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The local and landscape effects on bee communities in urban gardens

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Abstract

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Despite their ecological and economic importance we have little knowledge of how bees in urban environments respond to anthropogenic influences. I examined how bee richness and abundance responded to local and landscape factors in 30 urban gardens in Atlanta, GA. I sampled each site 4-5 times over the course of a 3-month period, using a standard netting protocol. I found that bee abundance is related to the garden area, floral density, floral richness, and surrounding canopy cover. Bee species richness was marginally negatively related to canopy cover. It appears that urban gardens can be managed to benefit bee communities even if seemingly isolated within developed areas. Efforts should be made to increase floral density within urban gardens with an emphasis on native plants. On a landscape level, urban planners should strive for greater connectivity between urban green spaces and peripheral areas to lessen the dominance of just a few synathropic species. Given the continuing trend of urbanization, it is imperative more ecological studies focus on urban environments so that we can begin forming better conservation strategies for metropolitan areas.

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Introduction

According to the US Census data, 50% of the United States population lives in the suburbs, while another 30% are city dwellers. Over 5% of the total surface area of the United States is covered by urban and other built-up areas (USCB 2001). This is more land than is covered by the combined total of national and state parks and areas preserved by the Nature Conservancy. Furthermore, the growth rate of urban land use in the United States is accelerating faster than the rate of land being preserved in the form of parks or as conservation areas (McKinney 2002). This is just a small part of a much larger global trend. Urbanization is increasing worldwide (United Nations Population Division 2005) and more than 87% of the Earth's land surface is not currently protected (Winfree, Griswold, and Kremen 2007). Human dwellings and infrastructure may occupy between 2.5 and 6 percent of the Earth, with approximately 10 percent of this area covered with impervious surfaces (Meyer and Turner 1992). As the population of humanity continues to grow it will become increasingly important for conservation efforts to understand and manage these built environments to maximize their ability to sustain biodiversity.

Recent trends in conservation biology and urban ecology such as countryside biogeography (Daily, Ehrlich et al. 2001) have lead to a proliferation of studies that explicitly investigate species' use of human-dominated habitats, as opposed to assuming that these habitats are inhospitable, as does more traditional studies based in the theory of island-biogeography. Many of these studies have discovered that anthropogenic habitats can support more species than had been previously assumed (Gascon, Lovejoy et al. 1999). For example, results from studies in a mosaic landscape of farms and forests in Costa Rica show that at least half of moth, mammal, butterfly, bird, and herbaceous and shrubby plant species commonly inhabit human-dominated habitats (Ricketts 2001; Mayfield et al. 2005; Mayfield and Daily 2005)

Pollinating insects, and bees in particular, are ideal for studying the impact of human influences on biodiversity. Bees represent a relatively speciose taxa and are therefore well suited for biodiversity analyses (Brosi 2007). Bees are considered keystone species whose disappearance could result in cascading effects throughout an ecosystem (Kevan 1991, LaSalle & Gauld 1993). They are also the most important pollinators for agricultural production (Klein 2007). The conservation of wild bee communities has gained prominence in light of the continued collapse of managed honey bee colonies in the United States and the putative "global pollination crisis" (Allen-Wardell et al. 1998, Kearns et al. 1998, Ghazoul 2005, Steffan-Dewenter et al. 2005, Biesmeijer et al. 2006, Potts et al. 2010).

Urbanization has a range of potential negative and positive impacts on bee communities. Large expanses of impervious surface in urban areas reduces and fragments the area available for plants and animals. A study that analyzed 130 effect sizes from 54 published studies recording bee abundance and/or species richness as a function of human disturbance found that both bee abundance and species richness were significantly, negatively impacted by habitat loss and fragmentation (Winfree et al. 2009). Over 80% of most downtown urban areas are covered by pavement and buildings (Blair and Launer 1997). Several studies have found that smaller urban habitat fragments have lower bee species diversity than larger urban fragments. (Cane et al. 2006; Viana et al. 2006; Nemésio and Silveira 2007; Hinners 2008). Impervious surface usually displaces the floral resources of an area, lowering the amount of pollen and nectar available to bees. Additionally, sealing the soil surface may impact ground nesting bee species and the vegetation removal could effect species that utilize trees for foraging and nesting (Steffan-Dewenter et al. 2001).

