

Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape

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Although urban areas are often considered to have uniformly negative effects on biodiversity, cities are most accurately characterized as heterogeneous mosaics of buildings, streets, parks, and gardens that include both ‘good’ and ‘bad’ areas for wildlife. However, to date, few studies have evaluated how human impacts vary in direction and magnitude across a heterogeneous urban landscape. In this study, we assessed the distribution of floral resources and flower-visiting insects across a variety of land uses in New York City. We visited both green spaces (e.g. parks, cemeteries) and heavily developed neighborhood blocks (e.g. with high or low density residential zoning) and used structural equation modeling (SEM) to evaluate the direct and indirect effects of median income, vegetation, and development intensity on floral resources and insects in both settings. Abundance and taxonomic richness of flower-visiting insects was significantly greater in green spaces than neighborhood blocks. The SEM results indicated that heavily-developed neighborhoods generally had fewer flower-visiting insects consistent with reductions in floral resources. However, some low-density residential neighborhoods maintained high levels of floral resources and flower-visiting insects. We found that the effects of surrounding vegetation on floral resources, and thus indirect effects on insects, varied considerably between green spaces and neighborhood blocks. Along neighborhood blocks, vegetation consisted of a mosaic of open gardens and sparsely distributed trees and had a positive indirect effect on flower-visiting insects. In contrast, vegetation in urban green spaces was associated with increased canopy cover and thus had a negative indirect effect on flower-visiting insects through reductions in floral resources. In both neighborhood blocks and green spaces, vegetation had a positive direct effect on flower-visiting insects independent of the influence of vegetation on floral resources. Our results demonstrate how inter-related components of an urban ecosystem can vary with respect to one another across a heterogeneous urban landscape, suggesting that it is inappropriate to generalize about urban systems as a whole without first addressing differences among component land use types.

The impacts of humans on landscape structure are perhaps most evident in cities. While ecological studies have often focused on the negative impacts of urbanization on biodiversity (Czech et al. 2000, McKinney 2006), cities are often located in biologically diverse areas (McDonald et al. 2008) and may contain large and/or regionally important natural features (Barthel et al. 2005). In addition, small human-created habitats such as gardens may contribute significantly to biodiversity in cities (Loram et al. 2007, Owen and Owen 1975). Thus, cities are most accurately characterized as fine-scale, heterogeneous mosaics of buildings, streets, parks, gardens and other green spaces (Cadenasso et al. 2007) that include both ‘good’ and ‘bad’ areas for wildlife. Across cities, biophysical factors that exert positive or negative effects on wildlife (e.g. building density, resources associated with surrounding vegetation) may be consistent across some neighborhoods (Warren et al. 2008) but can also rapidly shift, reflecting abrupt transitions in land use and zoning (Grimm et al. 2008).

Studies of urban ecology have commonly focused on ‘green spaces’ (e.g. cemeteries, parks, gardens), excluding more developed areas within cities (Pickett and Cadenasso 2008). However, evaluating biotic communities in commercial and residential neighborhood blocks is important because this is where humans spend most of their time, where most interactions with nature occur, and where most ecosystem services are likely to be actualized on a daily basis. Biodiversity has been shown to be inequitably distributed across cities (Turner et al. 2004), potentially due to fine-scale variation in vegetation and other biological resources. These differences are especially evident when comparing green spaces (e.g. parks, cemeteries) to residential/commercial neighborhoods, suggesting that factors affecting biotic communities may vary for these two land use types. In addition, there may be variation within each land use type. For instance, relative to single-family residential blocks, neighborhoods zoned as multi-family residential are characterized by tall buildings, which may obstruct

movement (Sneep et al. 2006) and increase mortality of some species, or which may have indirect effects by altering floral composition (Marco et al. 2008). Variation in socioeconomic factors also may play a role in structuring biotic communities in residential landscapes, as seen in positive associations between median household income and plant diversity (Hope et al. 2003). In both green spaces and developed neighborhoods, variation in the amount and types of vegetation (e.g. tree canopy and herbaceous cover) may affect nesting or feeding resources for wildlife.

A number of studies conducted in discrete urban habitats (e.g. city parks, meadow remnants, community and private gardens) have affirmed the importance of floral resources for floral-feeding insects such as bees (reviewed by Cane 2005, Hernandez et al. 2009). However, few studies have sampled across the spectrum of urban habitats, including residential, commercial, and different types of green spaces, to enable an evaluation of the effects of land use heterogeneity on biotic communities within cities (but see recent works of Hennig and Ghazoul 2011, Sattler et al. 2010, Wojcik 2011). In addition, while some studies have evaluated the impact of surrounding buildings, impervious surface, and green space on insects, few have identified specific mechanisms that underlie species-habitat relationships. This point is important because a negative impact of surrounding impervious surface on bees, for example, could be due to a variety of mechanisms such as reductions in gardens and/or floral resources (McFrederick and Lebuhn 2006), decreased nesting sites (Ahrné et al. 2009), and/or increased shading due to proximal buildings (Matteson and Langellotto 2010). Identifying the mechanisms responsible for any negative effects of urban land use is an important first step towards mitigation and effective conservation within urbanized landscapes.

The goal of this study was to identify proximate and ultimate determinates of the distribution of both floral resources and flower-visiting insects across a heterogeneous urban landscape. We quantified the presence of herbaceous flowering plants and flower-visiting insects (e.g. Diptera, Coleoptera, Lepidoptera, Hymenoptera) across a wide range of urban green spaces and residential and commercial blocks. We were specifically interested in the direct and indirect effects of development intensity and vegetation on floral resources and flower-visiting insects, and how these might vary between urban green spaces (with more vegetation and few proximal influences of built structures) and neighborhood blocks (with much less vegetation but more proximal buildings and other factors associated with development). To test these relationships, we used the analytic framework provided by structural equation models (SEMs). These models allowed us to explicitly examine the effects of human land use and floral resources on insect distributions in both neighborhood blocks and urban green spaces (Fig. 1). To our knowledge, this is the first study to evaluate direct and indirect effects of human land use on biotic communities across a highly heterogeneous and urbanized landscape.

Methods

To evaluate direct and indirect influences on flower-visiting insects in different urban habitats, we 1) quantified floral and insect distributions on transects across New York City, 2) used GIS with various spatial data sets to measure potential explanatory variables, and 3) evaluated relationships among variables using a SEM framework for both green spaces and neighborhood blocks. Because our sampling

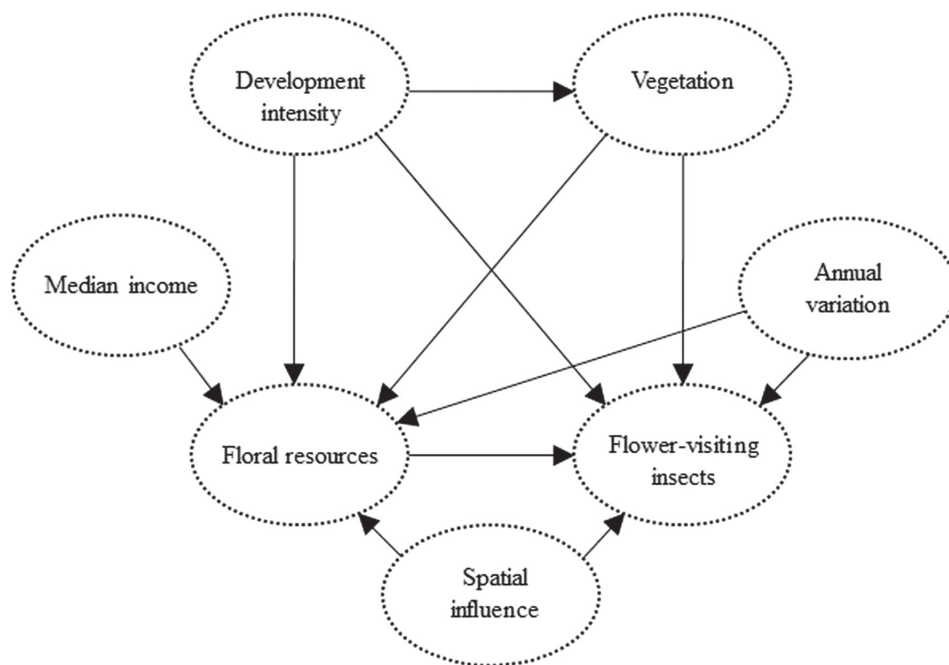


Figure 1. Original conceptual model for the relationship between floral resources and flower-visiting insects in urbanized landscapes. The link between floral resources and flower-visiting insects is well established. It is less certain how the other variables interact and influence flower-visiting insects directly or indirectly in urbanized landscapes.

design involved quantifying insects in heavily-populated neighborhoods, where fences and high levels of human disturbance are common, it was not possible to consistently collect insects using traditional methods (e.g. bowls and hand-netting). Therefore, we used a combination of visual identification, image capture, and specimen collection in this study.

