205.35	1563	0.771		
	Hal-small	746.81	1563	0.478		
	HB	2471.40	1563	1.581		
	Meg	379.75	1563	0.243		
	Abundance	7092.71	1563	4.538		
	Richness	1185.90	1563	0.759		
Total	And	8.00	1569			
	B. Cal	28.00	1569			
	B. Vos	1481.00	1569			
	Hal-large	250.00	1569			
	Hal-medium	1347.00	1569			
	Hal-small	848.00	1569			
	HB	2694.00	1569			
	Meg	384.00	1569			
	Abundance	10245.00	1569			
	Richness	2122.00	1569			

Table 5.4: The results of the ANOVA testing for daily variation in bee visitation to patches California Poppies in wildland landscapes, using a Bonferroni adjusted α of 0.0125.The * symbol indicates a significant result at the adjusted α.

	BeeTaxa	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	B. Cal	0.576	3	0.192	3.96	*0.009
	B. Vos	34.633	3	11.544	4.126	*0.007
	Hal-large	0.159	3	0.053	1.671	0.174
	Hal-medium	1.582	3	0.527	2.619	0.051
	Hal-small	0.242	3	0.081	0.434	0.729
	HB	4.574	3	1.525	4.05	*0.008
	Meg	0.039	3	0.013	1.21	0.306
	Abundance	62.4	3	20.8	5.004	*0.002
	Richness	6.371	3	2.124	3.604	0.014
Intercept	B. Cal	0.229	1	0.229	4.719	0.031
	B. Vos	321.192	1	321.192	114.809	0.000
	Hal-large	0.233	1	0.233	7.377	0.007
	Hal-medium	2.996	1	2.996	14.878	0.000
	Hal-small	4.051	1	4.051	21.835	0.000
	HB	6.05	1	6.05	16.071	0.000
	Meg	0.032	1	0.032	2.968	0.086
	Abundance	638.302	1	638.302	153.569	0.000
	Richness	150.401	1	150.401	255.233	0.000
Hour	B. Cal	0.576	3	0.192	3.96	*0.009
	B. Vos	34.633	3	11.544	4.126	*0.007
	Hal-large	0.159	3	0.053	1.671	0.174
	Hal-medium	1.582	3	0.527	2.619	0.051
	Hal-small	0.242	3	0.081	0.434	0.729
	HB	4.574	3	1.525	4.05	*0.008
	Meg	0.039	3	0.013	1.21	0.306
	Abundance	62.4	3	20.8	5.004	*0.002
	Richness	6.371	3	2.124	3.604	0.014
Error	B. Cal	13.294	274	0.049		
	B. Vos	766.547	274	2.798		
	Hal-large	8.665	274	0.032		
	Hal-medium	55.17	274	0.201		
	Hal-small	50.841	274	0.186		
	HB	103.142	274	0.376		
	Meg	2.929	274	0.011		
	Abundance	1138.87	274	4.156		
	Richness	161.46	274	0.589		
Total	B. Cal	14	278			
	B. Vos	1138	278			
	Hal-large	9	278			
	Hal-medium	59	278			
	Hal-small	55	278			
	HB	115	278			
	Meg	3	278			
	Abundance	1851	278			
	Richness	319	278			

Table 5.5: Summary of the regression models developed for the community of bees visiting California poppies in both urban and wildland landscapes. Models were developed using a stepwise backwards regression with a probability of removal set at $\alpha=0.05$. A significant model could not be generated for *Andrena* spp. and *Megachile* spp. in the wildland landscape due to low records for these groups in that landscape. Significant models could not be generated for *B. californicus* and for larger-bodied Halictids in either landscape. The abbreviations for the variables presented can be found in Table 5.1. The + and – symbols next to the variable indicate the direction of the correlation.

	Urban	**Wildland**
Community		
Abundance	poppy area (+) flw density (+)	flw density (+) floral richness (+)
Richness	poppy area (+) flw density (+) dist wui (-) dist rip (+)	flw density (+)
Taxon Groups		
Andrena spp.	dist rip (+)	ns model
Apis mellifera	flw density (+) floral richness (+)	patch area (-) poppy area (+)
B. califronicus	ns model	ns model
B. vosensenskii	poppy area (+) flw density (+) dist rip (+)	flw density (+) floral richness (+)
Halictids-small	dist rip (+) dist wui (-)	flw density (+)
Halictids-medium	dist wui (-)	poppy area (+) patch area (-) road class (-)
Halictids-large	ns model	ns model
Megachile spp.	flw density (+)	ns model

Table 5.6: The comparative models for bee visitation across both landscapes that indicated the importance of landscape context to forager activity. Only *B. vosensenskii* and medium sized Halictids were impacted by the greater land use context.

					[95% Conf.	**Interval]**
B. vosensenskii	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
d rip	0.0001338	0.0000610	2.190	0.030	0.000013	0.0002547
flw density	0.0402925	0.0136146	2.960	0.004	0.0133343	0.0672508
urban	-0.6177136	0.1231066	-5.020	0.000	-0.861477	-0.3739502
patch area	0.0041965	0.0011289	3.720	0.000	0.0019612	0.0064318
constant	0.3597906	0.1465154	2.460	0.016	0.0696756	0.6499056

F(4,119)=13.000 p=0.000
R-squared=0.3041 Adj R-squared=0.2807

					[95% Conf.	**Interval]**
Halictid-medium	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
urban	0.3010861	0.0943976	3.190	0.002	0.114201	0.4879711
d wui	-0.0000903	0.0000282	-3.200	0.002	-0.0001461	-0.0000345
constant	0.1466866	0.0738454	1.990	0.049	0.0004902	0.2928829

F(2,121)=6.69 P=0.0018
R-squared=0.0995 Adj R-squared=0.0846

Appendix 5.i: The visitation models for visitor abundance in both urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05.

					[95%ConfInterval]	
urban-abundance	**β**	**Std. Err.**	**t**	**p>|t|**	**lower**	**upper**
poppy area	0.008868	0.004008	2.210	0.029	0.000916	0.016820
flw density	0.108889	0.030779	3.540	0.001	0.047824	0.169954
constant	0.079757	0.271472	0.290	0.770	-0.458835	0.618350

F(2,100)=9.46 p=0.0002
R-squared=0.1591 Adj R-squared=0.1423

					[95%Conf.Interval]	
wild-abundance	**β**	**Std. Err.**	**t**	**p>|t|**	**lower**	**upper**
floral rich	0.498863	0.156127	3.200	0.005	0.170853	0.826873
flw density	0.206341	0.079042	2.610	0.018	0.040280	0.372402
constant	-0.686639	0.430207	-1.600	0.128	-1.590471	0.217192

F(2,18)=15.81 p=0.0001
R-squared=0.6373 Adj R-squared=0.5970

Appendix 5.ii: The visitation models for taxon richness in both urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05.