Landscaping and maintenance of residential and commercial areas typically involves removal of shrubs and dead wood and an increase in grasses and herbs. This could have a negative impact on the diversity of pollinators, whose diversity tends to have a positive correlation with plant species-richness (Bascompte, Jordano et al. 2003). Past studies have found urban bee communities responsive to both floral diversity and floral abundance (Matteson 2007, Ahrné 2009, Kearns and Oliveras 2009).

Because urban community gardens, communal areas divided amongst individuals, can be embedded within highly developed areas they are prime locations to study these different types of anthropogenic forces on bee diversity and abundance (Matteson and Langellotto 2010). I studied bee communities in 30 community gardens in the metro Atlanta area over gradients of landscape characteristics (including canopy cover). I also examined the local characteristics of garden area, floral richness, and floral abundance. Based on the findings of past studies (Dauber 2003 et. al, Matteson 2007, Kearns and Oliveras 2009, Ahrné 2009), I hypothesized that floral abundance and diversity within a garden will be the largest determinate of bee biodiversity and abundance. I predicted that areas with more canopy cover will have more abundant and diverse bee communities. Determining the relative importance these various influences will aid in developing priorities for conservation strategies for urban areas.

Methods and Materials

Study Area

The study gardens fall within a 30x30 km area of Atlanta, Georgia, USA. Several studies have compared urban bee populations to those found in nearby natural or peri-urban environs (Ahrné 2009, McIntyre 2001). The city of Atlanta is distinctive in that possesses far more tree cover than most major U.S. cities (Watt & Gunther, 2010). This relative abundance of trees allows a gradient analysis of the effect of tree removal entirely within an urban context. This is crucial since there are a multitude of environmental changes that result from urbanization, many of which could impact diversity and abundance.

Site Selection

I chose 30 community gardens that were dispersed throughout Metro-Atlanta (Table 1, Fig. 1). These sites were located making extensive use of online databases and correspondence with Atlanta organizations involved in community garden promotion. The number of purported gardens was greater than the actual number found. If these site locations are non-representative of the totality of community gardens, then I believe it results from a bias in the documentation of gardens. Sites were located a minimum of 500 m apart and at least 500 m from all known managed honey-bee colonies. The 500 m distance was chosen because it corresponds to the typical foraging distances of many bees (Gathmann and Tscharntke 2002; Greenleaf et al.2007).

Bee Sampling

During May-July 2010, I sampled foraging bees 4-5 times per site using aerial netting. I divided each garden into 10x10 m areas and employed a random number generator to select the sampling area for each site visit. Each netting session consisted of aerially netting bees for a 20-min period, between 8:00 and 14:00 hours. I rotated the temporal order that each site was visited during sampling days. To minimize collection bias, bees were netted in the order seen. No sampling occurred on days with precipitation or high winds.

Specimen Processing and Identification

I pinned all sampled bees and identified bee specimens in the laboratory to the finest taxonomic level possible following the nomenclature of Michener (2000). Additionally, representative specimens were selected for DNA barcoding. These specimens were photographed and a single leg removed and placed in a 96-well plate. These plates were then shipped to the University of Guelph where DNA extraction, amplification and sequencing took place according to the standard laboratory procedures followed at the Canadian Centre for DNA barcoding (CCDB, www.dnabarcoding.ca). These representative specimens in conjunction with the Barcode of Life Data Systems (BOLD, www.barcodinglife.org) allowed for augmentation and confirmation of the identification based on morphology. When lack of taxonomic treatments prevented identification to species, I used morphospecies designations that were constructed using specific characters in conjunction with DNA barcoding data.

Measuring Garden Attributes

I measured impervious surface area and canopy cover surrounding each site with data compiled by the Natural Resources Spatial Analysis Laboratory (NARSAL, http://narsal.uga.edu), using ArcGIS (ESRI, Redlands, CA, USA). I calculated total impervious and total canopy area via area percentages within a 500 m radius surrounding each garden. I quantified the total area of each garden using georeferenced orthographic photos combined with ground measurements.

I performed a complete census of all flowering plants on the second and fourth visit to each garden. All of the flowering plants were identified to at least the generic level and a majority were identified to the species level. The individuals identified only to the genus level should have a minimal impact on species diversity analyses because human cultivation typically results in garden plants that are different varieties of a single species rather than completely unique species. Because gardens varied in area, I measured flowering plant attributes in terms of density to prevent confounding with area effects.