Transect sampling

Floral resources and flower-visiting insects were quantified on 97 150 × 6 m transects in all five boroughs of New York City (Fig. 2). The 6 m width of the transect was chosen to include most flowers in front yards. Because most transects had few floral resources, quantification was not difficult. Sampling effort was also scaled to floral area along transects, enabling more time to evaluate pollinator abundance and richness on transects that had

denser floral resources. On each sampling day, we visited a wide variety of land use types in the city (e.g. city parks, high- and low-density residential). Transects were deliberately chosen so that all five boroughs of New York City and a variety of lands uses and human population densities were included. We had no prior knowledge of local floral resources or pollinator communities in the sampling locations. Transects were a minimum of 50 m from each other (mean nearest neighbor for green spaces = 453 m, range = 54 to 11 041 m; mean nearest neighbor for neighborhood transects = 248 m, range = 98 to 779 m). In total, 45 transects crossed through green spaces, including parks and cemeteries, while the remaining 52 transects crossed through residential and/or commercial neighborhoods. In green spaces, transects were located along paths, allowing sampling of adjacent habitats. If a path turned before reaching the 150 m sampling distance, we randomly choose a direction to turn and continued

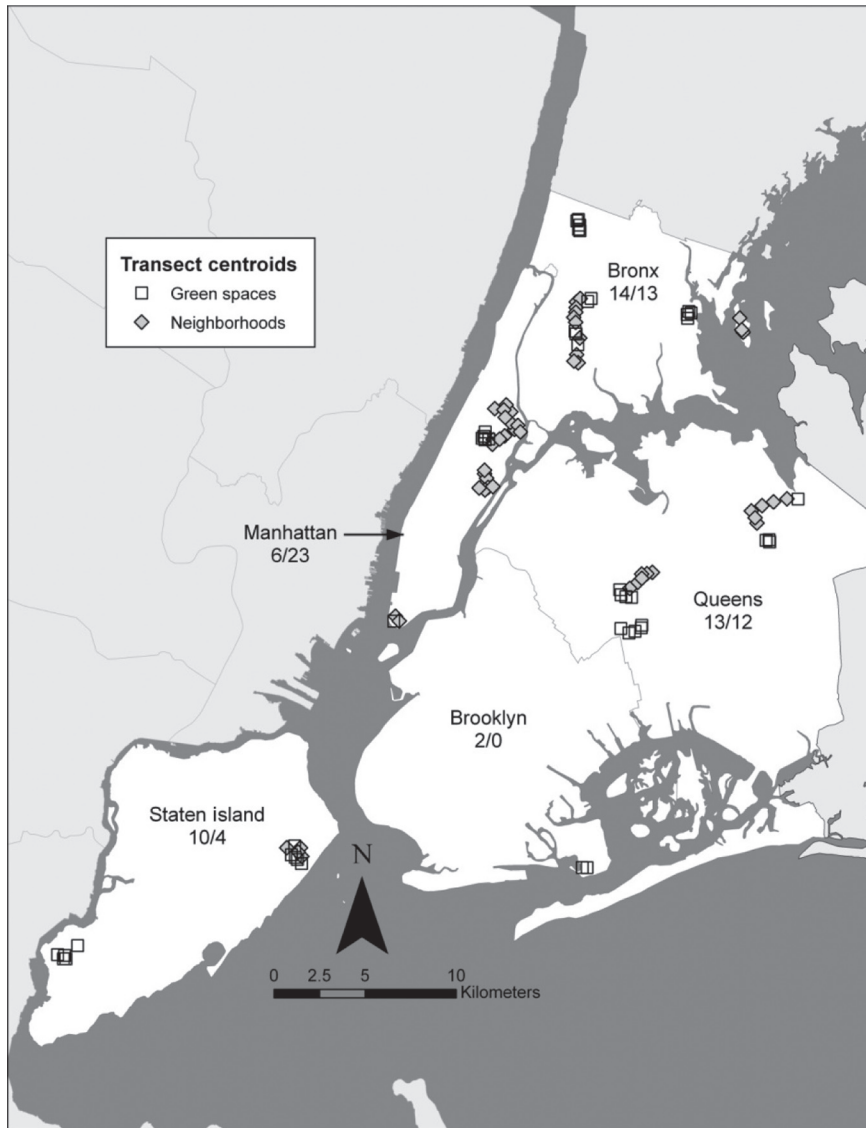


Figure 2. Map showing the centroid of 45 transects in green spaces and 52 transects in neighborhood blocks that were sampled for floral resources and insects in New York City. The five boroughs in New York City are white and labeled; numbers underneath borough names indicate the number of transects (green space/neighborhood) in each borough. Dark gray areas are water.

until 150 m was reached. All locations were sampled once between 10:00 and 15:00 on warm sunny days (21–27°C) between 15 July and 15 August in 2008 (seven transect sampling dates) and 2009 (four transect sampling dates), with different transects sampled each year to maximize sample size.

Transects were slowly walked at a uniform pace and any potential pollinators within transects were identified and recorded. Bees, flower flies and butterflies were recorded regardless of whether or not they landed on a flower. Other insects (non-Syrphid Diptera and all Coleoptera) were only counted if they were observed on a flower. The transect method employed is similar to standardized ‘Pollard’ walks used for butterfly monitoring (Pollard 1977). A difference, however, is that to facilitate identification of small insects, a 15-s observation was also conducted at any square meter within the transect having more than two flowers in bloom (‘flower sampling point’). At each flower sampling point, we recorded all flowering shrubs and herbaceous plants and took digital images to enable later identification to the lowest taxonomic level possible. Many plants in urban landscapes are cultivars or hybrids for which a species name does not exist (e.g. rosa ‘Henri Martin’) and for which taxonomic classification is challenging. For this reason, and to avoid giving weight to more easily identified taxa, identifications were standardized at the level of genera for our measure of floral richness. For flower identification, we used Peterson and McKenny (1996) and American Horticultural Society (2002). We quantified both abundance and taxonomic richness of floral resources on each transect. Floral abundance was measured as the total number of flower sampling points and floral richness was the number of unique genera per transect. Because the spatial distribution of flowers has been postulated to influence bees and other pollinating insects, we evaluated the spatial distribution of floral resources along transects by calculating the greatest linear distance between adjacent flower sampling points

(‘maximum floral gap’). Maximum floral gap was set at 150 m if there were no flower sampling points along the transect and 75 m if the transect had a single flower sampling point.

It was not possible to consistently net insects along all transects due to fences or lack of permission to sample from some sites. Therefore, insects landing on a flower head (anthers and/or stigma) were identified in the field to the lowest taxonomic level possible by KCM, who has extensive experience in this system (Matteson et al. 2008, Matteson and Langellotto 2010). While species- or genus-level determinations were possible for some groups in the field, we ultimately derived a measure of taxonomic richness based on 13 insect groups that could be visually differentiated without destructive sampling (Table 1). We choose these groups so as to not give extra weight to more easily identified groups (e.g. butterflies). However, we also collected insects opportunistically in the field and took digital images of others to enable later identification to species-level and to provide a complete list of species or genera observed across the study system (Appendix 1).

