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Wild bees and urban agriculture: assessing pollinator supply and demand across urban landscapes

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Abstract

Growing interest in urban agriculture has increased demand for pollination services. Most studies map pollination supply broadly, and do not consider the impacts of fine-scale urban land-use practices on the dynamics of pollination delivery, leaving a critical gap in our understanding of the pollinator supply-demand balance in urban landscapes. This study demonstrates a spatially-explicit framework, using Iowa City, IA (USA) as the case study region, for assessing the capacity of urban ecosystems to produce pollinator services in support of demand from urban agriculture. We estimate pollinator supply using the InVEST pollination model with detailed land-cover data produced through field survey and Bayesian hierarchical analysis, and we validate modeling results with bee abundance and richness data. We map social demand for pollinators using a kernel density estimation of urban agricultural sites and evaluate supply-demand budgets through spatial overlay analysis. Our results show that incorporating high-thematic-resolution urban land-use data substantially improves the performance of pollination supply modeling. Pollinator supply meets demand in 72% of the city. Surpluses occur in natural areas and heavily-vegetated, established residential neighborhoods, whereas deficits occur in resource-poor lawns. Our mapping framework stresses the key role of humans in modifying resource availability and pollinator services, and demonstrates the effectiveness of using disaggregated socio-economic data in urban land-cover classification for predicting pollinator supply. Our improved ability to identify spatial congruence and disparities in urban pollinator supply and demand can be used to inform pollinator conservation to support sustainable urban agriculture.

Keywords Urban agriculture · Wild bees · Pollination · Ecosystem service mapping · Ecosystem service supply · Ecosystem service demand

Introduction

Urban agriculture involves the development and transformation of urbanized land to support food production through community and private gardens, allotments, edible landscaping, and other productive uses. Urban agriculture is well-recognized in ensuring urban food security and proper nutrition, supporting local economies, reducing waste and pollution, and enhancing social cohesion (Armar-Klemesu 2000; Lovell 2010). In addition to honey bees kept by citizens, wild bees are particularly important in supplying urban agriculture with pollination services given that a wide variety of plants and fruits (e.g., tomatoes, apples, strawberries) in urban gardens and farms depend on animal pollinators to set fruit and seeds (Klein et al. 2007). The diverse wild bees that occur in large American cities such as Phoenix (Cane et al. 2006), New York (Matteson et al. 2008), San Francisco (Potter and

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LeBuhn 2015) and Chicago (Lowenstein et al. 2015) are the primary pollinators for urban agriculture (Matteson et al. 2008; Matteson and Langellotto 2010; Lowenstein et al. 2015; Tonietto et al. 2011).

Both the surrounding landscape context and local site attributes influence wild bee occurrence and foraging patterns (Ahrne et al. 2009; Wojcik 2011; Tonietto et al. 2011). In highly heterogeneous landscapes, these factors combine so that the distribution of pollinators and hence, pollination services, are uneven. Such relationships are less straightforward in urban ecosystems than agricultural or natural systems (Ricketts et al. 2008; Kennedy et al. 2013) because landscape heterogeneity occurs at a much finer grain. Gardens are often interspersed with areas of impervious surfaces, potentially altering bee community diversity and abundance.

Studies of the effects of urbanization on urban wild bees disagree with respect to their magnitude and direction. Some studies suggest that bee abundance and diversity increase with urban green space coverage and that bee diversity declines with increased impervious surface coverage in surrounding landscapes (Ahrne et al. 2009; Tonietto et al. 2011). In contrast, other studies show wild bee foraging dynamics to be strongly resource-driven with little if any effect of the urban matrix on species diversity and pollination efficiency (Winfree et al. 2008; Wojcik 2011; Potter and LeBuhn 2015). The patchy distribution of floral and nesting resources introduced by mosaics of trees, shrubs, gardens and other greenspaces in urban neighborhoods may contribute to this finding, for example, by providing stepping-stone habitat to support bees moving through urban landscapes. Several studies suggest that ornamental plants in urban residential neighborhoods can support bee diversity and abundance and, in turn, pollination services by mitigating the otherwise negative impacts of urban development (Frankie et al. 2009; Matteson and Langellotto 2010; Lowenstein et al. 2014). Landscape heterogeneity thus poses both opportunities and threats to urban wild bee communities and to associated pollination services. While small urban habitat patches can host rich wild bee communities, they may also experience regular disturbance that changes nesting site and food plant availability and/or accessibility. The patchy distribution of high-quality habitat may allow bees to persist in some urban settings, but in locations that may be distant from urban agriculture. Spatially-explicit estimation of the state, dynamics and availability of pollination services for urban agriculture could enhance understanding of these factors.

Mapping pollination services across landscapes generally follows one of three approaches. First, when spatially-explicit environmental and species occurrence data are available, empirical data-driven species-distribution models can be used to predict spatial patterns in pollination services (Polce et al. 2013). This method facilitates estimation of pollination services based on actual species occurrence and is thus likely to have high accuracy. However, field-sampling of bees across urban landscapes is costly in time and effort and is rarely applied in mapping urban pollination services.