					[95%Conf.Interval]	
urban-richness	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
dist wui	-0.000112	0.000052	-2.140	0.035	-0.000216	-0.000008
dist rip	0.274700	0.000082	3.360	0.001	0.000112	0.000437
flw density	0.041793	0.014318	2.920	0.004	0.013380	0.070206
poppy area	0.004665	0.001895	2.460	0.016	0.000905	0.008425
constant	0.198034	0.161251	1.230	0.222	-0.121962	0.518031

F(4,98)=7.57 P=0.0000
R-squared=0.2361 Adj R-squared=0.2049

					[95%Conf.Interval]	
wildland-richness	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
flw density	0.156092	0.037274	4.190	0.000	0.078077	0.234106
constant	-0.187182	0.228331	-0.820	0.423	-0.665084	0.290721

F(1,19)=17.54 p=0.0005
R-squared=0.4800 Adj R-squared=0.4526

Appendix 5.iii: The visitation models for *B. vosensenskii* in both urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05.

					[95%Conf. Interval]	
urban-*B. vosensenskii*	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
flw density	0.024767	0.011878	2.090	0.040	0.001199	0.048335
dist rip	0.000119	0.000055	2.170	0.033	0.000010	0.000228
poppy area	0.004089	0.001575	2.600	0.011	0.000964	0.007213
constant	-0.098466	0.121085	-0.810	0.418	-0.338724	0.141792

F(3,99)=6.40 p=0.0005

R-squared=0.1624 Adj R-squared=0.1371

					[95%Conf.Interval]	
wildland-*B. vosensenskii*	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
floral rich	0.329770	0.134632	2.450	0.025	0.046918	0.612622
flw density	0.157063	0.068160	2.300	0.033	0.013864	0.300261
constant	-0.5927399	0.3709793	-1.6	0.127	-1.372139	0.1866587

F(2,18)=10.57 p=0.0009

R-squared=0.5400 Adj R-squared=0.4889

Appendix 5.iv: The visitation models for *A. mellifera* in both urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05.

					[95%Conf.Interval]	
urban-honeybee	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
floral rich	0.092212	0.038704	2.380	0.019	0.015424	0.169000
flw density	0.044657	0.014001	3.190	0.002	0.016880	0.072435
constant	-0.300156	0.137730	-2.180	0.032	-0.573409	-0.026903

F(2,100)=7.54 p=0.0009

R-squared=0.1311 Adj R-squared=0.1137

					[95%Conf.Interval]	
wildland-honeybee	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
patch area	-0.020068	0.006682	-3.000	0.008	-0.034107	0.006029
poppy area	0.039844	0.013026	3.060	0.007	0.012477	0.067211
constant	0.080729	0.047483	1.700	0.106	-0.019030	0.180488

F(2,18)=4.75 p=0.0220

R-squared=0.3455 Adj R-squared=0.2728

Appendix 5.v: The visitation models for *Megachile* spp. in urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05. A significant model could not be made for wildland landscapes.

					[95%Conf.Interval]	
urban-*Megachile* spp.	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
flw density	0.0100394	0.004946	2.03	0.045	0.0002278	0.0198511
constant	-0.0608855	0.0437018	-1.39	0.167	-0.1475781	0.0258071

F(1,101)=4.12 p=0.0450

R-squared=0.0392 Adj R-squared=0.0297

Appendix 5.vi: The visitation model for *Andrena* spp. in urban landscapes. Models were constructed using backward stepwise regression with a probability of removal of α=0.05.

					[95%Conf.Interval]	
urban-*Andrena* spp.	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
dist rip	3.92E-06	1.50E-06	2.61	0.01	9.41E-76	9.00E-07
constant	-0.0022158	0.0019479	-1.14	0.258	-0.00608	0.0016484

F(1,101)=6.81 p=0.0104

R-squared=0.0632 Adj R-squared=0.0539

Appendix 5.vii: The visitation models for small and large halictids in both urban and wildland landscapes. Models were constructed using backward stepwise regression with a probability of removal of $\alpha=0.05$.

					[95%Conf.Interval]	
urban-hal small	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
dist wui	-6.4400E-05	2.7700E-05	-2.32	0.022	-0.00012	-0.00001
dist rip	1.8160E-04	4.3100E-05	4.21	0.000	0.00010	0.00027
constant	1.2468E-01	5.5213E-02	2.26	0.026	0.01514	0.23422

F(2,100)=8.92 p=0.0003

R-squared=0.1513 Adj R-squared=0.1344

					[95%Conf.Interval]	
wildland-hal small	**β**	**Std.,Err.**	**t**	**P>|t|**	**lower**	**upper**
flw density	0.0361288	0.0129522	2.790	0.012	0.0090195	0.0632382
constant	-0.0472313	0.0793428	-0.600	0.559	-0.21330	0.118835

F(1,19)=7.78 p=0.0117

R-squared=0.2905 Adj R-squared=0.2532

					[95%Conf.Interval]	
urban-hal medium	**β**	**Std.Err.**	**t**	**P>|t|**	**lower**	**upper**
dist wui	-0.000088	0.0000298	-2.950	0.004	-0.000147	-0.0000289
constant	0.4427187	0.0729882	6.070	0.000	0.2979298	0.5875076

F(1,101)=8.73 p=0.0039

R-squared=0.0796 Adj R-squared=0.0704

					[95%Conf.Interval]	
wildland-hal medium	**β**	**Std.Err**	**t**	**P>|t|**	**lower**	**upper**
poppy area	0.0322526	0.0140269	2.300	0.034	0.0026585	0.0618468
road class	-0.1727362	0.0717777	-2.410	0.028	-0.324174	-0.021298
patch area	-0.0168522	0.0072821	-2.310	0.033	-0.032216	-0.001488
constant	0.5154060	0.1828677	2.820	0.012	0.1295889	0.9012231

F(3,17)=3.00 p=0.0594

R-squared=0.3464 Adj R-squared=0.2310

CHAPTER 6 – DEFINING BIODIVERSITY WITHIN THE BUILT ENVIRONMENT

Introduction

Biodiversity, the term representing the concept of biological diversity, is both a measure and an important concept in modern ecological landscape management. At a basic level, the more different types of living things there are at a site, the greater the biodiversity. The definition of biodiversity is structured on the presence and variability of form, function, type, and heredity. This umbrella definition is commonly subdivided into the diversity held at three levels: genetic diversity, species diversity, and ecosystem diversity.