GIS variables

Previous work in this system indicated that local variables are more influential than landscape variables for explaining bee and butterfly species richness (Matteson and Langellotto 2010). In addition, initial analyses of Spearman’s correlations indicated that the proportion of canopy cover at a relatively small spatial scale (30 m) was generally more explanatory for flower-visiting insects than several larger spatial scales investigated (200, 350, 500 m; Appendix 2). Therefore, our SEM analyses evaluated the influence of vegetation (canopy and herbaceous cover) and development intensity in a 30 m buffer surrounding each transect. Vegetation was quantified as tree/shrub canopy cover (‘canopy cover’ hereafter) or herbaceous/grass cover (‘herbaceous cover’ hereafter) using a high-resolution map

Table 1. Flower-visiting insects encountered on 97 transects in green spaces and neighborhood blocks of New York City. The full list of species identified in this study is in Appendix 1.

Floral-visiting insect grouping	Order	Family/ super-family	Common genera/ species	Abundance (% of total)
Small bees (< 8 mm in length) [†]	Hymenoptera	Apidae, Colletidae, Halictidae	<i>Ceratina</i> , <i>Hylaeus</i> , <i>Lasioglossum</i>	347 (27%)
Bumble bees		Apidae	<i>Bombus impatiens</i> , <i>B. griseocollis</i> , <i>B. bimaculatus</i> , <i>B. citrinus</i>	197 (16%)
European honey bee		Apidae	<i>Apis mellifera</i>	147 (12%)
Other bees [‡]		Apidae, Andrenidae, others	<i>Xylocopa</i> , <i>Melissodes</i> , <i>Andrena</i>	118 (9%)
Leaf-cutter bees		Megachilidae	<i>Megachile</i>	56 (4%)
Solitary wasps [‡]		Sphecidae, Crabronidae	<i>Sphex</i> , <i>Isodontia</i> , <i>Cerceris</i> , <i>Philanthus</i>	67 (5%)
Social wasps [‡]		Vespidae	<i>Polistes</i> , <i>Vespula</i>	24 (2%)
Small flower flies	Diptera	Syrphidae	<i>Toxomerus</i>	62 (5%)
Flesh flies, house flies [‡]		Muscidae, Sarcophagidae	<i>Musca</i> , <i>Sarcophaga</i>	41 (3%)
Large flower flies		Syrphidae	<i>Syrphus</i> , <i>Eupeodes</i>	37 (3%)
Blow flies [‡]		Calliphoridae	<i>Phaenicia</i>	46 (4%)
Beetles [‡]	Coleoptera	Scarabidae, Mordellidae, others	<i>Popillia</i> , others	52 (4%)
Butterflies and diurnal moths	Lepidoptera	Pieridae, Nymphalidae, Lycaenidae, others	<i>Pieris</i> , <i>Vanessa</i> , <i>Celestrina</i> , <i>Melittia</i>	73 (6%)

[†]*Hylaeus* have distinctive white or yellow facial markings and, with practice, can be differentiated from *Lasioglossum* and *Ceratina* in the field. We grouped all three genera together because our sampling design did not involve closely inspecting small bees for facial markings.

[‡]*Xylocopa virginica* can be identified in the field but was included in this group because only nine individuals were observed in this study.

[‡]denotes opportunistic flower-feeders that were only counted if observed on a flower.

(pixel size = 0.81 m²) of New York City created by the USDA Forest Service, Northeastern Research Station (Myeong et al. 2001). We used Geospatial Modeling Environment (Beyer 2010) in conjunction with ArcGIS ver. 10 to quantify the amount of canopy cover and herbaceous cover in each 30 m transect buffer.

We also quantified several proxies of development intensity in 30 m buffers surrounding transects in developed neighborhoods. Human population density and median household income data were gathered from the US Census Bureau (United States Census Bureau 2006) at the spatial scale of census block groups. For transects that crossed block groups, we used an area-weighted mean to calculate each variable along the transect. We also measured building unit density and identified zoning classification (high- or low-density residential) from a 2001 municipal data set (Council on the Environment of New York City 2006). Building unit density was the total number of building units – including residential, commercial and office units – intersecting each 30 m buffer; this provided a proxy for the vertical and horizontal spatial extent of buildings in the vicinity of the transect (Matteson and Langellotto 2010). High-density, low-density, and commercial/mixed zoning types were classified according to the zoning of the majority of the lots (> 50% by area) in each transect buffer. Because there were no human residences in the green space transects (and thus very little variation in our measures of development intensity; Table 2), we did not analyze development intensity for the green space transects.

Structural equation modeling

We used structural equation modeling (SEM) to examine relationships among measured variables (Grace 2006). Classical SEM uses the variances and covariances in the dataset to test a series of linear relationships between variables. These relationships can be drawn as arrows between

Table 2. Measures of central tendency and dispersion for transects in green spaces and neighborhood blocks of New York City.

Variable	Green spaces (n = 45)	Neighborhood blocks (n = 52)
	Median (range)	Median (range)
Floral abundance	10 (0–41)	8 (0–37)
Floral richness	4 (0–19)	4 (0–20)
Maximum floral gap	74 (28–150)	74 (27–150)
Proportion canopy cover in a 30 m radius	0.53 (0.08–0.99)	0.06 (0.00–0.38)
Proportion herbaceous cover in a 30 m radius	0.26 (0.01–0.66)	0.03 (0.00–0.25)
Total building units in a 30 m radius	0 (0–6)	170 (13–1250)
Median household income	0 (0–0)	46 000 (11 500–94 800)
Population density per hectare	0 (0–0)	184 (18–870)
Insect abundance	9 (0–57)	2 (0–38)
Insect taxonomic richness	4 (0–10)	1.5 (0–8)

variables in a path diagram, providing an intuitive understanding of the hypotheses being tested. One advantage of this method is that it can explicitly examine both direct and indirect relationships between variables, thereby evaluating hypotheses about mediating factors. Another advantage is the ability to include latent variables to represent theoretical variables that cannot be measured directly. For example, floral resources are expected to be important to flower-visiting insects but it may not be precisely clear to which aspect of ‘floral resources’ insects are responding. We can therefore view floral abundance, richness, and spatial distribution as measures of a single latent construct that represents floral resources.

It is the usual convention in SEM to conceptualize that latent constructs are causes of the observed measured variables; therefore, arrows are directed outwards from the latent construct as seen in Fig. 3. It is then possible to evaluate a more general hypothesis by assessing relationships among latent variables, for instance, by testing whether the latent construct ‘development intensity’ (indicated by human population density, density of building units, and zoning type) influences the latent variables ‘vegetation’, ‘floral resources’ and ‘flower-visiting insects’.

We modeled the influence of development intensity, vegetation, and floral resources on insects using AMOS Graphics 17 (Arbuckle 2008), creating separate models for green-space transects and neighborhood transects. The initial model for green spaces included canopy and herbaceous cover (both indicators of the latent construct ‘vegetation’), floral richness, floral abundance and maximum floral gap along the transect (measures of ‘floral resources’), and flower-visiting insect taxonomic richness and abundance (as measures of the latent construct ‘flower-visiting insects’). Because bee and other insect populations can widely fluctuate through time (Roubik 2001) and because floral resources may vary annually as well, the year in which transects were surveyed (2008 or 2009) was also included in the initial model as possibly having a direct effect on ‘floral resources’ and ‘flower-visiting insects’. The initial model for neighborhood blocks included all of the above variables and the influence of the latent construct ‘development intensity’. In addition, to evaluate the effect of median income on floral resources, median income was included as a separate variable directly affecting floral resources.