Where pollinator occurrence data are unavailable, a second approach is used that relies on extrapolation techniques to estimate pollination based on generalized relationships between land cover, interpatch distance and pollination success (Maes et al. 2011; Schulp and Alkemade 2011; Schulp et al. 2014). One such study of farm sites identified an exponential decay function describing the negative association between pollinator visitation rates and distances from suitable pollinator habitat using data across multiple pollinator communities, crop species and biomes in rural agricultural systems (Ricketts et al. 2008). Although this relationship facilitated continental assessments of crop pollination (Maes et al. 2011; Schulp et al. 2014), it remains unclear whether such empirical knowledge can be applied to quantify pollination services in heterogeneous urban landscapes. It is likely that the simplification of urban landscapes into binary land categories (i.e., natural and semi-natural habitat vs. agricultural land) required in modeling this relationship could fail to account for the complexity of fine landscape elements that provide resources for bees (Kennedy et al. 2013).

A third approach to mapping urban pollination supply uses habitat models based on expert knowledge to identify landscape suitability for bees. The Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) pollination model exemplifies such an approach (Lonsdorf et al. 2009; Sharp et al. 2016). It combines land-cover data, expert assessments of nesting and floral resource availability, and pollinator life-history characteristics (i.e., nesting type, flight ranges) to generate a pixel-level bee abundance index. This model has been applied in numerous contexts and geographic locations, including global cropping systems (Kennedy et al. 2013), the entire conterminous US (Koh et al. 2016), European Union croplands (Zulian et al. 2013), and different agricultural settings in US states and Costa Rica (Lonsdorf et al. 2009; Chapin 2014; Groff et al. 2016). While these studies provide spatially-explicit estimates of pollination services, their focus on broad extents, coarse-resolution data and rural ecosystems tells us little about the applicability of this approach in urban areas.

Recent studies applied the InVEST model in identifying urban pollinator supply (Grafius et al. 2016; Davis et al. 2017; Stange et al. 2017). These studies assessed the capacities of urban land covers to provide pollination services through scenario analysis (Davis et al. 2017) as well as investigations of the influence of spatial (Grafius et al. 2016) and thematic resolution (Stange et al. 2017) on pollination models in urban areas. These studies improved our understanding of urban pollination supply, but did not quantify pollination demand or supply-demand relationships. Such relationships have been investigated in homogenous landscapes at moderate-to-coarse resolutions (30 m - 100 m) (Zulian et al.

2013; Schulp et al. 2014), but few fine-resolution studies of pollination supply-demand balances in heterogeneous landscapes exist (Kennedy et al. 2013; Olsson et al. 2015). This research gap is particularly apparent in urban settings (Grafius et al. 2016; Davis et al. 2017) where studies typically map only pollination supply, and do not consider the impacts of different urban land-use practices on the dynamics of pollination delivery, leaving a critical gap in our understanding of supply-demand relationships.

We develop a spatially-explicit, habitat model-based framework (Fig. 1) for assessing the capacity of urban ecosystems to supply pollination services to satisfy urban agricultural demands, thereby linking supply with demand while considering scale and land-cover dependencies. We demonstrate this approach in a case study area, Iowa City, IA, USA. We first refine land-cover data using an empirical model that predicts floral resource availability based on socio-economic data, then use the resulting land-cover dataset to implement the InVEST pollination model to identify fine-resolution variation in pollination supply. We employ kernel-density estimation to identify urban-agriculture hotspots and spatially link pollinator supply with demand. In so doing, we seek to address the following research questions:

1. How does pollinator supply and demand vary spatially in an urbanized landscape?
2. Are nationally-available socio-economic data related to estimates of pollinator habitat quality and can they be of value in assessing and managing pollination service supply?
3. Where and to what extent does pollination supply match demand from urban agriculture?

This study thus makes three key contributions. First, it identifies scale and land-cover dependencies inherent in modeling urban pollination and stresses the need to account for the spatial heterogeneity of urban landscapes in predicting pollination supply. Secondly, it demonstrates that socio-economic attributes are important indicators of land management practices that influence pollinator habitat quality and pollination supply. Finally, our findings increase our ability

