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Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study

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Abstract

Urban bee ecology is an emerging field that holds promise for advancing knowledge of bee community dynamics and promoting bee conservation. Published studies of bee communities in urban and suburban habitats are fewer than those documenting bees in agricultural and wildland settings. As land lost to urbanization is predicted to increase in coming years the necessity of studying urban bee populations is growing. We reviewed 59 publications on urban bee ecology with the following goals, to assess current knowledge, to highlight areas in need of further research, and to suggest applications of study findings to bee conservation. Identified trends in urban areas included the following, negative correlation between bee species richness and urban development, increase in abundance of cavity-nesters in urban habitats, and scarcity of floral specialists. Future directions for studying urban bee ecology include incorporation of landscape-scale assessments, conducting manipulative experiments and actively designing urban bee habitats.

Keywords

Urban ecology; Apoidea; bee ecology; bee species diversity; urban bees

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INTRODUCTION

Little is known about urban bee fauna as we are only beginning to document their community dynamics including patterns of species diversity and abundance. In agricultural and wildland settings, bees contribute to ecosystem function as pollinators of a majority of crop (Klein et al. 2007) and angiosperm species, with an estimated 85% of angiosperms relying on bee pollinators (Moldenke 1976; Simpson 1977; Moldenke 1979; Frankie and Thorp 2002). Their ubiquitous presence and importance in non-urban habitats has led to many publications on wild bee ecology and conservation but publications on urban bee ecology are much fewer.

Conversion of natural habitat can potentially affect bees by decreasing foraging resources, eliminating nesting site availability, fragmenting habitats and subjecting populations to anthropogenic pressures such as pollutants, pesticides, foot traffic, among other effects. Monitoring responses of bee populations to urbanization may identify underlying drivers shaping bee community dynamics–relationships that are currently obscure at best. Elucidation of causal relationships between community composition and habitat characteristics may provide information useful for bee conservation, especially as it applies to urban habitat construction.

Review Objectives

A theme of this review is the promotion of construction and enhancement of urban bee habitat using lessons learned from studies in urban bee ecology. The goals are to provide a current assessment of urban bee ecology and to suggest areas for future research with intent to increase bee conservation in urban habitats. We ask: which trends have been identified, which areas lack sufficient data and how can we apply current knowledge to bee conservation? We present and discuss scope and design of urban bee studies, emerging trends in urban bee ecology, and future directions for the field.

SCOPE AND DESIGN OF URBAN BEE STUDIES

Scope of Urban Bee Surveys

Urban bee surveys have been conducted in sites that varied according to, among other factors, density of development, remnant vegetation type, size or history of use. In this review we categorized the types of urban habitats surveyed based on broad descriptors to provide a context for evaluating trends in urban bee communities. In most of the surveys the authors classified habitats as "urban" without providing detailed descriptions. We note that although proximity to a built environment does constitute an urban setting, the term "urban" is general and does not allow for distinctions between habitats based on variation in ecologically significant characteristics. McIntyre et al. (2000) discussed the need for using quantitative descriptors when defining "urban" habitats. The use of an interdisciplinary concept of an urban habitat would promote comparison between urban ecological studies (McIntyre et al. 2000).

Many of the urban studies included in this review characterized study sites with a broad descriptor such as forest, garden, cemetery, or habitat fragment. Some studies provided coordinates and/or a reserve name when applicable but many more listed only "sites within city" or gardens. To illustrate, Antonini and Martins (2003) monitored three different site-types–secondary forest, weedy and swamp–on the campus of the Universidade Federal de Minas Gerais in Brazil, documenting higher bee species richness along the weedy transect. The study included a list of plant species visited by bees for the entire campus. Yet, the absence of detailed site descriptions or the inclusion of data such as floral diversity and abundance, % bare soil, land use patterns, etc. provided little context with which to evaluate the bee fauna in this area other than brief descriptions of each transect. Similarly, Saure (1996) surveyed sites in and around urban Berlin, documenting high species diversity but limiting description of his collection sites to "ruderal."

In order to evaluate trends in urban bee diversity we grouped urban bee studies based on broad survey site descriptions. In doing so, we used similar categorical classifications as provided in the publications. For future studies we propose the use of non-categorical descriptors that include quantified measurements of environmentally significant characteristics. Descriptors such as these will likely prove more valuable for evaluating trends in bee community composition.

METHODS

Based on descriptors used in urban bee surveys we created the following 5 site-type categories in order to group surveys that monitored similar sites: 1. remnant habitat, 2. managed gardens, 3. unmanaged (weedy) sites, 4. parks, and 5. home gardens. In defining the categories, we made assumptions regarding land use and management practices based on our own observations of such characteristics while working in regionally diverse urban areas. Many of the studies described survey sites based on the type of habitat present in the region, such as secondary forest, grassland or desert, these were defined as "remnant habitat" as they represented natural or semi-natural habitat. The "managed gardens" category included sites labeled as botanic and community gardens. Sites described as abandoned lots, weedy areas surrounding urban structures, and ruderal sites were placed in the "unmanaged (weedy) sites" category.