For each species living on the earth, three essential elements are necessary for survival: food, water, and cover. This is as true for human beings as it is for any other living being. The diversity of forms and functions seen within ecosystems provides and maintains the essential elements of life in the form of ecosystem services. Ecosystem services are defined as the set of direct and indirect benefits that are derived from healthy, sustainable, and functioning ecosystems (modified from Daily 1997 and Constanza et al. 1997). Correspondingly, the value of biodiversity can be seen in the value of ecosystem services. Efforts to create a tangible, manageable system for classification have sorted ecosystem services into 17 unique functions that interact with all aspect of life; supporting the underlying ecosystem functions, providing food and other products, regulating and buffering the environmental, and creating cultural and aesthetic landscapes (modified from Costanza et al. 1997). These services can be further sub-divided into their spatial scale of interaction with humans and other species (Costanza 2008), an approach that is particularly relevant when considering ecosystem and biodiversity management. Table 6.1 presents these ecosystem services with an interpretation of their function within urban systems. Global, non-proximal services include the regulation of climate and the atmosphere, as well as the general aesthetic value of diversity to human culture. Local proximal services provide environmental regulation at the local scale, mediating disturbance and local climate, treating water, buffering pollination, regulating pests and disease, and providing habitat. Directional services connect ecosystems and facilitate the movement of energy and matter. In situ services are responsible for the bounty of food and resources provided to humans and animals. Finally, user-related services provided genetic, cultural, recreational, and aesthetic resources.

When productivity and service provision is concerned, increased biodiversity corresponds to increased stability, resistance, longevity, and product derivation (Ehrlich et al. 1977; Aylward and Barbier 1992; Costanza and Daly 1992; Daily 1997). Biodiversity describes an ecological community and in many cases determines the fate of that community. Many authors and researchers have underscored the importance of maintaining and sustaining biodiversity in productive ecosystems, especially those that are directly related to human livelihoods such as temperate and tropical forests, wetlands, and agricultural systems. An increased measure of biological diversity within these ecological communities can increase the chances of success and long-term survival. Diverse systems are more stable and resistant to disturbance from both biotic (pest, weed, exotic species) and abiotic (fire, flood, wind) factors (Daily 1997). Ecosystems with compromised or reduced diversity are susceptible to regime shifts that can change their composition and evolutionary trajectory (Folke et al. 2004). For example, disturbances of ecosystems by anthropogenic factors (pollution, climate change, etc.) that consequently remove large numbers of species can eliminated functional groups, even entire trophic levels, and this reduction in biodiversity significantly changes the ecosystem. A loss of biodiversity and the resultant loss in ecosystem function can have substantial effects on the output of ecosystem services (Perring and Walker 1997). Clear examples are seen in economic agricultural systems where a loss of function translates into a loss of productivity and a further loss of livelihood.

The Value of Biodiversity

For all of its direct ecological value, biodiversity also serves cultural, recreational and spiritual roles. Scientist and philosopher E.O. Wilson has written extensively on the topic of biophila: the love of the living world (Wilson 1986). Humans are simply happier and more content when we are surrounded by an abundance of living things. We gravitate towards them, choosing to live within or near areas that are more complex in landscape and richer in species. The positive effect of the diverse and the biological in urban systems has been touted by urban theorist Jane Jacobs, who notes in her classic book, The Life and Death of Great American Cities (1961), that thriving neighborhoods are built on richness in culture and landscape. Increasing biodiversity within cities will not only improve ecological function (or the provision of ecosystem services) but also the residents' quality of life.

Quantifying Biodiversity

The concept of biodiversity implies an account of species numbers. Calculating the variability of species patterns involves a combination of the measurement of the richness (raw species or taxon numbers) and the distribution or variability of richness between multiple sites. Measures of diversity are more meaningful in the context of comparative assessments. This essential concept of spatial variability is apparent in urban landscapes, and will be discussed in more detail shortly.

Multiple methods have been developed to more accurately account for the diversity at a location. To help quantify this abstract term indices such as Simpson's D and E, Shannon's H, and Jaccard's Distance are often used to transform species lists into comparative metrics. At a more functional level, the proportions of species in important groups can be compared. Niche or guild structured concepts of diversity examine the functional roles that individual species fill within an ecosystem. These assessments, however, require a deeper understanding of the individual biology of species.

Dispersion and distribution can also be modeled across landscapes. Indexes of dispersion (and inversely aggregation) measure where species are located and how their associations with each other vary over the landscape. The variety of organisms at a locality, referred to as α-diversity, and the variation between localities, called β-diversity, describe the landscape level patterns of diversity. When both values are high they describe a region in which there are many unique local sites. This sum of the total diversity located with a landscape is the γ-diversity. Connectivity and isolation are the two primary characteristics of a landscape that further structure the patterns of plant and animal diversity by either facilitating or inhibiting movement, dispersal, and colonization.

Understanding the Diversity of Urban Landscapes

The interplay of biotic and abiotic features with the constructed, modified, and natural elements within the urban landscape creates a unique set of habitats within the urban system. The biotic elements of urban landscapes include the natural remnants of the landscape that existed before the city (fields, grasslands, forests, creeks, shorelines, etc.) and landscape features implemented by humans (street trees, parks, gardens, green spaces, etc.). A specific set of ecosystem characteristics are unique to the urban landscape, including: clearly defined borders and boundaries between land use types and ecological regions (Bolund and Hunhammar 1999); a dominance of structures related to human dwelling and daily life such as houses, buildings, roads, commercial areas (Rebele 1994); the existence of technological and industrial infrastructure (Meuser 1993), such as electrical power lines, telecommunications services, treatment facilities, etc.; and a generally higher proportion of non-native and exotic species. The urban ecosystem is the total assortment of these elements and their interactions with one another. The sharp distinction between land uses combined with the multitude of constructed and natural features creates a patchwork of different habitats abutting each other; resulting in a diverse mosaic of habitat that can be colonized and used by species.