Data Analysis

I tested the effect of total canopy area, total impervious surface area, floral diversity, floral density, and garden size on bee richness and abundance. Because the samples are count-based, I used generalized linear models assuming a poisson probability distribution. I found that impervious surface and canopy cover were highly correlated ($r = -.92$; Table 3). Therefore, I ran separate GLM models for both variables. I used a permutational MANOVA (McArdle and Anderson 2001, Anderson 2001) to investigate the effect of my explanatory variables on community structure using the Bray-Curtis index of dissimilarity. I used Moran's *I* and Mantel tests to measure possible spatial autocorrelation. For all analyses, I pooled all observations within sites to avoid pseudoreplication.

I analyzed data using the R statistical programming language (R Development Core Team, 2008), using the “vegan” package (Oksanen et al., 2006) for community ecological analyses, and the “ape” package (Paradis E., Claude J. & Strimmer K. 2004) for calculating Moran’s I.

Results

Overview

I sampled 1138 bees in four families, 11 tribes, 16 genera, and 28 species (species list in Table 2). The four most abundant bee species accounted for ~75% of sampled individuals: *Xylocopa virginica* (~39%), *Bombus impatiens* (~16%), *Bombus citrinus* (~11%), and *Bombus pensylvanicus* (~9%). Bee communities were not spatially autocorrelated (p = .911). Likewise, bee diversity did not show any pattern of spatial autocorrelation. Bee abundance was marginally spatially autocorrelated (Moran’s I = −-.069, p = 0.0507). However, I made the assumption that sites represented independent samples for all subsequent analyses.

Community Composition

The multivariate matrix permutation tests showed no correlation between bee community composition floral species richness, floral density, canopy cover, or impervious surface. Univariate tests also showed no relationship between community dissimilarity and floral diversity (F=1.36, p=.183), floral density (F=1.07, p=.40). Impervious surface and canopy cover were marginally significant but their corresponding p values never dropped below .08 in any of the tested combinations of variables.

Bee Richness and Abundance

Bee species richness and abundance displayed high variability between sites (Table 1). Generalized linear models (GLMs) showed that canopy area, impervious surface, floral density, floral richness, and garden area are all significantly and positively related to bee abundance (Table 4; Table 5; Fig. 2). For bee species richness, canopy cover was marginally negatively related (p=.08; Table 5; Fig. 3). I tested the influence of extreme values on this model and these significant relationships persisted even when outlying values were excluded from analyses.

Because *X. virginica* represented almost 40% of specimens I ran GLMs on the abundance of *X. virginica* and on bee abundance excluding *X. virginica* (Table 6). *Xylocopa* abundance showed a significant positive relationship with canopy area, floral density, floral richness, and garden area. However, bee abundance excluding *X. virginica* only showed a significant positive relationship with floral density.

Discussion

The bee assemblages sampled in this study were dominated by the generalist species *X. virginica*, *B. impatiens*, and *B. pensylvanicus*. Many urban bee surveys indicate 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). Cane (2006) found community shifts from specialist to generalist along gradients of increasing urbanization in Tucson, Arizona. As urban development replaces native or remnant habitat, native plants are replaced by non-native or horticultural plant species (Frankie et al. 2009). *B. citrinus* is a social parasite of *B. impatiens* and may be indirectly benefiting from this trend. Generalist bee species with broad tolerances appear to be favored in urban areas, while specialists suffer from the absence of their host plants and decrease in abundance. The lack of a significant relationship between bee abundance excluding *X. virginica* and floral diversity seems to counter this explanation. However, this may be because the most sensitive specialist species have already been locally extirpated from the developed neighborhoods of this study, as has been suggested for insect taxa in other cities (Kozlov 1996; Connor et al. 2003).

The positive relationship between bee abundance and floral richness and density are consistent with the findings of previous studies (McFrederick and LeBuhn 2006, Matteson 2007, Kearns and Oliveras 2009). The positive relationship between canopy cover and bee abundance is also commensurate with several other urban bee studies (Eremeeva 2004, Zanette et al. 2005, Matteson 2007). The significant effect of surrounding canopy cover and the lack of relationship between garden area and bee abundance in several of the GLMs suggests that urban green spaces cannot be treated as insular islands.