All of the measured variables except median household income were highly skewed and/or kurtotic. Therefore, we used the arcsin square root transformation for the proportion of herbaceous and canopy cover, and the log₁₀ transformation for the remaining variables. These transformations increased linearity of relationships among variables and decreased skewness and kurtosis, but the variable set still failed to meet the assumption of multivariate normality (Shapiro–Wilks test for multivariate normality, $W = 0.88$, $p < 0.001$ and $W = 0.89$, $p < 0.001$, respectively for green spaces and neighborhoods). Consequently, after transforming variables we assessed model fit using the Bollen–Stine bootstrapping procedure, which is robust to data that are not multivariate normal (Bollen and Stine 1992). In SEM, overall goodness of fit is commonly evaluated using a model χ^2 -statistic. A p-value less than 0.05 indicates a significant mismatch between

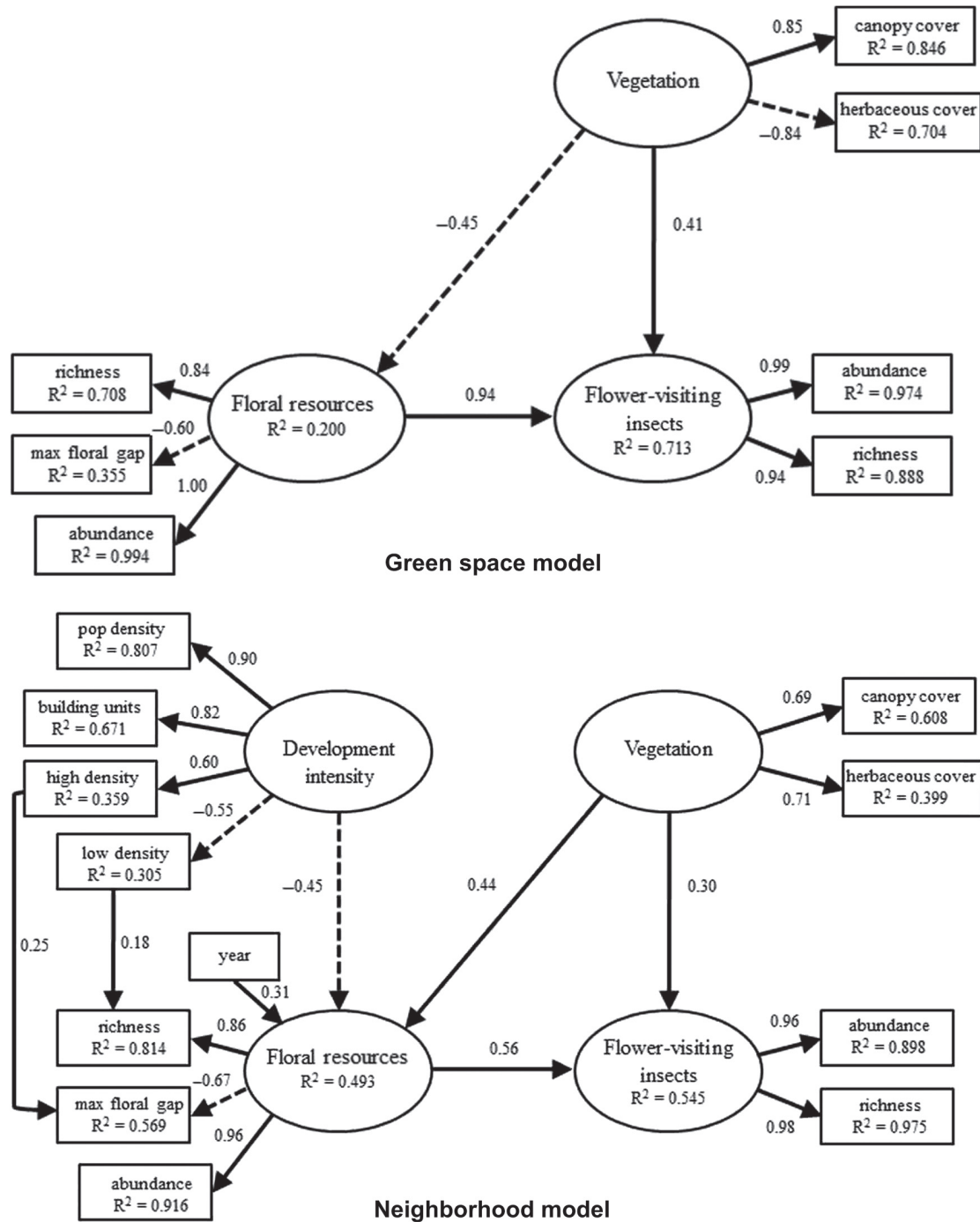


Figure 3. Final structural equation models explaining abundance and taxonomic richness of flower-visiting insects in green spaces (top) and neighborhoods (bottom) of New York City, USA. Rectangles indicate measured variables with associated R^2 values while ellipses show latent conceptual variables. Dashed arrows indicate negative path coefficients. Numbers adjacent to paths are standardized regression coefficients. Coefficients for canopy cover, abundance of floral resources, abundance of insects, and population density in neighborhoods were fixed at 1.0 to set the scaling of their respective latent constructs.

model and data, suggesting model respecification (usually involving additional linkages between variables). We also used the comparative fit index (CFI) as an indicator of model fit. CFI values range from 0–1 with values approximating 0.95 indicating a well-fitting model; this measure is more robust to small sample sizes than other commonly used measures of model fit (Hu and Bentler 1999).

To identify a ‘best’ final model for urban green spaces and neighborhood blocks, we followed the metamodelling approach of Grace et al. (2010). As a starting point, we used the theoretical model of insect diversity presented in Fig. 1, including ‘development intensity’ and median income in the neighborhood block model but not in the green space model. The initial models for both green spaces

and neighborhood blocks included all measured variables as indicators of their respective latent variables. We then sequentially removed the least influential measured variables or links as determined by the critical ratio of regression rate (regression weight divided by standard error). The final 'best' model was determined when the fit of the resulting model was adequate (based on Bollen–Stine χ^2 $p > 0.05$ and CFI approximating 0.95).

Bias-corrected standardized regression coefficients (β) for all paths in the final models were generated using Monte Carlo methods (based on 1000 randomizations taken with replacement). In addition to direct effects of the latent constructs, we assessed the indirect and total effects of all variables. Indirect effects were calculated as the product of the regression coefficients along compound paths (e.g. the coefficient for vegetation to floral resources multiplied by the coefficient for floral resources to flower-visiting insects) while total effects were calculated as the sum of the indirect and direct effects (Arbuckle 2008).

In SEM, it is necessary to specify a scale for the latent variables (Grace et al. 2010). This operation is typically accomplished by setting the regression coefficient equal to one for a measured variable that is positively associated and indicative of the latent construct of interest. We used the measured variables of population density, canopy cover, floral richness, and insect taxa richness to set scaling for their respective latent constructs. As a result, only R^2 values (not regression coefficients) were estimated for these measured variables.

Finally, we estimated the degree of spatial autocorrelation in both the observed variables and in the model residuals. To determine if spatial autocorrelation existed in the observed variables, we computed Moran's I as described in Harrison and Grace (2007) using the 'ape' package in R (Paradis 2006). To estimate spatial autocorrelation in model residuals, we used Bayesian estimation methods (Lee 2007) to impute values for the latent variables. This approach involved using Markov chain Monte Carlo simulation and Bayes theorem along with the missing data algorithm in Amos ver. 20 (Arbuckle 2011) to obtain estimates of latent variable scores. For each model, we averaged over 10 sets of latent variable scores, each score being based on 30 000 simulations. Imputed latent variable scores permitted direct examination of latent relationships, including an assessment of residuals. To determine if spatial autocorrelation existed in the model residuals, we again computed Moran's I.

Results

We surveyed a total of 97 transects in two contrasting urban settings. Over all transects, we recorded 111 plant genera (Appendix 3) and 1267 individual insects (Table 1) including 47 bee species and 29 other flower-visiting insect species or genera (Appendix 1). The most abundant flower-visiting insects were Hymenoptera (75% of all observations), specifically, bees (68%). Bees in the genera *Lasioglossum*, *Hylaeus* and *Ceratina* were particularly abundant (27% of all observations), as were bumble bees (16%), and the European honey bee, *Apis mellifera*

(12%). Other insect orders were less abundant, including Diptera (15% of all floral visitors), Lepidoptera (6%) and Coleoptera (4%).