Biodiversity in the floral community tends to be higher at urban sites than in the adjacent landscape (Thompson et al. 2003) due to the multitude of commercially available ornamental plant species and local land management practices, in particular gardens (Loram et al 2007; Loram et al 2008). Individual private landowners with an interest in gardening have produced the majority of highly biodiverse sites in urban areas. A resultant diverse fauna is associated with urban vegetation, including small mammals, birds, moths, butterflies, bees, and other insects. English author and scientist Jennifer Owen studied the diversity of species that visited her tiny Leicester garden over the course of 15 years (Owen 1991). To her surprise, and to that of many of her colleagues, she has accounted for more than 25 percent of the known national diversity in butterflies, moths, and beetles with her garden's quarter acre footprint. She also noted 55 species of birds and seven species of mammals. Similarly studies of urban garden ecosystems in North America (Matteson et al. 2008; Wojcik et al. 2008; Frankie et al. 2005; Tommasi et al. 2004), Europe (Young 2008; Smith et al. 2006; Gaston et al. 2005; Owen 1991), Asia (Jim and Liu 2001) and South and Central America (Nates-Parra et al. 2006; Taura and Laroca 2001) have documented abundant insects, birds, and even small mammal species associated with diverse urban gardens.

The construction of an urban landscape either removes or compromises the existing wildland. Indeed, the greatest global losses in biodiversity are attributed to land use change, and in particular activities associated with urban growth. The development of these new communities, however, often preserves remnant habitat and adds additional diverse plantings that attract a broader range of species. Although pre- verses post-development assessments are not available for all species groups, there does appear to be a trend towards increased diversity. The colonization of a site occurs when there is a new or unused habitat. Within the city, new and unused habitats are common and present an opportunity for inhabitation (Rebele 1994).

The common set of species that colonize the new habitats that are available in urban landscapes have been citied as generalists without significant ecological value to the local ecosystems (Murphy 1988). The most aggressive and robust local species are usually those that make it into urban landscapes. Less aggressive specialized species that rely on endemic microhabitats have been suggested to be far less common. Successful urban species often include insects that are generalists and pest (e.g., Argentine ants, mosquitoes, cockroaches, bed bugs) that have developed life histories associating them with humans. Many of these species are also public health concerns. The birds and small mammals within urban landscape that are generalists include commonly recognized species such as squirrels, raccoons, crows, pigeons, and rats. Exotic species are also consistently present in urban landscapes. These species are either broadly general in their habitat, accounting for their global distribution in wildland landscapes, or they have been able to colonize as they disperse with human population movement. The reality of the urban fauna, however, is that it includes a mix of species, many of which are locally native and specialized, and many of these species provide important ecological services within the city.

The urban environment is more functional and biodiverse than was originally thought. The next step is the conscious integration of this knowledge into green construction and green design – using appropriate species and techniques to promote functional biodiversity. Just as green design considers the needs of humans in the built environment, design for biodiversity should consider the needs of the organisms that will make up the ecological community at a site. At present, many projects set aside space for habitat, but few have the explicit goal of designing for biodiversity. This is not surprising. Much of the information about urban biodiversity still resides within academic journals and there is little in the current commercial literature that outlines procedures for enhancing biodiversity. Principles from urban ecology can be applied to green design to conserve and promote biodiversity in the urban built environment, especially with a focus on small-bodied arthropod species that are essential ecosystem service providers.

Planning and Building for Biodiversity

How a site is planned and landscaped can have a significant impact on the local ecosystem. Soil, slope, topography, and hydrology all affect the plant community at a site. The plant community, in turn, affects the animal community. Together, these elements make up the biological community of a site – they are the local ecosystem.

Constructing with nature in mind is nothing new. In 1969, Ian McHarg presented Design with Nature, a review of what has been done and what should be done to actively consider functional landscape construction. McHarg presented the classification and categorization of landscapes in terms of appropriate and inappropriate uses. Looking at the functional layers present across landscapes, McHarg approached the idea of sustainable development from the perspective of having the least impact on the function of the landscape. Approaches from the discipline of landscape ecology later considered the connection and flow of energy and products though the ecosystem, highlighting the function of features such as patches, corridors and edges in the structuring of diversity patterns (Forman and Godron 1986; Forman 1996; Dramstad et al. 1996; Turner et al. 2003).

A significant realization has been the degree to which species diversity patterns are increased at edges – the points at which one landscape type meets another. Edges, or ecotones, are areas where multiple ecosystems intersect and interact. At these sites there is a tendency for increased structure and habitat variability, and a resulting increase in overall biodiversity. Edges are a dominant feature in the urban mosaic, as one city block abuts another with a different land use.

Scale is also recognized as a factor that structures, defines, and explains patterns of species occurrence and diversity at the landscape level. Individual species assemblages respond to local and regional level factors at micro, meso, and macro scales. The focus of landscape-level investigations within cities, however, has traditionally been large – entire ecoregions, biomes, watersheds, and the total municipal boundary of the city. For the practitioner working on a city block, the theory, literature, and current guidelines often do not have the correct resolution to serve as guides to promoting biodiversity in small applications.

Site Planning Suggestions

Sites need not be vast and expansive to have a major impact on the local ecology. What landscape designers need to focus on is the microhabitats that exist, or can be created, on the site. The design should allow for efficient and comfortable movement through the landscape. Connectivity and heterogeneity have been shown to improve species movement through all landscapes (Fahrig 2003; McIntyre and Wiens 1999) including urban landscapes (Cartar and Real 1997; Dramstand et al. 1996). Heterogeneity in the biotic and abiotic habitat characteristics also plays a big role in increasing landscape use. Areas of light and shade are needed, as well as variation in the structure and topography of the landscape. Successful promotion of biodiversity is seen in design schemes that pay attention to the nonliving elements, such as rocks, slopes, and water features.

The best way to increase local biodiversity is to focus on α-diversity. This includes augmenting the number of plant species at a site. Diversity loves company. Rich, complex wildland landscapes house more species. Urban landscapes are no different in this respect. Mixed, diverse urban plantings correlate with increased urban fauna (Loram et al. 2007; Arngold et al 2006; Smith et al. 2006). Using locally native plant species, and focusing on plants that are important resources for local wildlife create a base upon which a more complex trophic structure will be built. Taking this a step further and targeting beneficial species that provide essential services, such as pollination and pest control, follows.