The GLMs appear to indicate that *X. virginica* are driving these patterns of abundance. The predominance of *X. virginica* likely results from its nesting habits in addition to its generalist character. *X. virginica* excavate nests in woody plant material such as dead branches, stalks, or stumps (Gerling et al., 1989). This may explain the relationship between greater canopy cover and greater abundance. However, *X. virginica* can also nest in wooden structures that accompany human settlement, for instance, the structural timbers of buildings. Bee species that nest in aboveground cavities have an advantage over ground-nesting species within urban environments. Urbanization often degrades nesting habitat for ground-nesting bees by transforming surface soil through landscaping or conversion to impervious surface. Several studies report higher abundance of cavity-nesting bee species in urban areas when compared to less developed areas (Cane 2005; Zanette et al. 2005; Cane et al. 2006; Hinners 2008; Matteson et al. 2008). Matteson et al. (2008) found an increase in cavity nesters in urban community gardens comparative to natural habitats.

These cavity-nesters might be so well suited for urban land conversion that they are competitively excluding other species of bees. This could explain the negative relationship seen between species richness and canopy cover. The fact that bee abundance excluding *X. virginica* was significantly related to floral density supports this notion of competitive exclusion. Increases in floral density increases food resources, lessening competition pressure.

Human influence has traditionally been presented in the literature in the form of an external force perturbing a “pristine” environment (Daily 2001, Daily et al. 2001). This conceptual framework is ill suited for human-dominated landscapes. Assuming that human action uniformly depresses the diversity and abundance of species within an ecosystem dismisses the possibility that the conservation value of urban environments can be increased through human decisions. In fact, many studies have found increases in bee diversity when comparing urban to native habitat (Cane 2006, Pawlikowski and Pokorniecka 1990, Winfree et al. 2007). This may be due to an increase in habitat heterogeneity that accompanies urbanization (Benton et al. 2003).

The positive relationship between floral density and bee abundance indicates that urban bee communities can benefit by increasing food supply through continuous management for areas with rich supply of flowering plants. Additionally, efforts should be made to increase floral diversity. This could be easily done in urban gardens by leaving a portion of garden unmanaged. This would increase flowering plants typically viewed as weeds and may benefit ground-nesting bees. Emphasis should also be placed on planting native species since they have been found to be more attractive to native bees (Frankie et. al 2005) and to increase total bee diversity (McIntyre 2001). The site with the highest abundance and richness within this study had a portion of the garden devoted to native plant species. Conservation efforts should not ignore the importance of these community allotment gardens. They typically display higher levels of floral diversity than most other urban green spaces due to the high number of gardeners with different flower preferences within each allotment area (Matteson and Langellotto 2010).

On a landscape level, urban planners should focus on improving colonization abilities by increasing connectivity among urban green spaces. Increased connectivity among suitable habitats within the landscape would increase the probability for females to find their way to breeding, nesting, and food sources. Greater connectivity with the less developed areas surrounding cities may enhance the ability of more sensitive species to persist in the presence of the synanthropic species that currently dominate.

Generalizations should not be extended over all urban environments. Metropolitan areas grow within particular historical and ecological contexts that may differ widely. Cities can differ in age, climate, geographic dispersion, or any number of factors that could affect how bee communities respond to different anthropogenic forces. Only through teasing apart the multifarious components of urban environments can we distill the relationships between human decisions and the physical components of human-dominated ecosystems in order to craft informed conservation strategies.

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Table 1: Summary data of bee sampling by site