The "parks" category was more broadly defined relative to the other site-type categories and included sites described as green areas, open space managed for recreation, zoological gardens, and open areas on university campuses. We reasoned that the site-types included in "parks" usually are not managed to provide diverse floral communities and likely exhibit similar characteristics in plant community composition and land management. We also made the assumption that, with the exception of zoological gardens, "parks" are generally designated for public recreation and often have high levels of unsupervised human usage and significant areas of lawn.

Several studies defined their study sites as "home gardens" and were categorized as such. We separated managed gardens from home gardens based on the assumption that managed gardens are likely to be older, allowing more time for bee species to discover and disperse to the habitat, and larger, thereby containing more nesting and foraging resources. For future bee surveys, floral diversity and abundance, native vs. non-native plant species, size, plant management techniques and availability of nesting resources are examples of variables that could be used to better define managed vs. home gardens.

RESULTS

Remnant habitats and managed gardens were studied more frequently than home gardens, parks, or unmanaged sites. Several comparative studies were included in more than one site-type category. Therefore, 68 site-type categorizations resulted from the 59 studies included in our review. Out of 68 categorizations, 17 surveys were conducted in remnant habitat: 10 in secondary forest, 1 in primary old growth, 3 in grassland habitats, 2 in desert and 1 in a swampy area (see Appendix I for list of studies). Managed gardens were included in 16 surveys. Unmanaged sites and parks were surveyed in 13 and 12 studies, respectively, and home gardens were monitored in 10 of the 68 categorizations.

Study Duration

The duration of sampling in urban bee surveys ranged from one season to greater than five consecutive seasons. Cane (2001) documented high temporal variation in bee species diversity and abundance indicating that short study duration can be problematic depending on study design and the questions of interest. Bee faunal surveys are often time and labor intensive leading researchers to limit the duration of sampling. We reasoned that the duration of a bee survey is relevant as temporal variation is a confounding variable that must be considered as part of a study analysis.

Studies evaluated in this review were categorized based on whether data were collected in 1 season, 2 consecutive seasons, or for more than 2 seasons. We define a season as spanning from the time of spring bee emergence to the cessation of fall bee activity. Of the studies that specified sample duration, 36% monitored for 1 season, 24% for 2 seasons and 40% for 3 or more seasons. While study duration of one season can provide diversity and abundance data for that year, variability of bee community composition makes identification of trends unlikely or misleading. Bees may respond within one season to fluctuations in climate and other biotic factors that may not be correlated with urbanization. Studies that were conducted for 3 seasons or more have the potential to provide more information on community response to urbanization. Owen (1991) surveyed arthropod diversity in her backyard garden, in Leicestershire England, for 15 years. Because of the long duration of the study, Owen was able to document fluctuations in species diversity over many years.

Study durations in excess of three years also provide the opportunity to evaluate effects of climatic fluctuations on bee communities. Many areas, including California, have experienced drought in the last several years. Our own observations of California bee fauna have analyzed bee species response to changes in precipitation. Surveys of the California Central Valley bee fauna revealed that species in the family Megachilidae decrease in abundance during a drought (G. Frankie, unpubl data). It is thought that the bees remain in their nests until favorable conditions resume (R. W. Thorp, unpubl. data). Evaluating the effects of climatic fluctuations is particularly important as global climate change becomes an imminent threat to animal populations worldwide.

Study Region

Globally, more studies were conducted in Brazil and North America than other regions. Study locations were divided into the following regions-Africa, Asia, Brazil, Europe, Germany, North America, South America and the United Kingdom (Figure 1). We separated Germany and Brazil from continental classifications to highlight the large number of studies conducted in these countries. Some of the earliest urban bee studies were conducted in Germany in the zoological parks and ruderal sites in and around Berlin (Dathe 1969, 1971 (cited in Saure 1996); Saure 1996). Urban bee research is lacking in Africa, Asia, and South America (other than Brazil) (see Appendix I).

In the interest of bee conservation, research efforts should be increased in developing regions as urbanization is expected to increase there dramatically. According to the United Nations the number of people expected to live in urban areas by 2030 is predicted to reach 5 billion, and in developing countries, 81% of the population will likely reside in towns and cities (UNFPA 2007). Although the loss of bee species as a result of urbanization is unavoidable, focusing research on specific regions may provide information that can then be used to influence development in urban regions by promoting open spaces designed to attract and support native bee species.