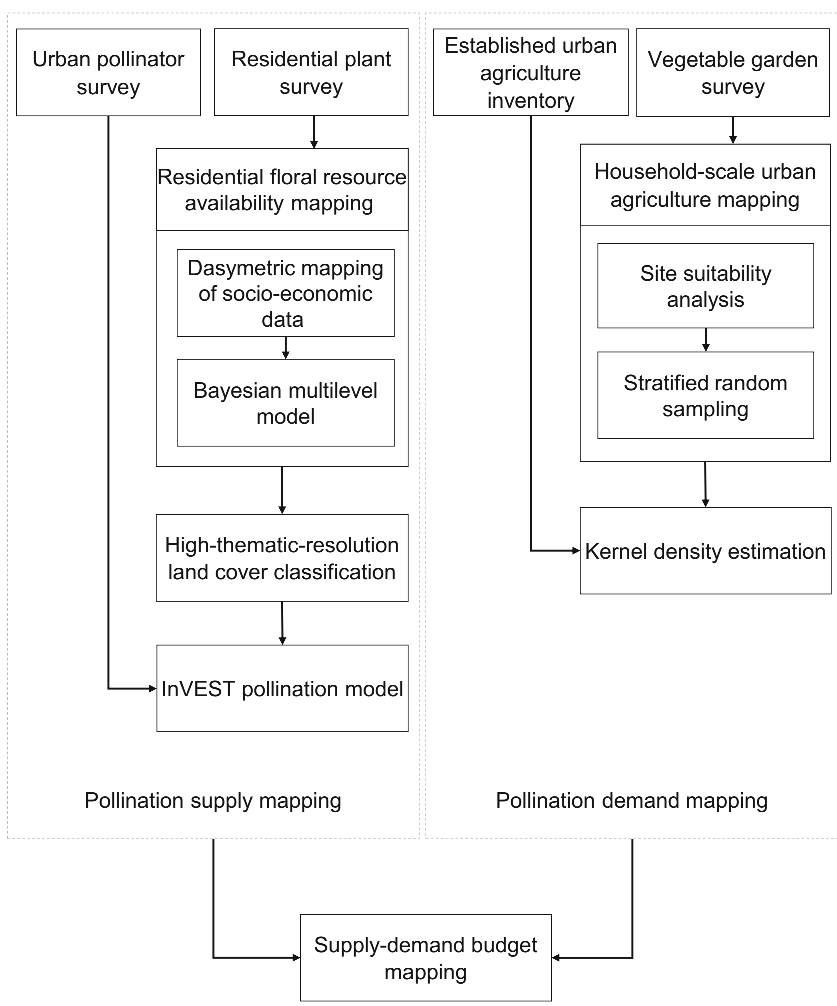


Fig. 1 Methodological diagram for mapping pollination supply-demand relationship

to quantify, map, and compare urban pollinator supply and demand at high spatial resolutions and could enhance urban landscape management to support both pollinator conservation and urban agriculture.

Methods

Study area

Iowa City is one of the most densely-populated cities in Iowa, with an estimated 2016 population of 74,000 and a population density of 1136 per km^2 (Fig. 2). Based on a high-resolution land-cover map (HRLC) for Johnson County (Iowa Department of Natural Resources 2012), the county that contains Iowa City, the dominant land covers in the study area include grass (i.e., lawns and semi-natural grasslands, 30%); roads and structures (14%); trees (23%); corn and soybean agriculture (28%); and water and wetlands (3%) (Appendix A, Table 1). The intensity of urbanization generally decreases with increasing distance from the city center. Crop fields dominate the edge of the city.

Data collection and preparation

Urban pollinator survey

We surveyed bees in five urban/suburban neighborhoods in 2015 (sites 1–5) and on two urban farms in 2010 (sites 6 and 7) (Fig. 2a). We chose the seven urban sites to represent land-cover variation and different study-area environments, based upon our knowledge of a series of site characteristics that may contribute to differences in pollinator community structure: level of imperviousness, neighborhood age (i.e., mean year built) (Appendix A: Table 3), presence of urban agriculture, and native plant diversity. We used established bee sampling protocols (Hendrix et al. 2010). Briefly, we netted bees from flowers on 1 ha plots at each site in June, July, and August when temperatures exceeded 15.6 °C and wind speeds were under 15 kph. Two collectors systematically visited all flowering plants in a plot to collect bees by netting for a total of 1 h in the morning and 1 h in the afternoon on each plot. We also collected bees using pan traps on days coinciding with netting. Pan trapping consisted of 12 bowls of 3 different fluorescent colors (blue, yellow and white) filled with soapy water. Bowls were placed roughly 9–10 m apart from one another on a transect through the middle of each site in the morning and contents were collected after 6 h. We identified bees to genus using Michener et al. (1994). We measured the mean inter-tegular span (i.e., distance between the wing bases in mm) of 5–10 specimens per genus. Based on this estimator of body mass, we predicted genus-specific typical foraging ranges using a power function (Greenleaf et al. 2007).

Residential plant and vegetable garden survey

We conducted 35 field surveys of herbaceous plants and residential gardens on cadastral parcels in nine study area residential neighborhoods in summer, 2017 (Fig. 2b). We focused on herbaceous plant richness because it is one of the most important limiting factors for wild bee communities (Roulston and Goodell 2011). We first selected 35 spatially-dispersed sampling sites using stratified random sampling. Residential neighborhood defined the stratum. The number of sampling sites in a neighborhood was proportional to neighborhood parcel density as identified using a parcel dataset from the Johnson County Assessor's Office. We surveyed all residential property parcels within a 250 m radius centered on each site. We chose 250 m as the radius because it is one of the lowest foraging ranges of bees encountered (Appendix, Table 2) and to maximize sample size (at least 22 residential parcels/site) while controlling cost in time and labor. In total, we sampled 4598 parcels, tallying the number of herbaceous plant genera per parcel in front and back yards from streets, sidewalks, and back-alleys. We scored each parcel to identify its relative plant genus richness as follows: 0 = monoculture turf grass; 1 = richness $\in \{1, 2, 3\}$; 2 = richness $\in \{4, 5, 6\}$; 3 = richness $\in \{7, 8, 9\}$; 4 = richness $\in \{10, 11, 12\}$; 5 = richness >12. During sampling, we also recorded the presence and absence of vegetable gardens (if observable) to support pollination demand mapping.