The work outlined in the previous chapters also indicates that the urban matrix, or the non-habitat elements present in the urban landscape, do not appear to have a significant affect on the occurrence of species at sites. Land use, various degrees of urbanization, and human disturbance do not preclude all species from visiting appropriate habitat. Species that have the ability to disperse or colonize through flight or that are small and have the ability to move within the landscape are accessing available habitat. To this end, many areas within the city that have not traditionally been considered part of the classically defined green space have the potential to become valuable and divers habitat.

The colonization of novel habitats is characteristic of range expansion and population evolution. A unique characteristic of urban landscapes is that they contain areas of new, vacant habitat that some species may be able to exploit (Rebele 1994). This new habitat within the urban landscape can take the form of classical green space that has been newly created. Urban habitat can also be more novel, representing elements of substrate, structure, and space that are unique and new. The rooftops of buildings are one of these unique habitat options.

Green Roofs and Urban Habitat

Green roof construction originated to interact with and mediate the various abiotic elements of urban systems (Marinelli 2006): precipitation, temperature, and noise. The biotic elements installed with the construction of green roofs create a new habitat that becomes available for colonization by species. The serendipitous functional ecosystems created through aesthetic and mechanical goals exemplify how the built environment can function as an ecosystem. Although definable in many ways, an ecosystem is the total sum of the interactions that occur between the living and non-living aspect of a landscape, and the interactions with the various living beings with each other.

Responding to the school of thought that green roofs are generally considered to be species poor, and particularly devoid of rare, endemic, and ground dwelling species, Brenneisen (2006) undertook a study of specially designed green roofs. Pooling information form successful projects in England, Germany, and from Switzerland, it is clear that species with mobility, even those that are generally ground dwelling, have the ability to colonize green roofs. A more detailed assessment of invertebrate diversity using green roof habitats compared to existing ground level green space in London found that the species occurrences were higher on rooftops, and that nearly 10% of these species were considered to be rare and/or listed as threatened (Kadas 2006).

There have already been projects with explicitly stated goals that target reviving the ecosystems within cities using rooftop green space. To counteract the trend in native species losses in Germany, as series of green roofs were installed in the mid 1980's that were planted with native grass species. The development of the ecological community that inhabited a series of extensive green roofs that have been installed for the past 20 years was recently catalogued (Kohler 2006). The set of roofs that was originally built for the purpose of re-introducing native plant species into urban landscapes provided sites of colonization for local flora. A floral survey concluded that 7% of the local wildland species that were common to the region had eventually colonized and been recorded on the rooftops.

Specific conservation goals have also been met with the habitat created on green roofs. In London, a series of grassy green roofs was constructed in the hopes of providing habitat for the rare black redstart (*Phoenicurus ochruros*), a bird species that has suffered declines due to land use change (Grant 2006). The project was successful in attracting the black redstart and there is growing interest in determining the set of other species, primarily invertebrates, that might also benefit from directed habitat development in the form of green roofs.

The green roof at the new California Academy of Science building in San Francisco's Golden Gate Park is an example of active habitat development, biodiversity promotion, and native species preservation together with aesthetic development. Quite contrary to the traditional turf-grass water retention systems that readily available as prefabricated roofing, the flora of the California Academy green roof is a representative mix of native species including: Strawberry (*Fragaria chiloensis*), Self Heal (*Prunella vulgaris*), Sea Pink (*Armeria maritima* ssp.), Californica Stonecrop (*Sedum spathulifolium*), Tidy Tips (*Layia platyglossa*), Goldfield (*Lasthenia californica*), Miniature Lupine (*Lupinus nanus*), California Poppy (*Eschscholzia californica*), and California Plantain (*Plantago erecta*) (California Academy of Sciences 2009). This variety of native plants is known to attract bees, flies, moths, and butterflies, including the Bay Checkerspot butterfly a listed State of

California endangered species. Early observations already indicated that faunal species are making use of the habitat and habitat resources provided three stories about the round.

The potential for sky habitats and aerial conservation corridors has been suggested for the Bay Checkerspot butterfly within the greater San Francisco Bay area. Much of the original migratory habitat for this species is currently urbanized. Ground-level habitat development competes with other social and economic uses within the city, the roof tops are free of such constraints. Rooftop habitat development, especially for winged species, presents a viable solution to habitat restoration without urban landscape removal. The vertical habitat potential present in within urban landscapes required a further examination.

The collective area of potential re-greening projects within urban landscapes must also be considered, as they can represent a significant increase in green space. For example, the development of many large commercial and industrial rooftop areas adds green space without removing any urban space. A calculation presented by Grant et al. (2003) suggests that if the available and green roof appropriate rooftop area in London were to be transformed, this would account for 26,000 hectares of new habitat, a figure that represents 28 times the area covered by Great Richmond Park in London. A similar calculation of the undocumented garden habitat that exist within the urban landscapes of Berkeley, California estimates 0.25 square kilometers unaccounted green space. This green space amounts to 1% of the total urban area covered by the city (City of Berkeley 2009). Although 1% seems minute, the total municipal green space in Berkeley accounts for only 7% of the landscape. Factoring in the additional garden green space increases the total green area in Berkeley by nearly 15%.

Active and conscience development of the urban biota supports the creation and preservation of ecosystems and the services that they provide. Urban landscapes in their very nature are systems that are built and managed. The management goals of the urban landscape should therefore extend beyond zoning, housing, transportation, commercial development, and recreation to include ecosystem service and biodiversity augmentation.

Getting Credit for Biodiversity?

Architects, planners, builders, and designers might be more likely to incorporate biodiversity into their plans if their work in this area can receive professional acknowledgement and recognition. Yet, when it comes to the green certification of construction projects, biodiversity is not rewarded as heavily as using sustainable harvested material and energy-efficiency measures. Choosing to increase the biodiversity of a site could raise a project from one certification level to another, simply through the interconnection of the concepts linked to biodiversity augmentation and established green building policies and practices. This interconnection is not obvious to practitioners and planners that are educated and trained outside of the ecological sciences, and is not clearly stated in the technical green building codes and literature. The incentives are less obvious, or sometimes not obvious at all, and the small efforts needed to achieve a biodiverse building site are not considered. The following narrative examines how reference to augmenting biodiversity is made, both directly and indirectly, in the current green building literature. Important concepts are extracted and presented for practitioners as a short list to consider in their project design.