Site Name	#	Bee Richness	Bee Abundance	Floral Richness	Floral Density	Area	Canopy Cover (m^2)
Anderson	1	2	12	9	3.36	103.27	78502.91
Boulevard	2	8	35	14	2.34	235.39	17907.46
Breakthru	3	4	6	7	0.48	113.5	69081.99
Brownwood	4	5	13	10	1.15	104.87	63162.85
Cabbagetown	5	10	54	24	6.49	111.3	15211.89
Four.Corners	6	7	36	7	1.3	106.5	33003.19
Gilliam	7	6	26	13	5.07	275.65	41340.65
Isaiah	8	6	69	18	3.51	297.14	90169.92
Kimpson	9	10	15	12	3.73	111.21	33409.4
Kirkwood	10	6	25	14	6.12	120.74	64675.44
Little.Nancy	11	4	29	9	5.13	193.75	103643.41
Mason Mill	12	9	31	22	1.36	486.76	71631.63
Mulberry.Fields	13	10	56	21	1.94	413.77	51563.47
Peachtree.Hills	14	9	56	24	4.98	321.28	92925.09
Poncey-Highland	15	11	40	20	6.12	501.01	28296.22
Rosa.Burney	16	8	37	5	0.91	420.1	10835.89
Scott	17	13	105	18	6.17	500.86	66550.11
Tobie.Grant	18	8	25	11	0.86	477.89	76146.57
EEC	19	8	32	11	0.46	397.91	67388.05
Dunwoody	20	6	46	20	2.3	841.95	68935.36
Edgewood	21	12	38	14	4.81	372.63	51563.47
Columbia	22	10	68	13	2.14	279.89	102634.17
Arcadia	23	8	63	18	3.71	145.49	60829.43
Mother.Clyde	24	6	14	14	2.45	427.08	50426.37
Mableton	25	6	28	21	1.89	965.82	58914
Avondale	26	5	54	9	3.95	219.04	88123.96
Dekalb	27	7	11	19	1.18	346.23	66569.59
Henderson	28	8	44	22	6.94	477.92	94431.48
Rose Circle	29	7	28	10	3.94	112.45	44907.46
Sullivan	30	12	42	14	1.77	512.23	47667.11

Table 2: Species summary list.

Family	Tribe	Genus	Species	No. Specimens
Apidae	Xylocopini	*Xylocopa*	*virginica*	445
	Bombini	*Bombus*	*impatiens*	182
			citrinus	120
			pensylvanicus	100
			griseocollis	1
			sp.	4
	Emphorini	*Ptilothrix*	*bombiformis*	47
		Melitoma	*taurea*	1
	Apini	*Apis*	*mellifera*	29
	Ceratinini	*Ceratina*	*calcarata*	7
	Eucerini	*Melissodes*	*bimaculata*	16
		Peponapis	*pruinosa*	7
		Svastra	*obliqua*	1
	Epeolini	*Triepeolus*	*remigatus*	1
Halictidae	Halictini	*Halictus*	*poeyi*	51
			confusus	9
			ligatus	2
			sp.	1
		Agapostemon	*virescens*	29
	Augochlorini	*Augochloropsis*	*metallica*	1
Megachilidae	Megachilini	*Megachile*	*exilis*	27
			campanulae	22
			mendica	19
			rotundata	4
			sp.	1
			sp.	1
		Coelioxys	*sayi*	1
Colletidae		*Colletes*	*Latitarsis*	2

Table 3: Pearson product-moment correlation coefficient for explanatory variables. (*) indicates statistical significance.

	Canopy	Impervious	Size	Floral Richness	Floral Abundance
Canopy Cover	1	-0.92*	0.07	0.09	0.06
Impervious	-0.92*	1	-0.2	-0.08	0.02
Size	0.07	-0.2	1	0.46*	-0.14
Floral Richness	0.09	-0.08	0.46	1	0.39*
Floral Abundance	0.06	0.02	-0.14	0.39*	1

Table 4: Garden characteristics and bee relative abundance and species richness. (*) indicates significant relationship. For both models df=24 (30 sample sites)

	Bee Abundance		Bee Richness	
	z	p	z	p
Floral Richness	3.4	6.74E-004*	1.3	0.21
Floral Density	4.78	1.72E-006*	0.49	0.62
Garden Size (m2)	1.79	7.28E-002*	0.62	0.58
Canopy Cover (m2)	2.44	1.46E-002*	-1.76	0.12

Table 5: Garden characteristics and bee relative abundance and species richness. (*) indicates significant relationship. For both models df=24 (30 sample sites)

	Bee Abundance		Bee Richness	
	z	p	z	p
Floral Richness	4.37	1.27E-005*	1.19	0.23
Floral Density	4.88	1.04E-006*	0.47	0.64
Garden Size (m2)	0.78	0.44	0.79	0.43
Impervious Surface (m2)	-2.37	0.018 *	1.75	0.08