Residential floral resource availability mapping

We developed a spatially-explicit predictive model following a social-ecological approach to estimate herbaceous plant genera richness in residential neighborhoods at the Census block level. While herbaceous plant richness is heterogeneous among residential properties, it follows predictable spatial patterns influenced by site physical characteristics (e.g., canopy coverage, slope, yard size) (Thompson et al. 2004; Cook et al. 2012). Social drivers, including population density, housing and neighborhood age, cultural identity, and economic and educational status influence herbaceous plant composition in residential yards (Martin et al. 2004; Kinzig et al. 2005; Grove et al. 2006; Luck et al. 2009; Schaeg 2017). Using our herbaceous plant survey data, we estimated mean relative plant genus richness for all 212 Census blocks that intersected residential neighborhoods for which we had sampled at least 30% of the surface area of the residential parcels. We selected twelve independent variables to represent key environmental, demographic and socioeconomic characteristics of Census blocks. These included four physical variables: LiDAR-derived tree canopy cover (Zhao and Sander 2015), slope (using a 3-m DEM from Iowa Geological and Water Survey 2010), yard size (non-built areas within residential parcels) and property built year (Johnson County Assessor's Office).

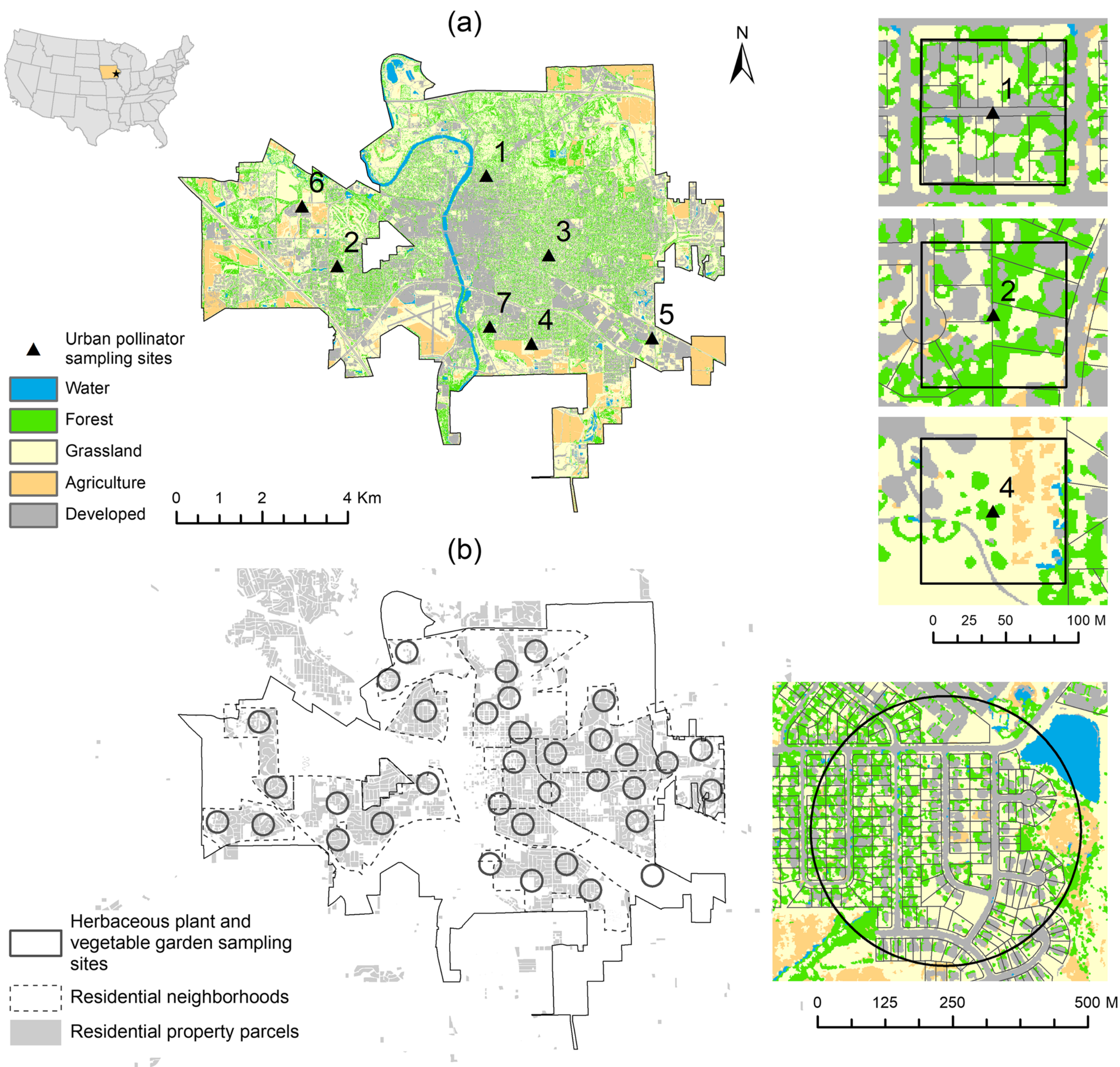


Fig. 2 Study area (Iowa City, IA) land cover. **a** Location of pollinator survey sites. The inset depicts land cover in three one hectare bee sampling plots. **b** Location of 35 residential garden survey sites. The inset depicts land cover and parcel boundaries for a 250-m-radius circular site in which we surveyed parcel-level herbaceous plants and vegetable gardens

We included eight additional variables in our predictive model using 2015 US Census American Community Survey (ACS) data: population density, population proportion Black, Hispanic, renter, limited English proficiency, with college and graduate degrees, and in poverty.