Green Building Systems and Greening

The United States Green Building Council (USGBC) Leadership in Energy and Environmental Design (LEED) certification system is the most widely practiced and well-understood green building certification system utilized by practitioners in North America. The LEED certification system is a tiered approval and verification system that assesses the environmental impacts of construction and development projects. The goal of LEED is to develop and promote green design through conscious development projects that use strategies to minimize the impact on energy and water consumption, emissions, waste generation, and both on- and off-site disturbance. The guidelines within the various LEED certification systems outline practices and procedures for Sustainable Sites, Water Efficiency, Energy and Atmosphere, Materials and Resources, Indoor Environmental Quality, Locations and Linkages, Awareness and Education, Innovation in Design, and Regional Priorities (USGBC 2009). The certification system allows practitioner to accumulate points towards four levels of certification: Certified, Silver, Gold, and Platinum.

The LEED rating system began as a scheme for evaluating and certifying the impact of new commercial construction projects (i.e., LEED New Construction), but has expanded to include homes (LEED Homes), existing building renovation and retrofits (LEED Existing Buildings: Operations and Maintenance and LEED Core and Shell), interior modifications for both retail and commercial applications (LEED Commercial Interiors and LEED Retail), institutions (LEED Healthcare and LEED Schools), and entire communities (LEED Neighborhood). LEED has been successful because it is a dynamic system that works with developers, consumers, researchers, and regulators.

The bulk of the negative environmental impact that results from human populations is attributed to the land lost in habitat conversion and the off-site impacts of developing: resource extraction and the subsequent habitat degradation at far-off localities, fuel consumption, and waste generation. Correspondingly, the bulk of the credits (points) given in the LEED ecological building system focus directly on the consumption of energy and resources and on the minimization of harmful chemicals that are all too common in products. The mediation of negatives is easily accounted for, but the development of positive landscapes is less clearly defined. A developer with a focus on air quality or a reduction in energy costs is presented with a guidebook that leads them to a path of health and efficiency. A desire to construct a site with a focus on biodiversity is less outlined, and the rewards are not as great within the current certification systems.

Of the 69 points available under the current LEED 2.2 certification for new construction (USGBC 2006), only two – within the Sustainable Site Credit category – are gained through directly providing landscape elements that can increase biodiversity. Sustainable Site Credit 5.1 deals with the creation of habitat or the mitigation of a removed habitat. It provides adequate guidelines and resources to a developer that wants to focus on this goal. The mitigation of habitat also is clearly outlined with a set of guidelines that dictate what kind and how much is needed. The promotion of general biodiversity is not directly stated. In fact, diversity is not mentioned directly. The implementation guidelines instead focus on species-specific interactions and plant animal relationships. It is explicitly stated that the developer should "Identify opportunities for site improvements that increase the area of native/adapted vegetation or other ecologically appropriate features" (USGBC 2006, p 68). Additionally research into the species that will likely utilize the site with a focus on "selecting plants that will help support these species by providing food, forage, or nesting sites" (USBGC 2006, p 68). LEED suggests contacting local native plant societies and conservation organizations to collect the required information.

Sustainable Site (SS) Credit 5.2 focuses on open-space provisioning. This credit is tricky because creating a single-species-dominated space, such as a large lawn area, qualifies for a credit, but does little to help increase biodiversity. Pastoral, grassy lawns provide little suitable habitat for most local species. This can be easily overcome, however, by adding bordering vegetation to the edge of the property. Edges where one type of vegetation abuts another often result in higher species diversity. Edges have been considered biodiversity hotspots for all types of organisms from birds (Whitaker and Montevecchi 1997) and mammals (Hansson 1998) to all sorts of insect species (Dueill et al. 2002; Tscharntke et al. 2002). The increased biodiversity at edges is often attributed to increased plant species richness and overall structural complexity that occurs at these sites.

Indirectly, two other LEED credit requirements can be met to maximize biodiversity at a site. Water Efficiency (WE) Credits 1.1 and 1.2 focus on reducing the need for irrigation by half; using native species can best tolerate local precipitation patterns will accomplish this goal. A subset of more tolerant native plant species will require no additional watering, eliminating the needs for any irrigation. These same water-tolerant native species will have associations with native animal species. More specifically, they will provide functioning habitat in harsher times, later into the season.

The Innovation in Design (ID) Credit 1 is an open-ended credit that invites innovation in technology and theory to the sustainable building process. Its intent is to reward exceptional performance in any existing credit to sustainability strategies not outlined in the current LEED program. A developer or contractor could propose an ID credit for providing a habitat that supports a vital community of plants and animals, even those not listed as of concern or endangered, through a landscape management plan.

Under a correctly outlined design plan, there is the potential that all five of these credits – SS 5.1 and 5.2, WE 1.1 and 1.2, and ID 1.1 – could be achieved, providing an ambitious project with five LEED points through the pursuit of a singular goal (Table 6.2). This efforct could potentially make the certification jump from Certified to Silver, Silver to Gold, or Gold to Platinum.

The newest of the U.S. Green Building Council's rating systems, LEED for Neighborhood Development (USGBC 2008b), provides slightly more detailed and directed reference for implementing biological diversity into the constructed landscape. They system is in the pilot phase and changes can be expected. Notable credits include Smart Location and Linkage (SLL) Prerequisite 3: Imperiled Species and Ecological Communities; SLL 9: Site Design for Habitat or Wetland Conservation; SLL 10: Restoration of Habitats or Wetlands; and SLL 11: Conservation Management of Habitats or Wetlands. Table 6.3 provides a more detailed breakdown of these credits. The focus remains on species or ecological communities known to be at risk for which there are likely to be conservation protocols and management plans. Those wishing to generally augment the local biodiversity of a planned community and retain LEED credit again must look creatively at these credits, or consider an ID credit.

Attempts to Get Credit

A number of ID credits submitted that include the active implementation of habitat development for local and native plants and animals, yet none explicitly stated that biodiversity was the focus. Just over three percent of the total submitted ID credits (6/188) focused on the interaction of the building site with local floral and fauna (USBGC 2008a). Of these six, two focused explicitly on habitat for wildlife: *Wildlife Friendly Design* and *Habitat for Urban Wildlife.* Only Wildlife Friendly Design was awarded. Habitat for Urban Wildlife was denied on the basis that pre-development conditions of this green-field site would have been more conducive to wildlife. This may or may not be true, but since there was no pre-development assessment of habitat quality, the assumption could not be nullified. The importance of monitoring and assessing biodiversity is highlighted in this example.