A unifying aspect of green space transects was the lack of buildings and a high proportion of canopy and herbaceous cover (median proportions of 0.53 and 0.26, respectively; Table 2) relative to neighborhood transects. In contrast, neighborhood transects greatly varied in human population density (range = 18–870 people ha⁻¹) and building density (range = 13–1250 building units in a 30 m buffer), and had much lower proportions of canopy and herbaceous cover (median of 0.06 and 0.03, respectively; Table 2). Despite major differences in the amount of vegetation and built structures, there were no significant differences between urban green spaces and neighborhood blocks in floral abundance (Mann–Whitney $U = 953$, $DF = 95$, $p = 0.114$), floral richness (Mann–Whitney $U = 1108$, $DF = 95$, $p = 0.208$), or maximum floral gap (Mann–Whitney $U = 1240$, $DF = 95$, $p = 0.612$). There were, however, significant differences in flower-visiting insect taxonomic richness (Mann–Whitney $U = 779$, $DF = 95$, $p = 0.003$) and abundance (Mann–Whitney $U = 699$, $DF = 95$, $p = < 0.001$), with green spaces having higher levels than neighborhood blocks in both cases.

Green space model

The final model for urban green spaces included the influence of vegetation (as indicated by canopy and herbaceous cover) and floral resources (indicated by floral richness, floral abundance, and maximum floral gap) on flower-visiting insects (indicated by abundance and taxonomic richness) (Fig. 3). This model did not significantly deviate from the data ($\chi^2 = 13.4$, $DF = 12$, Bollen–Stine bootstrap $p = 0.615$, CFI = 1.0) and explained 71.3% of the variation in flower-visiting insects. The variable 'year' was not included in the final model because it exhibited the lowest critical ratio of regression rate of all variables, for both floral resources and insects, and because each of these link removals increased the model CFI. Estimated errors for measured variables were minimal, ranging from 0 to 0.03. Vegetation exhibited a positive direct effect on flower-visiting insects ($\beta = 0.406$, 95% CI = 0.161/0.603, $p = 0.005$) but was negatively correlated with floral resources ($\beta = -0.448$, 95% CI = -0.673 / -0.119 , $p = 0.011$) and therefore had a negative indirect effect on flower-visiting insects ($\beta = -0.423$, 95% CI = -0.758 / -0.095 , $p = 0.011$). These opposing effects of vegetation on floral resources and insects resulted in a non-significant total effect of vegetation on flower-visiting insects ($p = 0.877$). Moran's I test results showed significant spatial autocorrelation in the observed vegetation variables ($p < 0.05$ for both canopy and herbaceous cover), but did not show evidence of significant spatial autocorrelation in the model residuals for floral resources and flower-visiting insects.

Neighborhood model

In addition to floral resources and vegetation, the final model for neighborhood blocks included the influences of

development intensity (Fig. 3). Direct links were removed sequentially in order of least influence as follows: Development intensity to vegetation, year to flower-visiting insects, and development intensity to flower-visiting insects. After removal of these variables and links, the resulting model did not significantly deviate from the data but the CFI value remained lower (0.923) than the standard threshold of 0.950. Therefore, we consulted a set of modification indices provided by the AMOS Graphics program that suggest ways to increase model fit (Arbuckle 2008). Of the suggestions provided, we considered the following two as being theoretically plausible in this system: 1) the effect of low-density residential zoning on floral richness, and 2) the effect of high-density residential zoning on the maximum floral gap. Addition of these two relationships resulted in a final model that fit the data well ($\chi^2 = 68.9$, $DF = 48$, Bollen–Stine bootstrap $p = 0.228$, $CFI = 0.943$; Fig. 3) and that explained 54.5% of the variation in flower-visiting insects. Estimated measurement error was less than 0.03 for all measured variables except building unit density (0.11) and low- and high-density residential zoning (0.13 for both). Moran's I test results detected significant autocorrelation in most observed variables for the neighborhood sample. However, there was no evidence of significant spatial autocorrelation in the model residuals for predicted latent factors.

In the final model for neighborhood blocks (Fig. 3), development intensity did not have a significant direct effect on insects. However, it did exhibit a significant negative indirect effect on insects ($\beta = -0.251$, 95% $CI = -0.487/-0.031$, $p = 0.034$). This relationship was mediated by a negative direct effect of development intensity on floral resources ($\beta = -0.451$, 95% $CI = -0.639/-0.201$, $p = 0.006$). Contrary to the relationship observed in the final model for urban green spaces (Fig. 3), vegetation was positively related to floral resources in neighborhood blocks ($\beta = 0.440$, 95% $CI = 0.116/0.893$, $p = 0.007$) and had a significant positive total effect on insects ($\beta = 0.545$, 95% $CI = 0.225/0.879$, $p = 0.005$).

The latent construct 'vegetation' represented different aspects of canopy cover and herbaceous cover in the models for green spaces and neighborhood blocks. In both models, the regression coefficient for canopy cover was fixed at 1.00 to provide scaling for the latent construct of vegetation (Grace et al. 2010). As a result, canopy cover was positively associated with vegetation in both settings. Herbaceous cover, however, was positively associated with vegetation in neighborhood blocks but negatively associated in green spaces (Fig. 3). This difference reflected contrasting relationships between herbaceous cover and canopy cover in neighborhood blocks (a positive association, Spearman's $\rho = 0.543$, $p < 0.001$) and green spaces (a negative association, Spearman's $\rho = -0.682$, $p < 0.001$) (Fig. 4).

Discussion

Although cities are commonly described as being heterogeneous (Rebele 1994, Cadenasso et al. 2007), few studies have investigated the effect of multiple urban land uses

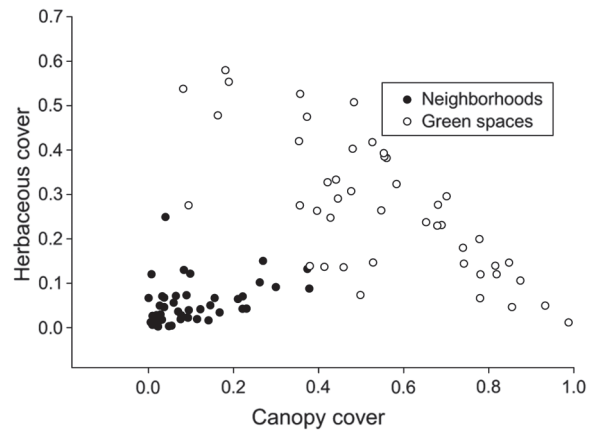


Figure 4. Associations between the measured variables (canopy cover and herbaceous cover) used as indicators of the latent construct 'Vegetation' for both neighborhood blocks ($n = 52$, Spearman's $\rho = 0.543$, $p < 0.001$) and green spaces ($n = 45$, Spearman's $\rho = -0.682$, $p < 0.001$).

on biotic communities (Sattler et al. 2010, Hennig and Ghazoul 2011, Wojcik 2011). This lack is partly because sampling in some urban environments (e.g. residential neighborhoods) can be logistically difficult. While our study design precluded sampling of all locations at the finest taxonomic resolution, it enabled multiple insights into how urban heterogeneity can affect biotic communities. Specifically, we found that land cover and its resultant effects on floral resources and flower-visiting insects greatly varied between green spaces and neighborhood blocks (Fig. 3). In addition, there was substantial variation in floral resources and flower-visiting insects within both green space and neighborhood block transects, further reflecting the variety of green space management and development intensity in cities. For instance, while some neighborhood blocks had a dearth of floral resources and flower-visiting insects, other neighborhood blocks (often low-density residential) had more floral resources and insects than some green spaces. These results highlight the importance of evaluating community composition across the entirety of the urban landscape to account for variation within and among land use types.