Because we sought to capture spatial heterogeneity in floral resource availability across urban neighborhoods, we refined our explanatory variables from a coarser to a finer resolution. Since the finest Census ACS data were at the block-group level, we used dasymetric mapping (Mennis 2003), an areal interpolation technique that uses ancillary data to redistribute data to finer resolutions. We firstly combined the 30-m National Land Cover Database (NLCD) 2011 Percent Developed Imperviousness data with parcel data to identify and remove uninhabited areas. We then assigned the remaining landscape pixels a high-, medium- or low-intensity development class according to a quantile classification of imperviousness. We sampled population density for block groups composed predominantly of each development class and calculated the fraction of the population in each development class by block group. We based derivation of this population fraction on both relative population density and areal coverage of each development classes following Mennis (2003). We weighted block group-level ACS data using the resulting fraction to derive population count estimates for individual pixels for each development class. Finally, we aggregated count estimates to blocks and calculated variables representing estimated proportions of block populations for the eight variables identified above.

We applied Bayesian hierarchical modeling to estimate block herbaceous plant richness using the rjags and coda packages in R version 3.3.3. This technique was appropriate for our survey design in which herbaceous plant richness data were nested within two geographical scales (i.e., Census block and residential neighborhood). We started with a highly parameterized model and used backwards selection guided by Akaike Information Criterion (AIC) scores and p-values to select a parsimonious covariate set for prediction. We assessed multicollinearity using variance inflation factors (VIF). We then fit a Bayesian linear regression model that assumes no neighborhood effects and two Bayesian mixed models that allow the intercept and slope parameters to vary with residential neighborhood, respectively ($n = 9$, Appendix A: Table 3). We selected our best-fit model for out-of-sample prediction ($n = 411$) based on Deviance Information Criteria (DIC) scores and Root Mean Square Error (RMSE) using leave-one-out cross validation. The resultant values allowed us to group residential property parcels intersecting these blocks into five land-use categories using a Jenks natural break classification of relative plant richness estimates. These new land-use classes were used to represent parcel-level floral resource availability in residential neighborhoods (Fig. 3a).

Mapping pollination supply

Developing a high thematic-resolution land-cover dataset

The original 1-m HRLC dataset defines fourteen land-cover classes, including three forest and two grassland classes (Appendix A: Fig. 1a & Table 1). Prior to modeling pollination supply, Dr. Stephen D. Hendrix (SDH), a bee expert, quantified the capacity of each HRLC class to support wild bees. It was evident in casual surveys that the HRLC grassland classes (i.e., Appendix A: Table 1, grass 1 & 2) did not adequately reflect variation in foraging resources within urban grassy areas, particularly in residential neighborhoods. Therefore, we developed a high thematic-resolution land-cover dataset, hereafter the ES land-cover dataset (ESLUC), to better-characterize pollinator habitat in such settings.

This process focused on refining the HRLC dataset to include distinctive urban plant richness categories reflecting variation in pollinator foraging resources. We first identified high-quality prairie using a map of native plant communities in Iowa City natural areas from the City of Iowa City to produce a GIS inventory of natural prairies. We also identified locations of major existing urban agricultural sites and digitized them in GIS (see "Mapping pollination demand" section for details). We then combined the natural prairies and urban agriculture layers with the HRLC dataset. We next used our floral resource availability map (Fig. 3a) to subdivide HRLC grass types in residential neighborhoods into five land-use categories characterized by different herbaceous plant richness. Specifically, inside residential parcels, we used if/then rules to reclassify HRLC classes to the new ESLUC classes as follows. We maintained water, wetland, forest, road, structure, and impervious classes, but reclassified grass1 and 2, cut hay, corn, soybean, barren, and fallow into five classes indicative of floral resource availability using the floral resource availability map developed in "Residential floral resource availability mapping" section. We then combined and converted all remaining grass 1 and 2 pixels from HRLC to one ESLUC class (i.e., grass). The final ESLUC dataset contained 20 land-cover classes: 2 water, 3 forest, 8 grass, 4 agricultural and 3 built (Appendix A: Fig. 1b) that provide a better thematic representation of classes with respect to bee habitat heterogeneity than the original HRLC (Appendix A: Fig. 1, insets).

The InVEST pollination model

We used the InVEST pollination model version 3.3.3 to model pollination supply (Sharp et al. 2016). Model inputs included the land-cover map developed above, information about nest site and floral availability by season for each land-cover type and a list of local bee genera and their life history traits, including typical foraging range, preferred nesting substrate and active flight seasons. The model assumes that surrounding floral abundance influences the local abundance of each bee genus, and that impacts decrease with increasing distance. Based on this assumption, the model smooths the floral resource availability surface using a Gaussian kernel of bandwidth equal to the typical genus-specific foraging range. It then multiplies the smoothed floral availability scores by a nest site availability score based on the nesting location (tree cavity or ground) of each genus and its availability by land-cover class. The resulting pollinator source score indicates pixel-level relative crop pollinator abundance. Finally, the pollinator source surface is smoothed to generate a pollination supply map that indicates pixel-level relative abundance of pollinators (Lonsdorf et al. 2009). Because this model is computationally intensive, we resampled the 1-m ESLUC map to 5-m resolution using the nearest neighbor technique to reduce model run time. We conferred with SDH to score each land-cover class in terms of its relative capacity to provide foraging and nesting resources by season (range: 0–1; Appendix A: Table 4). In general, natural prairies were assigned high scores (range = 0.7–1), followed by residential yards with high herbaceous plant richness, and forest types. Sites of urban agriculture and residential yards with moderate plant richness