Table 6: Garden characteristics and *Xylocopa* abundnace and bee abundance excluding *Xylocopa* (*) indicates significant relationship. For both models df=28 (30 sample sites)

	Xylocopa Abundance		Bee Abundance excluding *Xylocopa*	
	z	p	z	p
Floral Richness	4.91	8.97E-007*	0.61	0.54
Floral Density	4.92	8.63E-007*	2.15	0.03*
Garden Size (m2)	2.12	3.41E-002*	0.59	0.56
Canopy Cover (m2)	4.29	1.75E-005*	-0.33	0.74

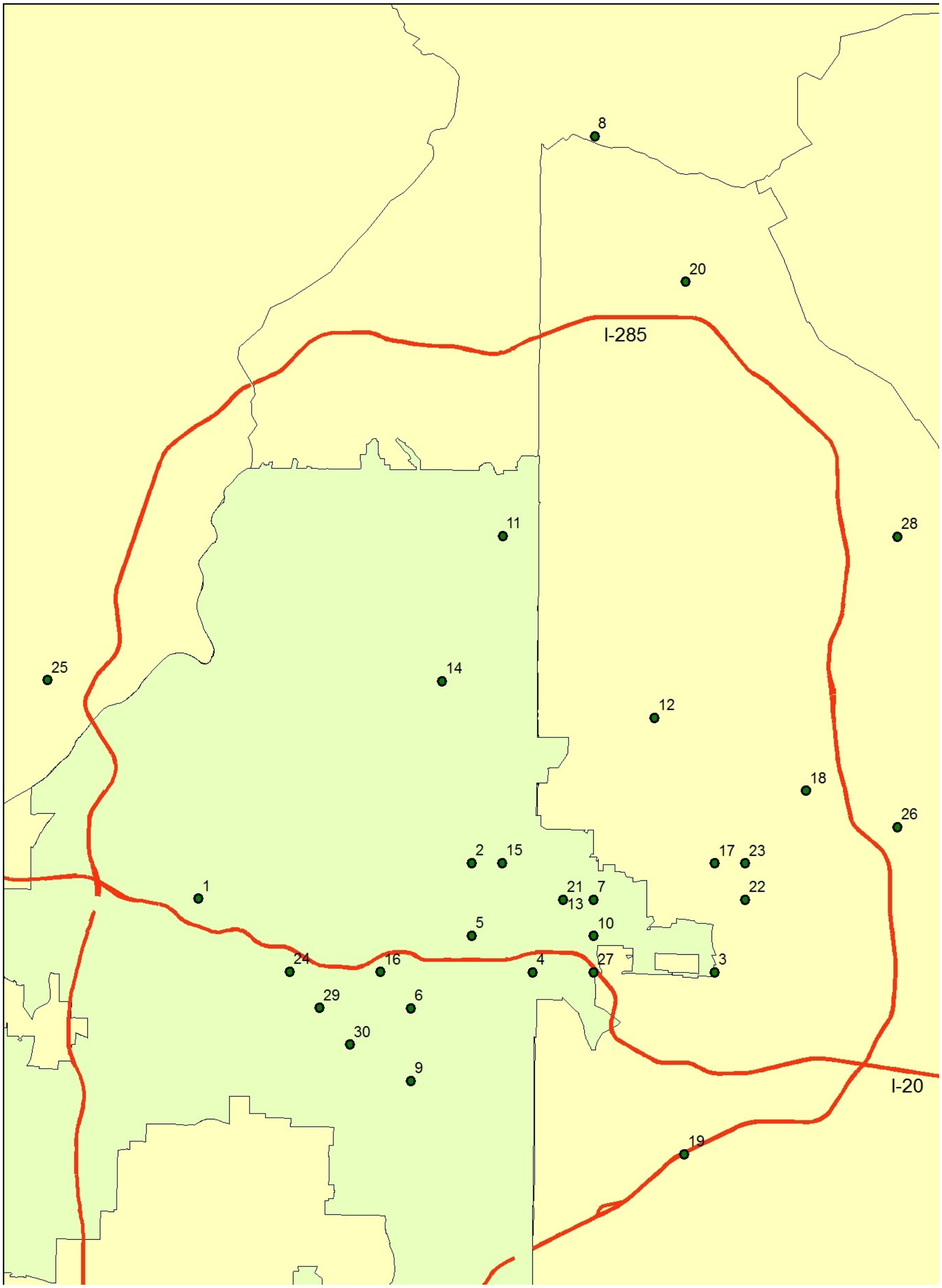

Figure 1: Map of the spatial orientation of sites. Green area represents the city limits of Atlanta. Numbers correspond to site # in table 1.