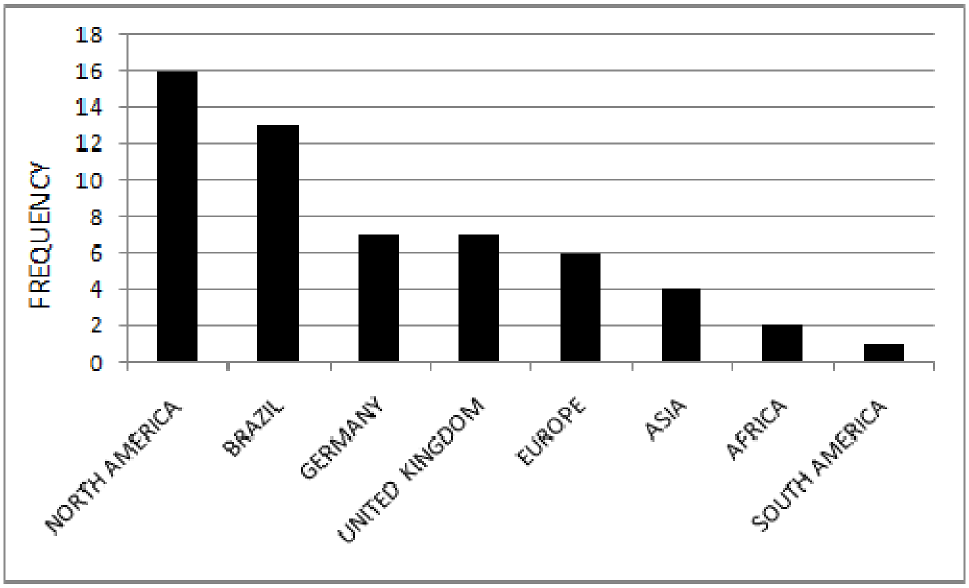

Figure 1. Urban bee studies categorized according to study region. To emphasize regional focus, Brazil is shown separate from South America and Germany separate from Europe.

TRENDS IN BEE COMMUNITY RESPONSE TO URBANIZATION

Bee Species Richness and Urbanization

Many of the urban bee studies surveyed different site types simultaneously, compared a site before and after urbanization, or measured habitat characteristics used as proxies for urbanization. Most studies concluded that urbanization is negatively correlated with bee species richness. Several studies evaluated degree of urbanization by quantifying characteristics of the landscape matrix such as % impervious surface or % arable land and concluded that bee species composition and richness was negatively correlated with anthropogenic modifications to surrounding habitat (Dauber et al. 2003; Ahrné 2008). Dauber et al. (2003) monitored 20 grassland sites in Germany and identified 5 land use types in the surrounding matrix revealing that bee species richness was positively correlated with % arable land and negatively correlated with urban development. In Sweden, Arhné (2008) measured % impervious surface in the landscape surrounding survey sites and reported lower species richness of bumble bees and cavity-nesting bees in areas containing a higher percentage of impervious surfaces. The findings reported in landscape scale studies emphasize the need to include matrix effects in analyses especially when considering bee species richness.

Similar to landscape scale studies, a majority of the comparative studies reported evidence of decreased bee species richness corresponding with increased development within the urban matrix. These studies compared urban, suburban or remnant habitat patches to natural areas (Owen 1991; McIntyre and Hostetler 2001; Eremeeva and Sushchev 2005; Matteson 2007; Fetridge et al. 2008; Matteson et al. 2008). Fetridge et al. (2008) and Matteson et al. (2008) compared bee community composition from urban community gardens to reference collections from surrounding natural areas. Fetridge et al. (2008) compared species richness of suburban and urban bee fauna in New York to nearby nature preserves, including the Black Rock Forest, and noted a general trend towards fewer ground-nesting bee species in densely urban habitats. In addition, the suburban bee fauna contained fewer species than the bee fauna in nearby natural habitats but had higher species richness than dense urban areas (Fetridge et al. 2008). Similarly, Matteson *et al*. (2008) compared bee faunal surveys conducted in community gardens of East Harlem and the Bronx to reference collections from three nearby natural areas, also including the Black

Rock Forest, and reported an increase in cavity-nesting species and an increase in exotic species in urban gardens. McIntyre and Hostetler (2001) conducted bee faunal surveys in urban and natural habitats simultaneously. This study documented lower species richness and abundance in urban areas than natural habitat that was located on the fringe of the city.

Smaller urban habitat fragments had lower bee species diversity than larger urban fragments. Several studies explored this relationship by sampling urban sites that varied in size and age (Cane et al. 2006; Viana et al. 2006; Nemésio and Silveira 2007; Hinners 2008). Cane et al. (2006) monitored desert patches containing *Larrea tridentata* in urban Tucson, Arizona and compared the bee community to that found in continuous desert patches located outside the urban boundary. In this survey, bee species diversity was reduced in small and older fragments but abundance was similar to that found in continuous desert patches (Cane et al. 2006).