Fig. 3 Floral resource availability for Iowa City residential parcels. **a** We grouped residential parcels into five categories based on relative plant richness estimated at the Census block level using the Bayesian random slope model (1 = low plant richness, 5 = high plant richness). **b** Examples of residential yards with relative floral resource availability ranging from 1 to 5. Photographs were taken by the authors

received moderate scores (range = 0.3–0.6), followed by rural monoculture agricultural classes and residential yards with low plant richness (score range = 0–0.2). Water, artificial structures (i.e. buildings, roads) and shadow do not provide floral or nesting resources, and thus scored zero. We considered all bee genera observed in the field except cleptoparasitic bees (i.e., *Coelioxys*, *Nomada*, *Sphecodes*) that do not directly interact with floral resources. For each genus, we assigned life history traits (i.e., typical foraging range and relative activity intensity for four flight seasons) using lab measurements ("Urban pollinator survey" section) and expert opinion (Appendix A: Table 2). We used equal weights for the different seasons and nesting guilds.

Model evaluation and validation

To investigate the robustness of InVEST model results to input land-cover data thematic and spatial resolution, we applied the InVEST model using both the HRLC and the ESLUC datasets at 5-m resolution as input data. We then carried out pairwise map comparisons, in which we visually and statistically contrasted spatial patterns identified using the HRLC with patterns identified using the ESLUC. In addition, we validated both modeled outputs with bee data collected from the urban sample plots. We used Pearson product-moment correlation tests coupled with Bonferroni outlier tests to assess whether the InVEST mean pollination supply scores for all grid cells within a 100 m × 100 m square buffer of sampling sites reflected the primary bee abundance and richness data collected from the field.

Mapping pollination demand

We defined *pollination demand* as the direct use of pollination services by established urban-agricultural entities (i.e., urban farms, community gardens, edible landscapes, community-supported agriculture (CSA)), and the estimated demand in residential yards based on neighborhood surveys (see 2.2.2. above). Demand mapping began with the compilation of locations of existing urban agriculture from a variety of data sources, including online catalogues and databases maintained by non-profit organizations (e.g., Iowa Local Foods Connection, Iowa Department of Agriculture & Land Stewardship, and Backyard Abundance), as well as social media (e.g., Facebook), government websites and personal communications. We visited all of these locations to confirm that they were urban agricultural sites, and then digitized the locations in ArcGIS v10.3.

Mapping of pollination demand from household-scale agriculture production followed two steps. We firstly delineated all non-built areas of residential parcels by overlaying the HRLC map and the parcel layer in a GIS, identifying these areas as productive space available for agriculture. We then narrowed down the choice of suitable residential yards for agriculture production by removing parcels on steep slopes (> 10%) or with limited productive space (< 4 m^2). Our residential garden survey suggested that 15% of study area residential yards have vegetable gardens and that garden density varies among neighborhoods (Appendix A: Table 3). We used stratified random sampling based on observed garden density by neighborhood to assign a subset of suitable private yards to have vegetable gardens, thereby spatially estimating sites of pollination demand for private home gardening. Unassigned suitable yards represent potential future urban garden demand.

We detected the spatial characteristics and significant hotspots of social demand for pollination services via a kernel density estimation using a Gaussian kernel function with a search radius determined by a spatial variant of Silverman's Rule-of-Thumb (Silverman 1986). The resulting smoothed surface indicated the density of urban agriculture across the study area, with higher values indicating higher demand for pollination services.

Supply-demand balance

We used the InVEST pollination map to indicate the biophysical supply of pollination and the kernel density map of urban agriculture to indicate pollination demand. To enable direct comparison between supply and demand, we first normalized demand and supply to a scale of 0 to 1 using linear feature scaling and classified these maps into areas with relative low and high supply and demand. We used a quantile classification scheme of supply and demand as follows: 0 = no supply/demand; 1 = very low (lowest quintile), 2 = low (second quintile), 3 = medium (third quintile), 4 = high (fourth quintile), 5 = very high (top quintile). We mapped relative differences between supply and demand by subtracting the supply layer from the demand layer to produce a supply-demand budget map with a range of −5 to 5. Here, a value of 5 represents a site with very high supply, but no demand (high surplus), and a value of −5 indicates a site that has high relative demand, but no supply (high deficit). Where supply matches the demand exactly, values are 0.

Results

Local wild bee and plant communities

We modeled 23 bee genera, 8 cavity-nesting and 15 ground-nesting, using the InVEST pollination model (Appendix A: Table 2). Mean bee genera richness per field site was 16 (standard deviation (SD) = 2) and mean monthly bee abundance was 76 (SD = 46) (Appendix A: Table 5). The highest percentage of residential yards (37%) in our floral resource surveys had relative plant richness scores of 1 (i.e., richness ∈ {1, 2, 3}). Mean relative plant richness per parcel was 2 (SD = 1) (i.e., richness ∈ {4, 5, 6}).