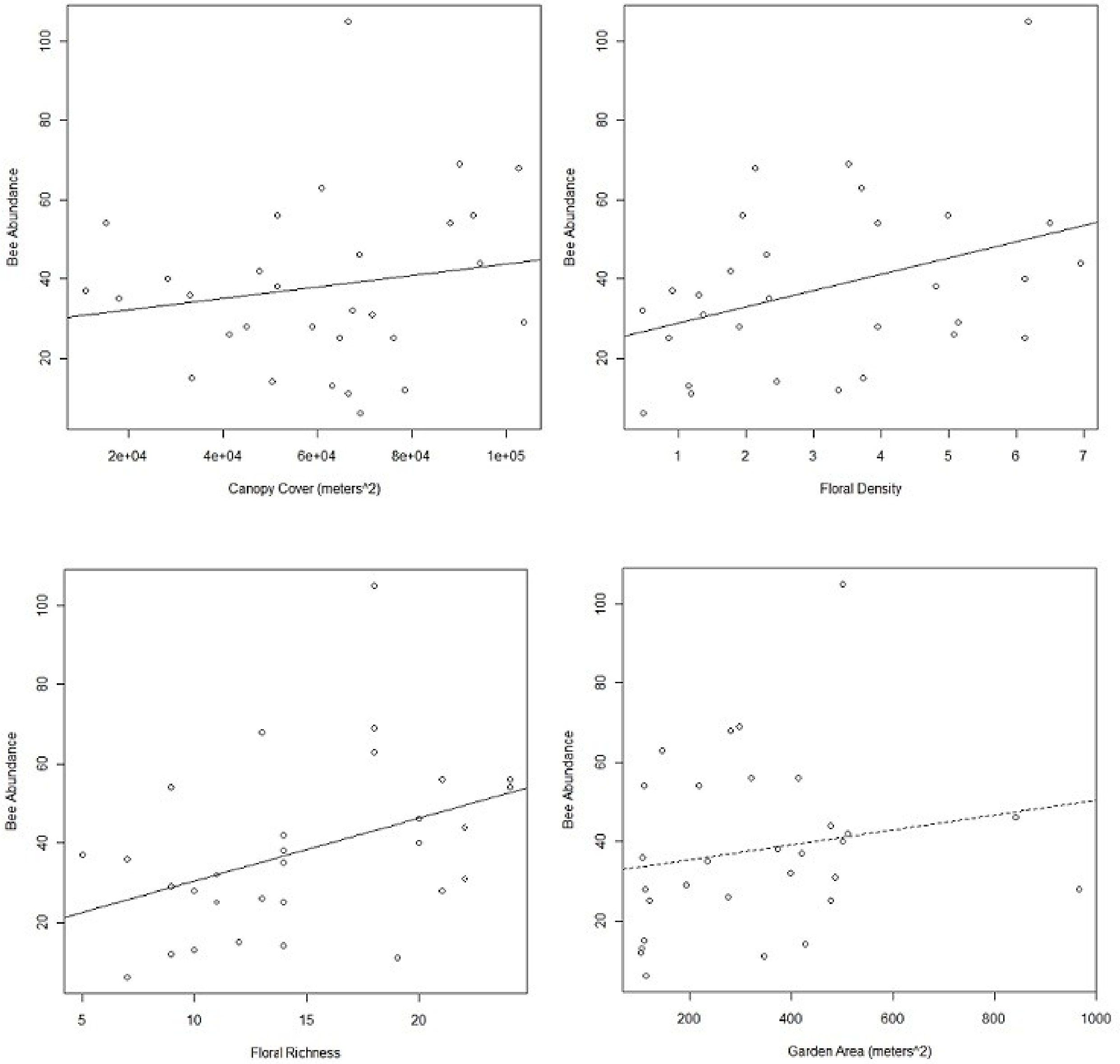

Figure 2. Relationships between bee abundance and canopy cover, floral density, floral richness and garden area. Lines are linear regression fit to show basic relationships. Solid lines indicate significant relationship while dotted lines show non-significant relationships.