Bee species from the families Colletidae and Andrenidae were conspicuously scarce in urban habitats. Of the studies that reported diversity of bee families, Colletidae was least diverse (Liow et al. 2001; Antonini and Martins 2003; Fetridge et al. 2008; Hernandez et al. in review). The only study that reported high abundance, but not richness, for Colletidae was Hisamatsu and Yamane (2006). The increased abundance in this study was putatively the result of increased floral resources for an oligolectic colletid, a floral specialist on one or several plant genera within a family, as a nearby plant community in a Japanese marsh was dominated by two of the floral hosts for this species. Species from Andrenidae, species of this genera are largely ground-nesters and early spring fliers, were also rare in urban habitat patches (Owen 1991; Antonini and Martins 2003; Hernandez et al., in review).

In some groups of bees, such as bumble bees, species richness increased in urban areas relative to surrounding natural habitat. Winfree et al. (2007) compared continuous forest to disturbed forest and an urban area in the New Jersey Pinelands Biosphere Reserve and reported the highest bee species diversity for the urban area. McFrederick and LeBuhn (2006) surveyed bumble bee diversity in urban San Francisco, California and surrounding areas. Their findings indicated competitive exclusion by one bumble bee species when sites were surrounded by an open landscape such as a forest, or other natural habitat, often leading to greater bumble bee species richness in urban rather than suburban or natural areas within the urban matrix. Ecological variables such as habitat structure, floral diversity and competitive interactions clearly have an influence on bee community dynamics, as was demonstrated by these studies. Further investigations may identify urban habitat characteristics that are positively correlated with bee diversity.

Cavity-Nesters in Urban Habitats

Several studies reported higher abundance of cavity-nesting bee species in urban areas and remnant habitat fragments comparative to suburban sites or continuous natural habitat (Cane 2005; Zanette et al. 2005; Cane et al. 2006; Hinners 2008; Matteson et al. 2008). In Tucson Arizona, Cane et al. (2006) documented a 10-fold increase in cavity-nesters in desert habitat fragmented by urban development compared to continuous fragments of desert. Hinners (2008) monitored bee communities in grassland fragments in Colorado and compared them to continuous grassland habitat, documenting an increase of cavity-nesters and a corresponding decrease in ground-nesters in grassland fragments. Furthermore, Matteson *et al*. (2008) found an increase in cavity nesters in urban community gardens compared to natural habitats.

The propensity for abundance of cavity nesting species to increase in urban areas raises several questions: are cavity-nesters increasing in urban areas as a result of manmade nesting sites, and, are the diversity and abundance of cavity-nesting bees in urban areas reaching levels higher than those traditionally documented in surrounding natural habitats? A general lack of knowledge regarding bee nesting highlights the need for future research on this aspect of bee ecology.

Decrease in Floral Specialists with Urbanization

Many of the urban bee surveys reviewed indicated that floral specialists are scarce in urban habitats (Cane 2005; Frankie et al. 2005; Cane et al. 2006; McFrederick and LeBuhn 2006; Fetridge et al. 2008; Frankie et al. 2009). As urban development replaces native or remnant habitat, overall floral diversity tends to decrease and/or be replaced by a combination of native and non-native or horticultural plant species (Frankie et al. 2009). In reporting on the bee community sampled from a small urban garden, Hernandez et al. (in review) noted a conspicuous lack of specialist bee species. However, once sunflowers (*Helianthus annuus*) and a species from the family Cucurbitaceae were planted, the specialists *Diadasia enavata* and *Peponapis pruinosa*, respectively, were found foraging on the host plants (Hernandez et al. in review). Although surveys including notes on floral specialists are rare, it is likely that further surveys will support the trend that floral specialists are absent from urban areas. Manipulative experiments in which plants are introduced to attract specialist foragers would be valuable towards assessing the presence of these bees in urban and surrounding habitats.

FUTURE DIRECTIONS

Assessing Landscape Scale Effects

While biotic characteristics of a habitat patch are undoubtedly strong determinants of urban bee community structure, much can be learned by applying the principles of landscape ecology. Traditional ecological studies, including many studies included in this review, focus on describing or quantifying animal communities in one or several habitat patches, this approach is valuable for evaluating diversity and abundance of a community within in a specific habitat patch but is limiting if the goal is to identify causal factors or drivers of community structure. Landscape ecology addresses the effects of habitat heterogeneity on ecological processes at varying spatial scales (Hanski 1999; Lawton 2000; Turner 2001). Application of Levin's (1976) principles, suggests consideration of factors such as the uniqueness of a local habitat, successional stage of vegetation, and species dispersal ability when analyzing animal community dynamics.

Within the context of landscape ecology, identification of biologically relevant spatial scales for bee species provides the basis for evaluating putative causal relationships between landscape characteristics and bee community dynamics. In urban areas, it is rare that bees can meet their nesting and foraging requirements in one habitat patch. This follows a basic ecological principle: most species depend on several different habitats (Rosenzweig 1995). Evaluation of matrix effects within a relevant scale will likely depend on species specific factors such as foraging distance, dispersal ability and nesting site preferences. Cane (2005), identified the condition of the environmental matrix as important in shaping urban bee communities and proposed evaluating environmental matrices based on distance between suitable sites for bees, availability of pollen and nectar and nesting site availability.