Conclusions

Biodiversity is an important factor in the healthy functioning and sustainability of an ecosystem. Its assessment and measurement is not complicated, but applying and valuing biodiversity is. The debate continues in the academic world as to how biodiversity translates into product and function (Perrings 1995). There is little argument to biodiversity being important and integral, but without a comparative metric the acceptance of managing for biodiversity will be difficult. Developing greener cities calls for an understanding of how ecological communities interact. Efforts to green the built environment have started with the core of the constructed structure. New insights into the richness of urban landscapes and the successes that greening efforts have had will allow the process of creating and managing urban ecosystems to develop further.

Acknowledgements

I would like to thank the editorial staff at Urban Land Magazine for their enthusiastic acceptance of the original article idea. Sean Fine was an exceptional study buddy as we worked towards professional LEED accreditation. Miranda Gardiner was enormously helpful with the interpretation of LEED ID credits and other Green Building certification systems.

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Figures, Tables, and Appendices

Table 6.1: A presentation of the 17 ecosystem services proposed by Constanza et al 1997, with abbreviated annotations indicating the proposed Costanza 2004 categorizations. A description of each service is provided from wildland systems as well as the provision and relevance of the service in urban systems. The abbreviations indicated are as follows: *GNP*= Global non-proximal; *LP*= Local proximal; *DF*= Directional and flow related; *InS*= In situ and point of use related; *UMR*= User movement related.

Ecosystem Service	**Description**	**Traditional Wildland example**	**Urban example/urban ecosystem element providing the service**
1. Gas regulation *GNP*	A regulation of the atmospheric concentration of gases such as CO_2/O_2; O_3; SO_x; etc.	Forests and grasslands across the globe.	Urban trees and other urban vegetation.
2. Climate regulation *GNP*	The regulation of temperature, precipitation, and greenhouse gas formation.	Forests and grasslands across the globe. Bodies of water (oceans and large lakes).	Urban forests and urban trees; the overall urban green space. Urban riparian areas.
3. Disturbance regulation *LP*	Buffering against significant environmental change.	Forests, coastal wetlands, riparian areas, etc.	Healthy and intact riparian areas within cities.
4. Water regulation *DF*	The regulation of the flow of water and hydrology.	Riparian areas and coastal marshland regions.	Lawns and open space; managed biological retention basins and constructed wetlands; green roofs.
5. Water supply *DF*	The storage and retention of water.	Wetlands, lakes, rivers, fields, grasslands, and forest ecosystems.	Lawns and open space; managed biological retention basins and constructed wetlands; green roofs.
6. Erosion control *DF*	The retention of soil.	Intact root systems that prevent wind and water erosion of soil, as well as water bodies that store sediment.	Urban grasslands and lawns, riparian areas, and the urban forest as well as other managed landscapes.

Table 6.1, continued:

Ecosystem Service	**Description**	**Traditional Wildland example**	**Urban example/urban ecosystem element providing the service**
7. Soil formation *DF InS*	Processes that create and maintain soil.	The erosion of rocks and the decomposition of organic materials.	The erosion of rocks and the decomposition of organic materials in urban open space, private gardens, agricultural plots, and remnant natural areas.
8. Nutrient cycling *DF*	Storage, cycling, and acquisition of nutrients.	Plants, invertebrates, and microbes associated with these processes.	Plants, invertebrates, and microbes associated with these processes.
9. Waster treatment *LP*	The recovery of nutrients and the breakdown of excessive contents.	Microbes, plants, and animals, as well as chemical pathways.	Microbes, plants, and animals, as well as chemical pathways.
10. Pollination *LP*	The movement of angiosperm gametes and the resultant production of food.	Wildland and agricultural pollinator community.	Urban pollinators, such as resident urban bees.
11. Biological control *LP*	The control and regulation of trophic dynamics.	Keystone predators/parasitoids and other natural enemies.	Urban resident predators such as raptorial birds of prey, spiders, small predatory mammals, natural enemies, etc.
12. Refugia *LP*	Habitat for resident and transient organisms.	Nurseries, migratory habitats, overwintering grounds, and regional residential habitats for each species.	General habitat features found within the urban landscape, that support the lifestyles of certain urban resident and transient species.
13. Food production *InS*	The production of primary products that are used as energy sources for secondary consumers.	Animal products (fish and hunted game), agricultural animals, agricultural crops, fruits, and nuts, as well as gathered food products.	Urban agriculture, community gardens, and fruiting street trees that are part of the urban forest.

Table 6.1, continued:

Ecosystem Service	**Description**	**Traditional Wildland example**	**Urban example/urban ecosystem element providing the service**
14. Raw material *InS*	The production of primary products that are used as raw materials.	The production of lumber, fuel, and fibers.	Certain resources in small amounts can be derived from urban resources that can be used as lumber, fuel, and fiber.
15. Genetic resources *UMR*	The sources of unique biological materials that can be used for medicine, science, and technology.	The total genetic resources held in all of the unique and locally adapted ecosystems.	The set of genetic resources possessed by species that are adapted to urban landscapes.
16. Recreational *UMR*	Opportunities for recreational activities.	Wildland visitation, eco-tourism, sporting.	Areas of open space provide sites for recreation and sporting, and in many cases are frequented by tourists.
17. Cultural *GNP UMR*	The total non-commercial aspects of ecosystems.	Aesthetic, spiritual, educational, and scientific potential of ecosystems.	The set of aesthetic, spiritual, educational, and scientific elements that are unique to urban systems and define the lifestyle of urbanites.

Table 6.2: LEED Credits both directly and indirectly related to increasing biodiversity at a site.

LEED Credit		Possible Points	Applicability
Sustainable Sites		**2**	Directly Related
SS 5.1	Protecting or restoring habitat	1	Habitat that is diverse and supports local species is created
SS 5.2	Maximizing open space	1	An area is set aside for the purpose of creating space for plants and animals
Water Efficiency		**2**	Indirectly Related
WE 1.1	Reduction need for irrigation by 50 percent	1	Many plants that are appropriate for increasing biodiversity are also locally adapted to low water condition
WE 1.2	No irrigation	1	A section of the abovementioned plants will not require any water external water inputs.
Innovation in Design		**1**	
ID 1.1	Innovation in design	1	A rigorous landscape management plant that pushes maximizing biodiversity may qualify as a significant innovation

Table 6.3: LEED Neighborhood credits that consider biodiversity promotion.