The largest discrepancies between green spaces and neighborhood blocks were the lack of buildings in green spaces and vegetation in neighborhood blocks. Specifically, green spaces had nine times more canopy cover and seven times more herbaceous cover than developed neighborhood blocks in a 30 m buffer around transects (Table 2). Interestingly, despite having much less vegetation, neighborhood blocks did not have lower floral richness or abundance, or greater maximum floral gap. This finding is likely due to the presence of numerous ornamental flower beds in proximity of residential and commercial buildings. However, despite the similarity in measured floral resources between green spaces and neighborhood blocks, the effect of floral resources on flower-visiting insects was nearly twice as large in green spaces ($\beta = 0.94$) than in neighborhood blocks ($\beta = 0.56$). Considering that many common garden flowers are exotic and/or horticultural cultivars that may provide relatively little pollen and/or nectar

(Comba et al. 1999), this result makes sense. Also, in support of this, several flower cultivars that are common in neighborhood blocks but not green spaces (e.g. *Petunia*, *Impatiens*, *Hydrangea*, *Rosa*, *Viola*, *Lilium*) were relatively unattractive to flower-visiting insects (KCM unpubl.). This variation in 'floral quality' also may have contributed to the lower explanatory power of the model for neighborhood blocks ($R^2 = 0.545$) relative to the model for green spaces ($R^2 = 0.713$). In support of this idea, post hoc removal of the above flower genera from the neighborhood block model increased the effect of floral resources on flower-visiting insects and also increased the explanatory power of the model. This finding suggests that floral composition and identity may be especially important in urban landscapes where floral resources vary widely in pollen and nectar availability. In more 'natural' settings, such as nature reserves, abundance and diversity of floral resources have also been linked to abundance and diversity of bees (Potts et al. 2003).

In addition to variation in the effect of floral resources, there were differences in the relationship between vegetation and floral resources for green spaces and neighborhood blocks. Surrounding vegetation was positively associated with floral resources in neighborhood blocks but negatively associated in green spaces, reflecting differences in vegetation in these two settings. In neighborhood blocks, herbaceous cover and canopy cover increased together, but in green spaces, herbaceous cover decreased with increasing canopy cover, likely due to different uses of green space (e.g. ball fields versus forest trails). Therefore, in neighborhood blocks, the latent construct 'vegetation' represented a mosaic of open gardens and sparsely distributed trees increasing together, while in urban green spaces 'vegetation' represented increasing canopy cover at the expense of open herbaceous cover (Fig. 4). The negative relationship between vegetation and floral resources in green spaces may reflect the shading effect of tree canopy on flowering herbaceous plants. This effect has also been seen in non-urban settings, where canopy cover is often negatively related to flowering plant density and bee abundance (Hoehn et al. 2010, Grundel et al. 2011). Conversely, the positive impact of vegetation on floral resources in neighborhood blocks is likely due to floral resources that increase with the 'savannah-like habitat' of open gardens, vegetated lots, and sparsely distributed canopy cover.

In both urban settings, vegetation had a positive direct effect on flower-visiting insects independent of the impact of vegetation on floral resources. This result may reflect increased nesting sites in areas with more vegetation. For instance, most bee species in New York City construct nests in soil, cavities, or plant stems (J. S. Ascher unpubl.) and proxies of nesting resources have been shown to be an important factor for bees in a variety of settings (Moretti et al. 2009, Grundel et al. 2011). Nesting resources may be especially limiting in urban areas due to a high proportion of impervious surface or heavily compacted soil (Cane 2005) although this hypothesis has not been empirically evaluated.

Studies conducted across a gradient of urbanization have suggested that abundance and richness of butterflies

and bees may be optimized at intermediate levels of urban development (Blair and Launer 1997, Winfree et al. 2007), although the mechanisms underlying this pattern are not clear. In this study, development intensity did not directly influence insects or vegetation (Fig. 3). Instead, increasing development intensity inhibited flower-visiting insects specifically by reducing floral resources. High-density residential neighborhoods in New York City are typically characterized by relatively few gardens and tall apartment buildings, which can increase shading (Matteson and Langellotto 2010) and decrease floral resources. The lower diversity of floral resources in these high-density residential areas may also result from uniform management of flowering plants around large apartment buildings. Although we found a negative impact of increasing development intensity in New York City, studies carried out in less populated landscapes may exhibit the opposite pattern if floral resources increase with urban development.

We did not find a significant relationship between median household income and floral richness (Spearman's $\rho = -0.030$, $p = 0.853$). In contrast, a study conducted in Phoenix, Arizona (USA) found a positive association between median income and plant diversity, termed the 'luxury effect' (Hope et al. 2003). New York City may provide an exception to the luxury effect for at least two socio-ecological reasons. First, while median household income is very high in some high-density residential areas, particularly in Manhattan, these areas tend to have few flowers due to the high development intensity. Second, the presence of >700 community gardens, which are often located in lower income neighborhoods (Englander 2001), may help to maintain equitable floral diversity across income levels in New York City. This observation suggests that the 'luxury effect' may be less applicable in densely populated cities similar to New York City.

While some of our transects were close together, there was no residual spatial autocorrelation in either model. However, the raw data from the neighborhood sample did show spatial autocorrelation for most variables. This indicates that many environmental variables (canopy cover, herbaceous cover, floral resources) are spatially autocorrelated in urban neighborhoods. In contrast, lack of residual spatial autocorrelation in our response variables suggests little spatial structuring due to biotic processes such as dispersal and competition. Sattler et al. (2010) found spatial variables to explain less than 7% of the variation in bee community composition in three Swiss cities. These authors postulated that a high level of disturbance in cities reduces the influence of biotic processes that can lead to spatial structuring of communities. Our finding of a lack of spatial autocorrelation in model residuals provides some support for this idea.

A limitation of this study is that we did not collect insects at all locations and identify them to the species-level. Different bees and other flower-visiting insects may exhibit idiosyncratic responses to biophysical variables due to varying nesting and floral requirements (Murray et al. 2009). However, lower-resolution taxonomic data from visual observations have been found to correlate strongly with specimen-based data (Kremen et al. 2011). Furthermore, considering the large differences in our findings for

urban green spaces and neighborhood blocks, it seems unlikely that our general conclusions would be largely altered by finer resolution data. Nevertheless, it is valuable to evaluate species- or guild-specific responses to urban land use heterogeneity (e.g. to determine which species drop out or persist in more heavily developed neighborhoods) and this is a major goal of our ongoing research. Another limitation of this study is that our sampling protocol provided a limited snapshot of the entire seasonal activity of insects. While our sampling was deliberately conducted during the period of peak activity for many insects, sampling during other time periods could result in different findings. For instance, sampling in early spring may demonstrate a positive correlation between canopy cover and floral resources in green spaces due to blooming of many trees and spring ephemerals during this time.

Conclusions

We found differential impacts of vegetation and floral resources on flower-visiting insects in urban green spaces and along neighborhood blocks. Insects in neighborhood blocks were positively influenced by a mosaic of open vegetation (canopy and herbaceous cover increasing together) through associated increases in floral resources and potential increases in nesting sites. In contrast, in green spaces, high levels of canopy cover came at the expense of herbaceous cover, decreasing floral resources and resulting in a negative indirect effect on flower-visiting insects. Floral resources had a positive impact on insects in both settings but the magnitude of the effect was greater in green spaces. In addition, for neighborhood blocks, development intensity indirectly decreased flower-visiting insects by reducing floral resources. These results may have implications for urban agriculture and the maintenance of wild plant populations in cities.

This study demonstrates how biophysical variation in cities (e.g. buildings, vegetation, etc.) can directly and indirectly affect biotic communities, and how these effects may vary in direction and magnitude for different urban settings. Given the proximity of green spaces and residential/commercial neighborhoods in urban areas, shifts in ecological effects may occur over very short spatial scales in cities. This finding suggests that the oft-cited heterogeneous mosaic of land uses in urban landscapes may result in an equally heterogeneous tapestry of mechanisms affecting urban biota.