It is likely that biologically relevant spatial scales for bees vary with factors such as land use, density of development, distribution of open areas, etc, identifying these factors for each study site will likely improve our understanding of urban bee community responses to anthropogenic habitat alteration. Miller et al. (1997) examined one such approach as they created general landscape descriptors that encompassed several types of land use (most anthropogenic in nature) that were ecologically relevant for evaluating community patterns of birds and vascular plants located within 2 watersheds in Pennsylvania. It is possible that factors such as % impervious surface, % green space, distance between habitat patches, floral diversity, etc. could serve as landscape descriptors in urban bee studies. Distance from source populations (natural habitat areas) is another important factor to consider.

Experimental Studies of Bee Community Dynamics

The use of experimental methodology in urban bee studies is rare. Of the 59 studies evaluated for this review, 2 used a manipulative approach. Two experimental studies that utilized an experimental approach focused on bumble bee and trap nesting species. Goulson et al. (2002) monitored larval and pupal growth rate and end of season nest size of *Bombus terrestris* nests in three habitat types and found that nests located in suburban study sites increased in size at a faster rate than nests in both farmland with no set aside natural habitat and farmland with hedgerows. They concluded that the suburban area contained higher plant abundance than the farmland plots thereby providing more and higher quality foraging resources than the other sites (Goulson et al. 2002). Gaston et al. (2005) conducted an experiment to test the effectiveness of 5 different methods for increasing biodiversity in urban gardens in Sheffield, United Kingdom. As part of the experiment, they provided trap nests and artificial bumble bee nests and monitored nest useage. Their findings indicated that wasps utilized trap nests more than bees. Although two bee species, *Osmia rufa* and a *Hylaeus* sp., did use the nests their abundance was low. Interestingly, bumble bees were found foraging in the garden but did not utilize the artificial nests provided (Gaston et al. 2005). Our own California urban bee research combines manipulative garden management techniques with monitoring of the foraging bee community. We conducted sampling in an urban garden before and after the addition of 36 bee attractive plants and documented an increase in bee species diversity from 2 to 23 species (Pawalek et al., in review). While these studies are valuable, further experimentation is needed to establish causal relationships between bees (social and solitary species) and environmental characteristics.

Construction and Enhancement of Urban Bee Habitats

The expansion of urban areas is unavoidable but there is potential for conserving bee species by promoting inclusion of bee friendly green spaces within the urban matrix. How do we balance the needs of urban bees for suitable forage and nesting resources with the needs and aesthetic preferences of the public? Some site-types may be more suitable for development within the urban matrix than others. For example, managed community and botanic gardens can be ideal for developing bee habitat if administrating organizations are interested in bee conservation. Leaving patches of remnant habitat and/or creating public parks during development can provide bee habitat while also creating a pleasing landscape for urbanites. In contrast, ruderal sites, although they support a diverse bee community, are considered unsightly by urbanites and are often paved over or the vegetation removed. Home gardens and other sites outside the realm of city planning are unique in that their creation and maintenance are based on individual home-owner or organizational preferences. A pollinator park under development in Guelph, Canada provides an illustration of community effort to construct and enhance urban bee habitat. The proposed pollinator park will cover 45 hectares of an old municipal dump and will be planted with pollinator friendly flowering plant species (http://www.pollinator.ca/guelph). From our observations and surveys of urban bee habitats throughout California we have identified techniques in garden design and plant management that seem to increase environmental suitability for bees. For example, stability of resource availability through time enhances attractiveness for establishment of pioneer and successional populations of bees.

CONCLUSION

Little is known about urban bee ecology. The numbers of surveys have increased but represent significantly fewer published studies than exist for bee ecology in wildland and agricultural regions. Survey site descriptions included in urban bee faunal surveys are lacking in detail thereby preventing analyses capable of discerning which habitat characteristics affect urban bee communities. In addition, study duration is frequently limited to one to two seasons. Detection of habitat dependent trends requires multiple years of data collection. Finally, urbanization is predicted to occur rapidly in developing countries yet our assessment of study regions indicate a paucity of studies in areas other than North America, Brazil, and perhaps Germany.

Several trends in urban bee community composition were evident in the reviewed literature: 1. Bee species richness was lower in urban areas compared to suburban areas and natural habitats, 2. Abundance, and in some surveys, species richness of cavity-nesting bee species was higher in urban areas, and 3. Diversity and/or abundance of specialist bee species decreased in urban areas, this often coincided with a decrease in ground-nesting bee species.