LEED Neighborhood Credit	Credit Goals	Implementation	Applicability
PreReq 3: Imperiled Species and Ecological Communities	Protect imperiled species or ecological communities.	Avoid site selection that will cause a negative interaction with an at risk species or ecosystem. If interaction occurs, follow mediation guidelines.	In the mediation process diverse landscapes can be created under the umbrella of species conservation, alternatively many species can be targeted at the same site.
SLL 9: Site Design for Habitat or Wetland Conservation	Conserve native wildlife habitat, wetlands and water bodies.	Work with local agencies to identify local conservation priorities. Protect and conserve locally significant habitat and provide buffers around development.	The plan of action can include an appropriately chosen habitat development plant that opens the door for local wildlife use and colonization.
SLL 10: Restoration of Habitats or Wetlands	Restore wildlife habitat and wetlands harmed by previous human activities.	Use only native plants to create habitat equal to or greater than 10% of the project footprint.	High diversity can be strived for in this planting. The native plants selected will likely have biophilic associations with local fauna.
SLL 11: Conservation Management of Habitat or Wetlands	Conserve native wildlife habitat, wetlands and water bodies.	Create a long-term monitoring and management plan for on-site habitats and integrate it into local agency conservation planning.	The monitoring and management plan can address the continual maintenance of high local plant and animal diversity.

CONCLUSION

The impact the humans have on the environment and the conservation of biological systems are all too often presented as stories of loses – habitat degradation, species declines, ecosystem malfunctioning, and no happy ending. The account of some species, however, within certain elements of anthropogenic systems might tell another story, with a happier ending. Increasing attention is been given to the impact that urbanization has on biodiversity and ecosystem functioning. Generally, the growth and development of cities is viewed as a process that removes natural systems. Yet, the city is not devoid of functional ecology and ecosystem services. Most notably, the areas of green space and the managed flora that are present within cities that provide aesthetic and recreation value to humans also provide habitat for other species.

Within the urban fauna there are certain ecologically important anthophiles that interact with the available floral resources. Viable communities of these organisms exist. The current loses of species and species functions in pollinator communities may in part be mediated by the new habitat and new niches that are developed in some cities. Bees appear to be as pervasive in urban ecosystems as they are in some terrestrial ecosystems. Perhaps the biology of bees – their small size, mobility, and behavioral plasticity (even in species with narrow host ranges) – enables them to survive in modified landscapes. Perhaps it is the shared aesthetic of humans and bees – the mutual desire for flowers – that allows bees to persist within the city limits.

A review of the academic literature on bees in urban landscapes highlighted significant gaps in the knowledge capacity of the discipline. A subset of these knowledge gaps have been addressed in this dissertation work including: understanding new habitat colonization, how patterns of phenology and seasonality are manifested within cities, the variability of bee visitation within and between populations of floral resources, the characteristics that determine resource attractiveness in multiple landscapes, and the local drivers of floral visitation and foraging patterns.

The research finding of the preceding chapters can be summarized into an optimistic chronicle that accounts how the active search for food continues in urban landscapes, as it would have in wildland systems. Urban land use does not inhibit or preclude bees from visiting flowers. Habitat development is a possibility that has a great potential for success when the floral preferences of bees are taken into consideration. Urban bees show variability in their occurrence and preference in their visitation patterns. Resource abundance, defined as the total number of flowers present at a site, drives the general patterns seen in visitor abundance and taxon richness, but land use, and residential land use in particular, increases bee occurrences at some sites. Urban and wildland species assemblages are different, but carry on in similar manners, focusing on resource quality and an optimization of foraging, regardless of the greater landscape context.

Habitat development

The biological traits and ecological trends exhibited by urban bees have many analogies with wildland bee ecology. Previously documented bee-plant associations are generally conserved within urban landscapes. Seasonal bee visitation patterns are paralleled at urban resources, but certain phenologies are extended due to garden management and urban heat island effects. The potential of newly constructed habitats that are designed to attract certain species has been verified. The long-standing evolutionary relationships between bees and their food plants are conserved within urban landscapes.

Variability in resource visitation

Significant intra- and inter-resource variability was documented from tropical urban landscapes. The greater regional landscape context determined the presence and absence of bee species foraging at a resource, as well as their relative dominance patterns within the urban bee community. In this respect, populations of floral resources within similar regional landscapes had congruent bee faunas. Local inter-resource variability was driven by the individual characteristics of the resource, and in particular the number of flowers that were available to foragers. The daily variability in bee visitors was high, and is presumed to be driven by the individual characteristics of the floral resources, such as nectar volume fluctuations and perhaps also the daily climatic factors. Clear seasonal trends were not evident in the patterns of usage seen over an extended time, suggesting again that another set of factors might be driving the temporal visitation patterns of bees.

Comparing bee visitation throughout the city

Examinations of local-scale foraging dynamics within urban systems established that resource quantity is the significant overall driver of bee visitations patterns. The total abundance of bees recorded at a site and the taxonomic richness of these individuals generally increased as resource availability increased. In the tropical dry forest cities of Bagaces, Cañas, and Liberia in Costa Rica, resource quantity was measured as the number of individual flower that a *T. stans* resource possessed. The spatial clustering of *T. stans* across the landscape can also be considered a measure of resource quantity within a neighborhood, and was also shown to increase visitation patterns. In the coastal grassland cities of Berkeley, Emeryville, and Oakland in California, resource quantity was measured as the number of individual flowers in a patch of *Eschscholzia californica*, as the size of the patch, and as the density of flowers within the patch. Larger patches with more poppies that were denser attracted more bee visitors.

The urban and the wildland

From the work conducted in California, patterns of species occurrences and resource usage between urban and wildland landscapes could be examined. The raw numbers of visitors and taxa were unchanged between the two landscapes, but the composition of each fauna was shown to be quite different, with larger species more prevalent in the wildands and smaller species more common in the city. In both the urban and the wildland landscapes, resource quantity remained the dominant driver of bee visitation patterns. Wildland foragers were more drawn to resource patches with higher floral species richness. In the Costa Rica study, residential neighborhoods experienced increased visitor numbers from certain species, suggesting that the richness of the resource base might also influence some species-specific visitation patterns. In all of the landscapes, however, resources that were abundant in flowers were successful in attracting bees.

These results are optimistic and constructive for the conservation and management of bees and the pollination services that they provide within urban landscapes. The urban landscape and the land use characteristics that define urban systems are not inhibiting resource usage by bees. Bees are finding and using rich floral resources, regardless of their location. In this light, any available portion of the urban landscape has the potential to serve as viable habitat for bees. Conserving species within cities and managing populations of bees within urban landscapes for beneficial applications, such as urban agriculture, has budding potential.