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References

- Ahrné, K. et al. 2009. Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. – *PLoS One* 4: e5574.
- American Horticultural Society. 2002. *Encyclopedia of plants and flowers*. – DK Publishing.
- Arbuckle, J. L. 2008. *IBM SPSS Amos 17 user's guide*. – Amos Development Corporation, SPSS Inc.
- Arbuckle, J. L. 2011. *IBM SPSS Amos 20 user's guide*. – Amos Development Corporation, SPSS Inc.
- Barthel, S. et al. 2005. History and local management of a biodiversity-rich, urban cultural landscape. – *Ecol. Soc.* 10: article no. 10.
- Beyer, H. 2010. Geospatial modelling environment. ArcGIS Extension. < www.spatial ecology.com >.
- Blair, R. B. and Launer, A. E. 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. – *Biol. Conserv.* 80: 113–125.
- Bollen, K. A. and Stine, R. A. 1992. Bootstrapping goodness-of-fit measures in structural equation models. – *Sociol. Meth. Res.* 21: 205–229.
- Cadenasso, M. L. et al. 2007. Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. – *Front. Ecol. Environ.* 5: 80–88.
- Cane, J. H. 2005. Bees' needs challenged by urbanization. – In: Johnson, E. A. and Klemens, M. W. (eds), *Nature in fragments: the legacy of sprawl*. Columbia Univ. Press, pp. 109–124.
- Comba, L. et al. 1999. Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens. – *Ann. Bot.* 83: 369–383.
- Council on the Environment of New York City. 2006. *Open accessible space information system for New York City*. – CUNY Mapping Service at the Center for Urban Research The Graduate Center / CUNY.
- Czech, B. et al. 2000. Economic associations among causes of species endangerment in the United States. – *Bioscience* 50: 593–601.
- Englander, E. 2001. *New York's Community Gardens – a resource at risk*. – Trust for Public Land.
- Grace, J. B. 2006. *Structural equation modeling and natural systems*. – Cambridge Univ. Press.
- Grace, J. B. et al. 2010. On the specification of structural equation models for ecological systems. – *Ecol. Monogr.* 80: 67–87.
- Grimm, N. B. et al. 2008. Global change and the ecology of cities. – *Science* 319: 756–760.
- Grundel, R. et al. 2011. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. – *Ecol. Appl.* 20: 1678–1692.
- Harrison, S. and Grace, J. B. 2007. Biogeographic affinity contributes to our understanding of productivity–richness relationships at regional and local scales. – *Am. Nat.* 170: S5–S15.
- Hennig, E. I. and Ghazoul, J. 2011. Plant–pollinator interactions within the urban environment. – *Persp. Plant Ecol. Evol. Syst.* 13: 137–150.
- Hernandez, J. L. et al. 2009. Ecology of urban bees: a review of current knowledge and directions for future study. – *Cities Environ.* 2: < <http://digitalcommons.lmu.edu/cgi/viewcontent.cgi?article=1036&context=cate> >.
- Hoehn, P. et al. 2010. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. – *Biodiv. Conserv.* 19: 2189–2200.
- Hope, D. et al. 2003. Socioeconomics drive urban plant diversity. – *Proc. Natl Acad. Sci. USA* 100: 8788–8792.
- Hu, L.-t. and Bentler, P. M. 1999. Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. – *Struct. Eq. Model.* 6: 1–55.
- Kremen, C. et al. 2011. Evaluating the quality of citizen-scientist data on pollinator communities. – *Conserv. Biol.* 25: 607–617.

- Lee, S. Y. 2007. Structural equation modeling: a Bayesian approach. – Wiley.
- Loram, A. et al. 2007. Urban domestic gardens (X): the extent and structure of the resource in five major cities. – *Landscape Ecol.* 22: 601–615.
- Marco, A. et al. 2008. Gardens in urbanizing rural areas reveal an unexpected floral diversity related to housing density. – *Comptes Rendus Biol.* 331: 452–465.
- Matteson, K. C. and Langellotto, G. A. 2010. Determinates of inner city butterfly and bee species richness. – *Urban Ecosyst.* 13: 333–347.
- Matteson, K. C. et al. 2008. Bee richness and abundance in New York City urban gardens. – *Ann. Entomol. Soc. Am.* 101: 140–150.
- McDonald, R. I. et al. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. – *Biol. Conserv.* 141: 1695–1703.
- McFrederick, Q. S. and Lebuhn, G. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? – *Biol. Conserv.* 129: 372–382.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. – *Biol. Conserv.* 127: 247–260.
- Moretti, M. et al. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. – *J. Anim. Ecol.* 78: 98–108.
- Murray, T. et al. 2009. Conservation ecology of bees: populations, species and communities. – *Apidologie* 40: 211–236.
- Myeong, S. et al. 2001. Urban cover mapping using digital, high-spatial resolution aerial imagery. – *Urban Ecosyst.* 5: 243–256.
- Owen, J. and Owen, D. F. 1975. Suburban gardens: England's most important nature reserve? – *Environ. Conserv.* 2: 53–59.
- Paradis, E. 2006. Analysis of phylogenetics and evolution with R. – Springer.
- Peterson, R. T. and McKenny, M. 1996. Wildflowers. – Houghton Mifflin Company.
- Pickett, S. T. A. and Cadenasso, M. L. 2008. Linking ecological and built components of urban mosaics: an open cycle of ecological design. – *J. Ecol.* 96: 8–12.
- Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. – *Biol. Conserv.* 12: 115–134.
- Potts, S. G. et al. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? – *Ecology* 84: 2628–2642.
- Rebele, F. 1994. Urban ecology and special features of urban ecosystems. – *Global Ecol. Biogeogr. Lett.* 4: 173–187.
- Roubik, D. W. 2001. Ups and downs in pollinator populations: when is there a decline? – *Conserv. Ecol.* 5: <www.ecologyandsociety.org/vol5/iss1/art2/>.
- Sattler, T. et al. 2010. Response of arthropod species richness and functional groups to urban habitat structure and management. – *Landscape Ecol.* 25: 941–954.
- Snep, R. P. H. et al. 2006. How peri-urban areas can strengthen animal populations within cities: a modeling approach. – *Biol. Conserv.* 127: 345–355.
- Turner, W. R. et al. 2004. Global urbanization and the separation of humans from nature. – *Bioscience* 54: 585–590.
- United States Census Bureau. 2006. 2006 population estimates. – US Census Bureau.
- Warren, P. S. et al. 2008. Plants of a feather: spatial autocorrelation of gardening practices in suburban neighborhoods. – *Biol. Conserv.* 141: 3–4.
- Winfree, R. et al. 2007. Effect of human disturbance on bee communities in a forested ecosystem. – *Conserv. Biol.* 21: 213–223.
- Wojcik, V. A. 2011. Resource abundance and distribution drive bee visitation within developing tropical urban landscapes. – *J. Pollination Ecol.* 4: 48–56.

Appendix 1. Flower-visiting insects identified along 97 transects in green spaces and neighborhood blocks of New York City. This list includes determinations based on visual inspection in the field (V), insect specimens (S), and/or digital images (I). Species determinations of bees using specimens were primarily made by J. S. Ascher but also J. Gibbs (for some additional *Lasioglossum*).

Order	Family	Species	Determination	
Hymenoptera	Colletidae	<i>Hylaeus hyalinatus</i>	S	
		<i>Hylaeus leptocephalus</i>	S	
		<i>Hylaeus mesillae cressoni</i>	S	
	Halictidae	<i>Hylaeus modestus modestus</i>	S	
		<i>Augochlora pura pura</i>	S	
		<i>Agapostemon sericeus</i>	S	
		<i>Agapostemon virescens</i>	S, V	
		<i>Halictus confusus confusus</i>	S	
		<i>Halictus ligatus</i>	S	
		<i>Halictus rubicundus</i>	S	
		<i>Lasioglossum cattellae</i>	S	
		<i>Lasioglossum cressonii</i>	S	
		<i>Lasioglossum ephialtum</i>	S	
		<i>Lasioglossum imitatum</i>	S	
		<i>Lasioglossum marinum</i>	S	
		<i>Lasioglossum obscurum</i>	S	
		<i>Lasioglossum pectorale</i>	S	
		<i>Lasioglossum quebecense</i>	S	
		<i>Lasioglossum subviridatum</i>	S	
		<i>Lasioglossum versatum</i>	S	
		<i>Lasioglossum weemsi</i>	S	
		<i>Lasioglossum zophops</i>	S	
		Megachilidae	<i>Osmia pumila</i>	S
			<i>Megachile centuncularis</i>	S
			<i>Megachile frigida</i>	S

(Continued)

Appendix 1. (Continued).