Some proposed future directions for the field of urban bee ecology are to approach analyses of urban bee community dynamics utilizing techniques from landscape ecology, employ manipulative studies to determine causal relationships between bee habitat utilization and ecologically significant habitat characteristics, and participate in active construction and enhancement of urban bee habitats. We propose that an overriding goal of urban bee research be the conservation of this group through the application of our knowledge of bee habitat utilization, including foraging and nesting needs, towards the construction of enough suitable urban habitats to support a subset of natural populations in urban areas.

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LITERATURE CITED

Alvos-Dos-Santos, I. 2003. Trap-nesting bees and wasps on the University Campus in Säo Paulo, southeastern Brazil (Hymenoptera: Aculeata). Journal of the Kansas Entomological Society 76(2):328-334.

Antonini, Y. and R.P. Martins. 2003. The Flowering-Visiting Bees at the Ecological Station of the Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil. Neotropical Entomology 32(4):565-575.

Ahrné, K. 2008. Local management and landscape effects on diversity of bees, wasps and birds in urban green areas. PhD dissertation, Swedish University of Agricultural Sciences. 56 pp.

Cane, J.H. 2001. Habitat fragmentation and native bees: a premature verdict? Conservation Ecology 5(1):3.

-------. 2005. Bees, pollination, and the challenges of sprawl pp. 109-124. In Johnson, E.A. and M.W. Klemens (Eds.). Nature in fragments: the legacy of sprawl. Columbia University Press, New York, New York. 382 pp.

Cane, J.H., R.L. Minckley, L. Kervin, and T.H. Roulston. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Application 16:632–644.

Clark, T.E. and M.J. Samways. 1997. Sampling arthropod diversity for urban ecological landscaping in a species-rich southern hemisphere botanic garden. Journal of Insect Conservation 1:221-234.

Comba, L., S.A. Corbet, A. Barron, A. Bird, S. Collinge, N. Miyazaki, and M. Powell 1999a. Garden flowers: insect visits and the floral reward of horticulturally-modified variants. Annals of Botany 83:73–86.

Comba, L., S.A. Corbet, L. Hunt, and B. Warren. 1999b. Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens. Annals of Botany 83:369-383.

Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems and Environment 98:321–329.

Eremeeva, N. I. and D.V. Sushchev. 2005. Structural changes in the fauna of pollinating insects in urban landscapes. Russian Journal of Ecology 36(4):259-265.

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

Frankie, G.W. and R.W. Thorp. 2002. Pollination and pollinators, pp. 919-926. In Resh, V. and R. Carde (Eds.). Encyclopedia of Insects. Academic Press, San Diego, California. 1266 pp.

Frankie, G.W., R W. Thorp, J.C. Pawelek, J.L. Hernandez, and R. Coville. In Press. Urban bee diversity in a small residential garden in Northern California. Journal of Hymenoptera Research.

Frankie, G.W., R.W. Thorp, M. Schindler, J. Hernandez, B. Ertter, and M. Rizzardi. 2005. Ecological patterns of bees and their host ornamental flowers in two northern California cities. Journal of the Kansas Entomological Society 78:227– 246.

Frankie, G.W., R.W. Thorp, J.L. Hernandez, M. Rizzardi, B. Ertter, J.C. Pawalek, S.L. Witt, M. Schindler, and V.A. Wojcik. 2009. Native bees are a rich natural resource in urban California gardens. California Agriculture. 63(3):113-120.

Gaston, K.J., R.M. Smith, K. Thompson, and P.H. Warren. 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodiversity and Conservation 14:395–413.

Goulson, D., W.O. H. Hughes, L.C. Derwent, and J.C. Stout. 2002. Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. Oecologia 130:267–273.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209-219.

Herrmann, M. 2007. Bees and wasps (Hymenoptera, Aculeata) on Fuerstenberg Hill in Constance, Germany. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau. 97(1): 75-102.

Hernandez, J.L., G.W. Frankie, R.W. Thorp, and M. Schindler. In Review. Bee visitation (Hymenoptera: Apoidea) in a newly constructed urban garden in Berkeley, California.

Hinners, S.J. 2008. Pollinators in an urbanizing landscape: effects of suburban sprawl on a grassland bee assemblage. PhD Dissertation, University of Colorado. 24 pp.

Hisamatsu, M. and S. Yamane. 2006. Faunal makeup of wild bees and their flower utilization in a semi-urbanized area in central Japan. Entomological Science 9:137-145.

Kearns, C.A. and D.M. Oliveras. 2009. Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. Journal of Insect Conservation 13:655–665.

Klein, A.M., B.E. Vaissière, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274:303-313.

Laroca, S. and A.I. Orth. 2002. Melissocoenology: historical perspective, method of sampling, and recommendations to the "Program of conservation and sustainable use of pollinators, with emphasis on bees" (ONU), pp.217-225 In Kevan, P. and V.L. Imperatriz Fonseca (Eds.). Pollinating Bees - The Conservation Link Between Agriculture and Nature - Ministry of Environment / Brasília.