Residential yards with floral and nesting resource scores of 4–5 (≥10 genera) comprised about 10% of sampled parcels and were concentrated in medium-density residential areas near downtown Iowa City. Areas along the urban fringe consisting predominantly of newer, larger lots had lower scores. Based on the stepwise AIC procedure (Appendix A: Table 6), three covariates, population proportion below the poverty level (VIF = 2.04), proportion with college degrees (VIF = 1.76), and year the property was built (VIF = 1.22), were incorporated in the multilevel model and used to predict relative residential yard plant richness by Census block (Appendix A: Fig. 2a & 2b). The Bayesian random slope model was identified as the best model with lowest DIC = 525.6 and RMSE = 0.776 (Appendix A: Table 7 and Fig. 2c). Education level (slope coefficient = 0.244, $p < 0.001$) was significantly and positively associated with higher plant richness, whereas the year of property construction was significantly negatively correlated (slope coefficient = −0.551, $p < 0.001$). The strength of these relationships varied among neighborhoods (Appendix A: Fig. 2d). Only one neighborhood (Appendix A: Table 3, neighborhood 4) with older housing, predominantly apartments rented to university students, had a significant negative correlation between poverty and plant richness (slope coefficient = −0.288, $p < 0.001$).

We produced our residential parcel floral resource availability map using the estimated plant richness scores and a natural breaks classification (Fig. 3a). The first class occurred mainly on the urban fringe and included properties characterized by heavily-managed turf grass or unmanaged lawns with common weeds (see Fig. 3b [1]) and thus low floral resource availability. The second, third and fourth classes included residential yards with low (≤3 genera, see Fig. 3b [2]), medium (4–6 genera, see Fig. 3b [3]) and high (7–9 genera, see Fig. 3b [4]) plant richness. The fifth class, which occurred predominantly in centrally-located, older, medium-density neighborhoods, exhibited the highest herbaceous plant richness (≥10 genera, see Fig. 3b [5]) and floral availability. Our results indicate that urban residents typically maintain small (mean = 1228.3 m^2, SD = 1731.9 m^2, range: 32.72–41,088.00 m^2), resource-rich urban gardens.

Pollination supply from urban ecosystems

Both the ESLUC-based InVEST pollinator source map (Fig. 4a) and the HRLC-based map (Fig. 4b) show considerable variation in relative pollinator abundance across Iowa City. High pollinator sources occurred in high-quality forest and grasslands (e.g., natural forest, prairie preserves) and residential yards with high plant richness. Low pollinator sources occurred in downtown and southern Iowa City, the urban fringe, and industrial, commercial, and newer residential areas.

The maps of relative pollinator abundance we produced using the improved thematic resolution ESLUC model (Fig. 4a) differed substantially from the HRLC-based map (Fig. 4b). The ESLUC map identified isolated high-quality pollinator habitat patches surrounded by lower quality habitat (e.g., residential yards in densely-developed areas, medium-sized natural grasslands near the urban outskirts, Fig. 4a), while the HRLC-based model (Fig. 4b) showed smoother patterns and failed to capture these details. The contrast between the two pollinator-source maps was particularly high in semi-natural grasslands and open spaces (e.g., golf courses, airport, rural vacant lots). Overall ESLUC- and HRLC-based pollinator source values were only weakly correlated ($r = 0.42$, $p < 0.001$).

Our validation analysis indicated that using the higher thematic-resolution ESLUC improved model performance. Bonferonni-adjusted outlier tests indicated no outliers in the data (i.e., no studentized residuals with Bonferonni, $p < 0.05$). ESLUC-based pollinator source scores exhibited significant, positive correlations with both observed bee abundance (Fig. 4c, $r = 0.93$, $p = 0.002$) and genus richness (Fig. 4e) ($r = 0.85$, $p = 0.016$). The HRLC-based pollinator source scores were not significantly correlated with observed bee abundance and genus richness (Fig. 4d and f).