Order	Family	Species	Determination
		<i>Megachile pugnata pugnata</i>	S
		<i>Megachile rotundata</i>	S
		<i>Megachile sculpturalis</i>	S, V
		<i>Megachile texana</i>	S
		<i>Coelioxys octodentata</i>	S
		<i>Pseudoanthidium nanum</i>	S
	Apidae	<i>Xylocopa virginica</i>	I, V
		<i>Ceratina calcarata</i>	S
		<i>Ceratina dupla dupla</i>	S
		<i>Melissodes agilis</i>	I, V
		<i>Melissodes bimaculata bimaculata</i>	I, S, V
		<i>Melissodes subillata</i>	S
		<i>Anthophora terminalis</i>	S
		<i>Peponapis pruinosa</i>	I, S, V
		<i>Bombus bimaculatus</i>	S
		<i>Bombus citrinus</i>	S
		<i>Bombus fervidus</i>	I, S, V
		<i>Bombus griseocollis</i>	I, S, V
		<i>Bombus impatiens</i>	I, V
		<i>Apis mellifera</i>	I, V
		<i>Epeolus lectoides</i>	S
		<i>Ptilothrix bombiformis</i>	S
	Sphecidae	<i>Isodontia</i> spp.	V
		<i>Sphex ichneumoneus</i>	V
		<i>Sphex pensylvanicus</i>	V
	Scoliidae	<i>Scolia dubia</i>	V
	Vespidae	<i>Vespula maculifrons</i>	V
		<i>Vespula germanica</i>	V
		<i>Polistes dominulus</i>	I, V
	Vespidae	<i>Monobia quadridens</i>	V
Diptera	Calliphoridae	<i>Lucilia</i> spp.	I, V
	Muscidae	<i>Musca domestica</i>	I, V
	Sarcophagidae	<i>Sarcophaga</i> spp.	V
	Syrphidae	<i>Eupeodes/Syrphus</i> spp.	I, V
		<i>Toxomerus</i> spp.	I, V
Coleoptera	Scarabaeidae	<i>Popillia japonica</i>	I, V
	Mordellidae	<i>Mordella/Mordellistena</i> spp.	I, V
Lepidoptera	Pieridae	<i>Pieris rapae</i>	I, V
	Nymphalidae	<i>Vanessa atalanta</i>	V
		<i>Vanessa cardui</i>	V
		<i>Danaus plexippus</i>	V
		<i>Polygonia interrogationis</i>	V
	Lycaenidae	<i>Celestrina ladon</i>	I, V
		<i>Everes comyntas</i>	V
	Papilionidae	<i>Papilio troilus</i>	V
		<i>Papilio polyxenes</i>	V
	Hesperiidae	<i>Phyciodes tharos</i>	V
		<i>Epargyreus clarus</i>	V
		<i>Poanes</i> spp.	V
	Sesiidae	<i>Melittia cucurbitae</i>	V

Appendix 2. Spearman's correlations between the proportion of canopy cover at different spatial scales and the latent variables of 'floral resources' and 'flower-visiting insects' in green spaces and neighborhoods of New York City.

Buffer size for which canopy cover was measured	Green spaces		Neighborhood blocks	
	Floral resources	Flower-visiting insects	Floral resources	Flower-visiting insects
30 meter	-0.393	-0.025	0.342	0.324
200 meter	-0.138	-0.076	0.302	0.211
350 meter	-0.191	-0.048	0.035	0.016
500 meter	-0.079	0.095	-0.102	-0.087

Appendix 3. Flower genera identified along 97 transects in green spaces and neighborhood blocks of New York City. Observation location includes plants identified just along neighborhood block transects (N), just in green space transects (G), or in both transect types (B).

Family	Genus	Observed location(s)
Agavaceae	<i>Hosta</i>	B
Apiaceae	<i>Daucus</i>	B
Apocynaceae	<i>Apocynum</i>	G
Asclepiadaceae	<i>Asclepias</i>	B
Asteraceae	<i>Achillea</i>	B
	<i>Ageratum</i>	G
	<i>Aster</i>	G
	<i>Centaurea</i>	B
	<i>Cichorium</i>	B
	<i>Cirsium</i>	G
	<i>Coreopsis</i>	B
	<i>Echinacea</i>	B
	<i>Erigeron</i>	B
	<i>Eupatorium</i>	G
	<i>Galinsoga</i>	N
	<i>Helianthus</i>	B
	<i>Heliopsis</i>	N
	<i>Lactuca</i>	N
	<i>Leucanthemum</i>	B
	<i>Osteospermum</i>	N
	<i>Rudbeckia</i>	B
	<i>Senecio</i>	B
	<i>Solidago</i>	B
	<i>Symphotrichum</i>	G
	<i>Tagetes</i>	B
	<i>Taraxacum</i>	B
	<i>Veronia</i>	G
Balsaminaceae	<i>Impatiens</i>	B
Begoniaceae	<i>Begonia</i>	N
Brassicaceae	<i>Brassica</i>	N
	<i>Lepidium</i>	B
Caprifoliaceae	<i>Diervilla</i>	N
Caprifoliaceae	<i>Lonicera</i>	G
Caryophyllaceae	<i>Dianthus</i>	B
	<i>Silene</i>	N
Celastraceae	<i>Euonymus</i>	B
Chenopodiaceae	<i>Chenopodium</i>	N
Cleomaceae	<i>Cleome</i>	N
Commelinaceae	<i>Tradescantia</i>	N
Convolvulaceae	<i>Ipomoea</i>	N
Crassulaceae	<i>Hylotelephium</i>	B
Cucurbitaceae	<i>Cucurbita</i>	G
Fabaceae	<i>Chamaecrista</i>	G
	<i>Cytisus</i>	G
	<i>Lotus</i>	G
	<i>Lupinus</i>	N
	<i>Medicago</i>	N
	<i>Melilotus</i>	B

(Continued)

Appendix 3. (Continued).

	<i>Securigera</i>	G
	<i>Thermopsis</i>	G
	<i>Trifolium</i>	B
Geraniaceae	<i>Geranium</i>	B
	<i>Pelargonium</i>	B
Hemerocallidaceae	<i>Hemerocallis</i>	B
Hydrangeaceae	<i>Hydrangea</i>	B
Lamiaceae	<i>Agastache</i>	B
	<i>Lavandula</i>	N
	<i>Mentha</i>	G
	<i>Monarda</i>	G
	<i>Nepeta</i>	G
	<i>Prunella</i>	G
	<i>Salvia</i>	B
	<i>Stachys</i>	N
Liliaceae	<i>Lilium</i>	B
Lobelioideae	<i>Lobelia</i>	N
Lythraceae	<i>Lythrum</i>	G
Malvaceae	<i>Alcea</i>	N
	<i>Hibiscus</i>	N
	<i>Malva</i>	G
Manyanthaceae	<i>Nymphoides</i>	G
Oleaceae	<i>Ligustrum</i>	N
Onagraceae	<i>Circaea</i>	B
	<i>Oenothera</i>	N
Oxalidaceae	<i>Oxalis</i>	B
Phytolaccaceae	<i>Phytolacca</i>	B
Plantaginaceae	<i>Antirrhinum</i>	G
	<i>Digitalis</i>	G
	<i>Penstemon</i>	G
	<i>Plantago</i>	N
Polemoniaceae	<i>Phlox</i>	B
Polygonaceae	<i>Persicaria</i>	B
	<i>Polygonum</i>	B
Pontederiaceae	<i>Pontederia</i>	G
Portulacaceae	<i>Portulaca</i>	N
Ranunculaceae	<i>Clematis</i>	N
	<i>Delphinium</i>	B
	<i>Ranunculus</i>	B
Rosaceae	<i>Aruncus</i>	N
	<i>Rosa</i>	B
	<i>Spiraea</i>	B
Saxifragaceae	<i>Astilbe</i>	N
	<i>Heuchera</i>	N
Scrophulariaceae	<i>Buddleja</i>	B
Solanaceae	<i>Nicotiana</i>	G
	<i>Petunia</i>	B
	<i>Solanum</i>	B
Tropaeolaceae	<i>Tropaeolum</i>	N
Verbenaceae	<i>Lantana</i>	B
	<i>Verbena</i>	N
Violaceae	<i>Viola</i>	B
Vitaceae	<i>Ampelopsis</i>	B
Vitaceae	<i>Vitis</i>	N