Lawton, J.H. 2000. Community ecology in a changing world. Ecology Institute. Oldendorf/Luhe, Germany.

Levin, S.A. 1976. Spatial patterning and the structure of ecological communities. Lectures on mathematics in the life sciences (some mathematical questions in biology 8:1-35.

Liow, L.H., N.S. Sodhi, and T. Elmquist. 2001. Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. The Journal of Applied Ecology 38(1):180-192.

López-Uribe, M.M., C.A. Oi, and M.A. Del Lama. 2008. Nectar-foraging behavior of Euglossine bees (Hymenoptera: Apidae) in urban areas. Apidologie 39:410-418.

Loyola, R.F. and R.P. Martins. 2009. On a habitat structure-based approach to evaluating species occurrence: cavity-nesting Hymenoptera in a secondary tropical forest remnant. Journal of Insect Conservation 13:125-129.

Matteson, K.C. 2007. Diversity and conservation of insects in urban gardens: theoretical and applied implications. PhD Dissertation, Fordham University. 227 pp.

Matteson, K.C., J.S. Ascher, and G.A. Langellotto. 2008. Bee richness and abundance in New York City urban gardens. Annals of the Entomological Society of America 101(1):140-150.

McFrederick, Q. and G. LeBuhn. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? Biological Conservation 129:372-382.

McIntyre, N. E., K. Knowles-Yánez, and D. Hope. 2000. Urban ecology as an interdisciplinary field: differences in the use of "urban" between the social and natural sciences. *Urban Ecosystems* 4:5-24.

McIntyre, N.E. and M.E. Hostetler. 2001. Effects of urban land use on pollinator (Hymenoptera: Apoidea) communities in a desert metropolis. Basic and Applied Ecology 2:209-218.

Miller J.N., R.P. Brooks and M.J. Croonquist. 1997. Effects of landscape patterns on biotic communities. Landscape Ecology 12(3):137-153.

Moldenke, A.R. 1976. California pollination ecology and vegetation types. Phytologia 34:305-361.

-------. 1979. Pollination ecology as an assay for ecosystem organization: convergent evolution in Chile and California. Phytologia 42:415-454.

Nemésio, A. and F.A. Silveira. 2007. Orchid Bee Fauna (Hymenoptera: Apidae:Euglossina) of Atlantic Forest Fragments inside an Urban Area in Southeastern Brazil. Neotropical Entomology 36(2):186-191.

Nates-Parra, G., A. Rodríguez-C., and E.D. Vélez. 2006. Stingless bees (Hymenoptera:Apidae: Meliponini) in Oriental mountain cemeteries from Colombia. Acta Biológica Colombiana 11(1):25-35.

Owen, J. 1991. The Ecology of a Garden: The First Fifteen Years. Cambridge University Press, Cambridge. 403 pp.

Pauw, A. 2007. Collapse of a pollination web in small conservation areas. Ecology 88(7): 1759-1769.

Pawalek, J.C., G.W. Frankie, R.W. Thorp, M. Przybylski. 2009. Modification of a community garden to attract native bee pollinators in urban San Luis Obispo, California. Cities and the Environment 2(1):article 7. http://escholarship.bc.edu/cate/vol2/iss1/7 (accessed 12/18/2009).

Raw, A. 1988. Nesting biology of the leaf-cutter bee *Megachile centuncularis* (L.) (Hymenoptera: Megachilidae) in Britain. The Entomologist. 107(1):52-56

Rosenzweig, M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge UK. 436 pp.

Saure, C. 1996. Urban habitats for bees: the example of the city of Berlin, pp. 47-53. In Matheson, A., S. L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams (Eds.). The Conservation of Bees, Linnean Society Symposium Series No. 18. Academic Press. 254 pp.

Simpson, B.B. 1977. Breeding systems of dominant perennial plants of two disjunct warm desert ecosystems. Oecologia 27: 203-226.

Silva, C.L., S.C. Augusto, S.H. Sofia, and I.S. Moscheta. 2007. Bee diversity in *Tecoma stans* (L.) Kunth (Bignoniaceae): importance for pollination and fruit production. Neotropical Entomology. 36(3): 331-341.

Smith R.M., K.J. Gaston, P.H. Warren, and K. Thompson. 2006. Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. Biodiversity and Conservation 15:2515-2545.

Taura, H.M., S. Laroca, J.F. Barbosa, and J. Rodrigues. 2007. Melissocoenotics Hymenoptera, Anthophila) in the *Parque Florestal dos Pioneiros*, Maringá, PR (southern Brazil) — I. Relative abundance and diversity. Acta Biol. Par., Curitiba 36(1-2): 47-65

Tommasi, D., A. Miro, H.A. Higo, and M.L. Winston. 2004. Bee diversity and abundance in an urban setting. Canadian Entomologist 136(6): 851-869.

Turner, M.G., R.H. Gardner, and R.V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag. New York. 401 pp.