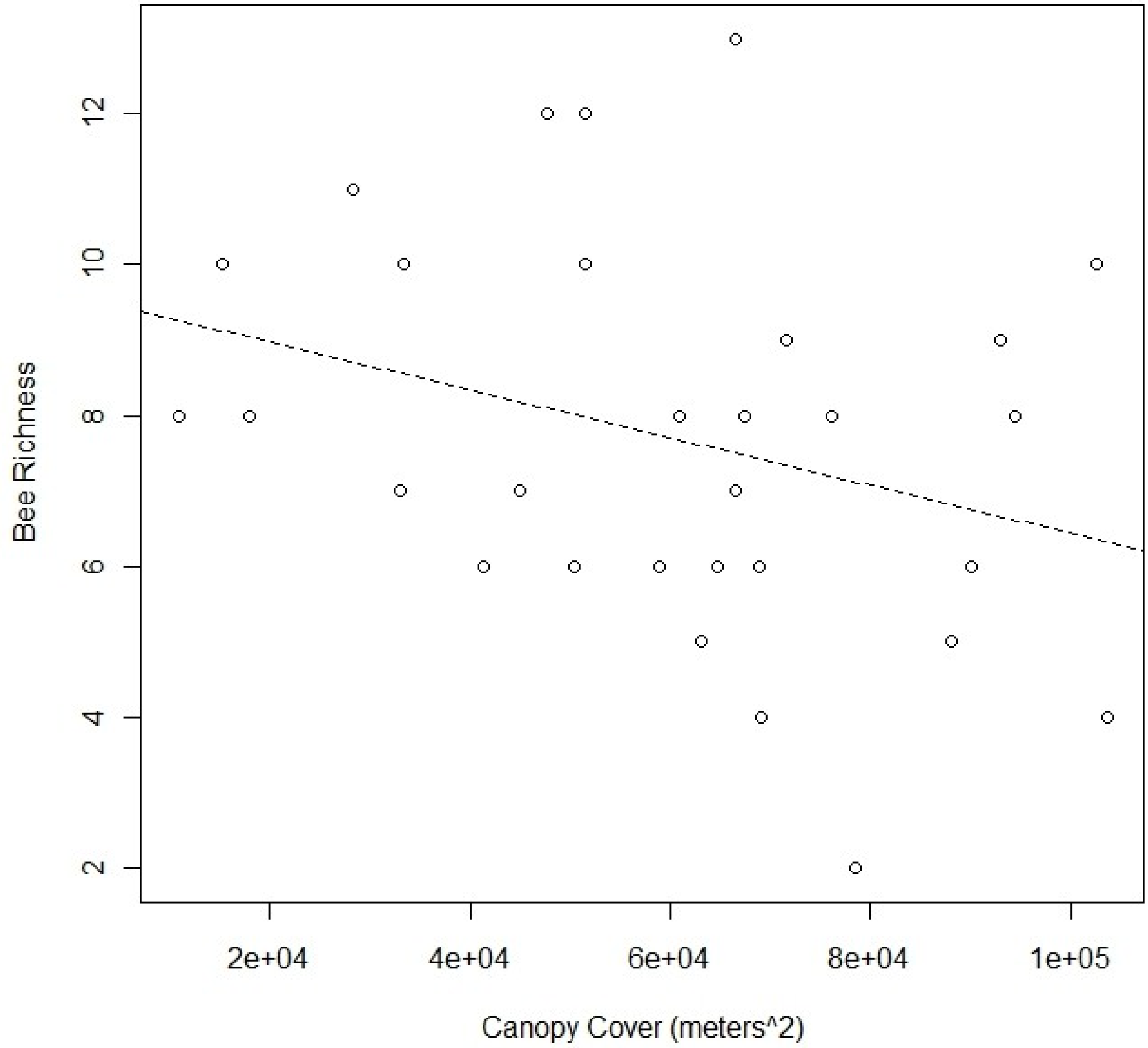

Figure 3. Relationship between bee richness and canopy cover. The dotted line represents linear regression fit to indicate the directionality of the marginally significant relationship.