United Nations Population Fund. 2007. State of the World Population: unleashing the potential of urban growth. http://www.unfpa.org/swp/2007 (accessed 27 March 2009).

Viana, B.F., A.M. Costa de Melo, and P. Dias Drumond. 2006. Variation in the structure of habitat affecting solitary bees and wasps composition in urban forest fragments of Atlantic forestry in northeastern Brazil. Sitientibus serie Ciencias Biologica 6(4):282-295.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology 21(1):213-223.

Wojcik, V.A., G.W. Frankie, R.W. Thorp, and J.L. Hernandez. 2008. Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. Journal of the Kansas Entomological Society 81(1):15-28.

Zanette, L.R.S., R.P. Martins, S.P. Ribeiro. 2005. Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. Landscape and Urban Planning 71:105-121.

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Appendix I. List of urban bee studies included in review, includes site-type characterization, study duration (number of seasons) and study region. Studies in which duration was not available are designated with a --.

REGION	SITE-TYPE	DURATION	STUDY CITATION
AFRICA	Managed garden	1	Clark and Samways 1997
	Remnant habitat (fynbos)	2	Pauw 2007
ASIA	Managed garden	--	Sakagame and Fukuda 1973 (cited in Cane 2005)
	Park	--	Ikudome 1992 (cited in Cane 2005)
	Remnant habitat (swamp)	1	Hisamatsu and Yamane 2006
	Remnant habitat (forest)	1	Liow et al. 2001
BRAZIL	Park	>2	Alvos-Dos-Santo 2003
	Park	--	Camargo and Mazucato 1984 (cited in Cane 2005)
	Park	--	Knoll et al. 1993 (cited in Cane 2005)
	Park	1	Taura et al. 2007
	Park	1	Zanette et al. 2005
	Remnant habitat (forest)	--	Laroca et al. 1982 (cited in Cane 2005)
	Remnant habitat (forest)	1	Loyola and Martins 2009
	Remnant habitat (forest)	1	Nemésio and Silveira 2007
	Remnant habitat (forest)	>2	Viana et al. 2006
	Remnant (forest, swamp), unmanaged	1	Antonini and Martins 2003
	Unmanaged site	>2	Laroca and Orth 2002
	Unmanaged site	2	Lopez-Uribe et al. 2008
	Unmanaged site	--	Silva et al. 2007
EUROPE	Managed garden, park	--	Ahrné 2008
	Park	--	Noskiewicz (cited in Cane 2005)
	Unmanaged site	--	Banaszak 1982 (cited in Cane 2005)
	Unmanaged site	--	Berezin et al 1995 (cited in Cane 2005)
	Unmanaged site	>2	Eremeeva and Suschev 2005
	Unmanaged site	--	Jacob-Remacle 1984 (cited in Cane 2005
GERMANY	Managed garden	--	Bischoff 1995 (cited in Cane 2005)
	Managed garden	--	Küpper 1999 (cited in Cane 2005)
	Managed garden	--	Rieman 1995 (cited in Cane 2005)
	Park	--	Dathe 1969, 1971 (cited in Cane 2005)
	Remnant habitat (grassland)	2	Dauber et al. 2003
	Remnant habitat (forest)	>2	Hermann 2007
	Unmanaged site	>2	Saure 1996
NORTH AMERICA	Home garden	>2	Frankie et al. In Press
	Home garden, managed, unmanaged	>2	Frankie et al. 2002
	Home garden, managed, unmanaged	>2	Frankie et al. 2009
	Home garden, remnant (desert)	1	McIntyre and Hostetler 2001
	Managed garden	2	Fetridge et al. 2008
	Managed garden	2	Hernandez et al. In Review
	Managed garden	>2	Matteson et al. 2008
	Managed garden	>2	Matteson 2007
	Managed garden	2	Wojcik et al. 2008
	Park, remnant (forest)	2	McFrederick and LeBuhn 2006
	Remnant (desert)	2	Cane et al. 2006
	Remnant (grassland)	--	Hinners 2008
	Remnant (grassland)	>2	Kerns and Oliveras 2009
	Remnant habitat (forest)	1	Winfree et al. 2007
	Unmanaged, home garden	>2	Frankie et al. 2005
	Unmanaged site, managed garden	1	Tommasi et al. 2004

Appendix I – Continued on next page.

Appendix I – Con't

REGION	SITE-TYPE	DURATION	STUDY CITATION
SOUTH AMERICA	Park	--	Nates-Parra et al. 2006
UNITED KINGDOM	Home garden	>2	Gaston et al. 2005
	Home garden	>2	Owen 1991
	Home garden	1	Smith et al. 2006
	Managed garden	2	Comba et al. 1999a
	Managed garden	2	Comba et al. 1999b
	Unmanaged site	1	Goulson et al. 2002
	Unmanaged site	--	Raw 1988