Pollination demand from urban agriculture

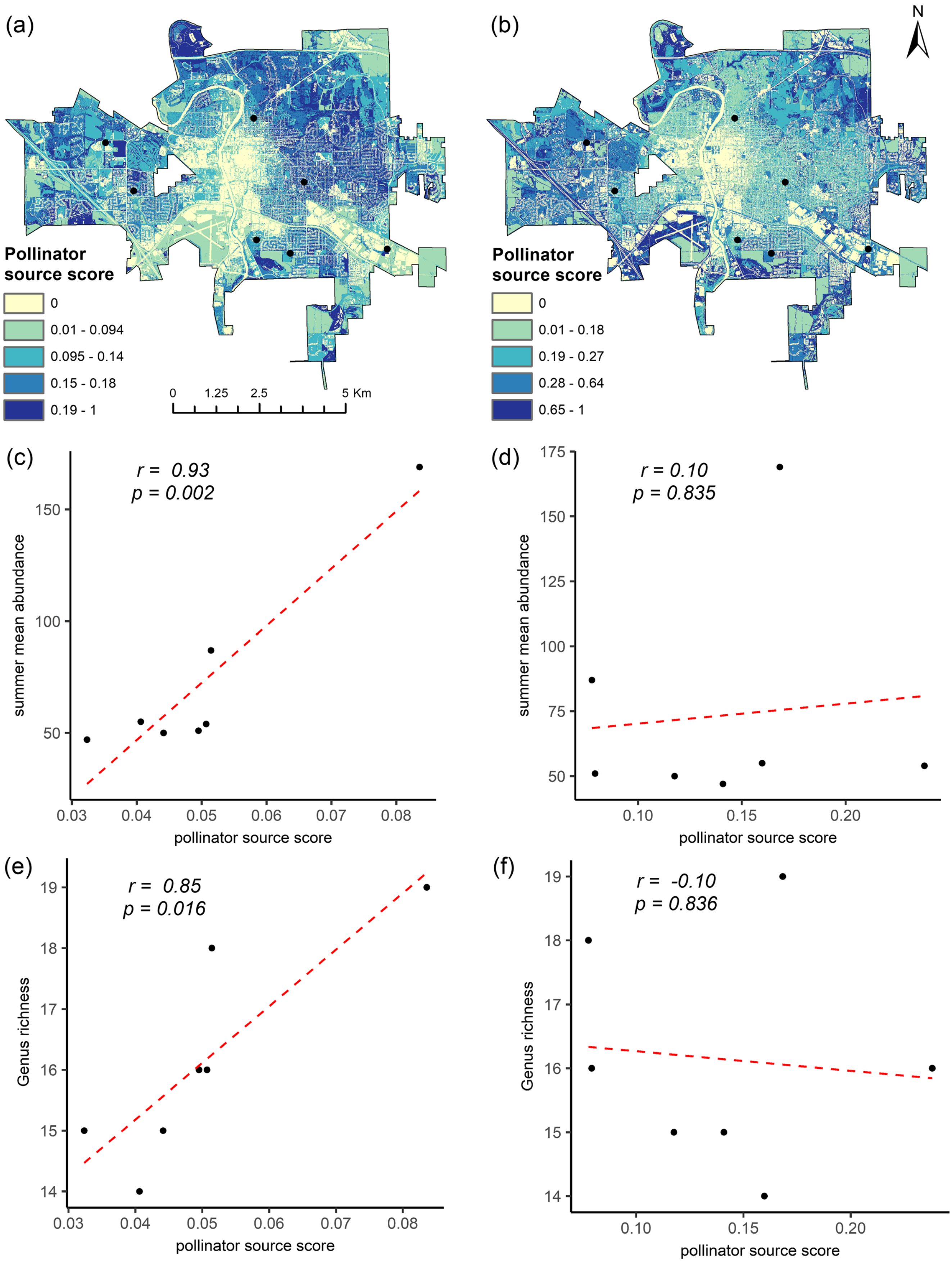
We identified 32 urban agricultural sites: 9 community gardens, 6 school gardens, 4 CSAs, 7 edible landscapes and 6 urban farms (Fig. 5a). In addition, 15% (763) of parcels surveyed revealed some type of gardening practice (e.g., raised vegetable beds, vegetable pots, front/backyard gardens) (Fig. 5b). Home garden density in neighborhoods ranged from 8% - 24% (Appendix A: Table 3). Urban agriculture covered 4.1% of Iowa City's land and was unevenly distributed (Fig. 5c). While small home vegetable beds were widespread in medium-density housing districts, larger urban farms and allotment gardens were sparsely-dispersed in low-density urban fringe areas. Using stratified-random sampling based on field-identified garden densities in different neighborhoods, we estimated the existence of an additional 2228 home gardens (but do not indicate exact locations of these home gardens).

Analysis of supply-demand balance

Pollination supply showed clear spatial patterning (Fig. 6a). Areas of very high supply (value = 5) covered about 20% of the study area, occurring in a large forested patch and older residential neighborhoods in the northern part of the city and in smaller patches in western and southern Iowa City including natural and semi-natural areas. Very low and low pollination supply (value = 1 & 2; 40%) occurred in downtown Iowa City where impervious surfaces dominate, and in highly-impervious areas of eastern and southeastern Iowa City characterized by recent development and low floral resource availability.

Demand exhibited a different distribution (Fig. 6b). Areas of high and very high pollination demand (value = 4 & 5; 26%) covered large areas of central, eastern, and southern Iowa City and patches in western Iowa City. Conversely, very low supply and low demand (value = 1 & 2; 37%) occurred in areas of industrial agriculture (i.e., corn, soybean monocultures) and in industrial northern and far southern portions of the city. Pollination demand was zero in 23% of the study area.

The supply-and-demand balance showed clear spatial patterning (Fig. 6c). Here positive values indicated that supply exceeds demand (a budget surplus), while negative values indicate the reverse (a budget deficit). We found balanced pollination budgets in 16.4% of the study area (value = 0). More land had a pollination budget surplus (36.4 km^2) than had a budget deficit (29 km^2). Areas of high pollination surplus (value = 4 & 5; 12.92%) were predominantly located in the heavily-vegetated residential neighborhoods in the north and south of the city and in natural grassland and forests.


(a)
Pollinator source score
0
0.01 - 0.094
0.095 - 0.14
0.15 - 0.18
0.19 - 1
0 1.25 2.5 5 Km
(b)
N
Pollinator source score
0
0.01 - 0.18
0.19 - 0.27
0.28 - 0.64
0.65 - 1
(c)
r = 0.93
p = 0.002
summer mean abundance
pollinator source score
(d)
r = 0.10
p = 0.835
summer mean abundance
pollinator source score
(e)
r = 0.85
p = 0.016
Genus richness
pollinator source score
(f)
r = -0.10
p = 0.836
Genus richness
pollinator source score

◀ **Fig. 4** Pollinator source maps showing relative pixel-level pollinator abundance based on the ESLUC (**a**) and HRLC (**b**) datasets with locations of pollinator sampling sites locations (●). Relationships between the ESLUC- (**c**) and HRLC-based (**d**) pollinator source scores and observed bee abundance and between the ESLUC- (**e**) and HRLC-based (**f**) pollinator source scores and observed bee richness

High pollination deficits (value = −5 & -4; 0.16%) occurred in a north-south band across central Iowa City including high-poverty, dense residential neighborhoods dominated by rental property and new housing estates with low floral resource availability.

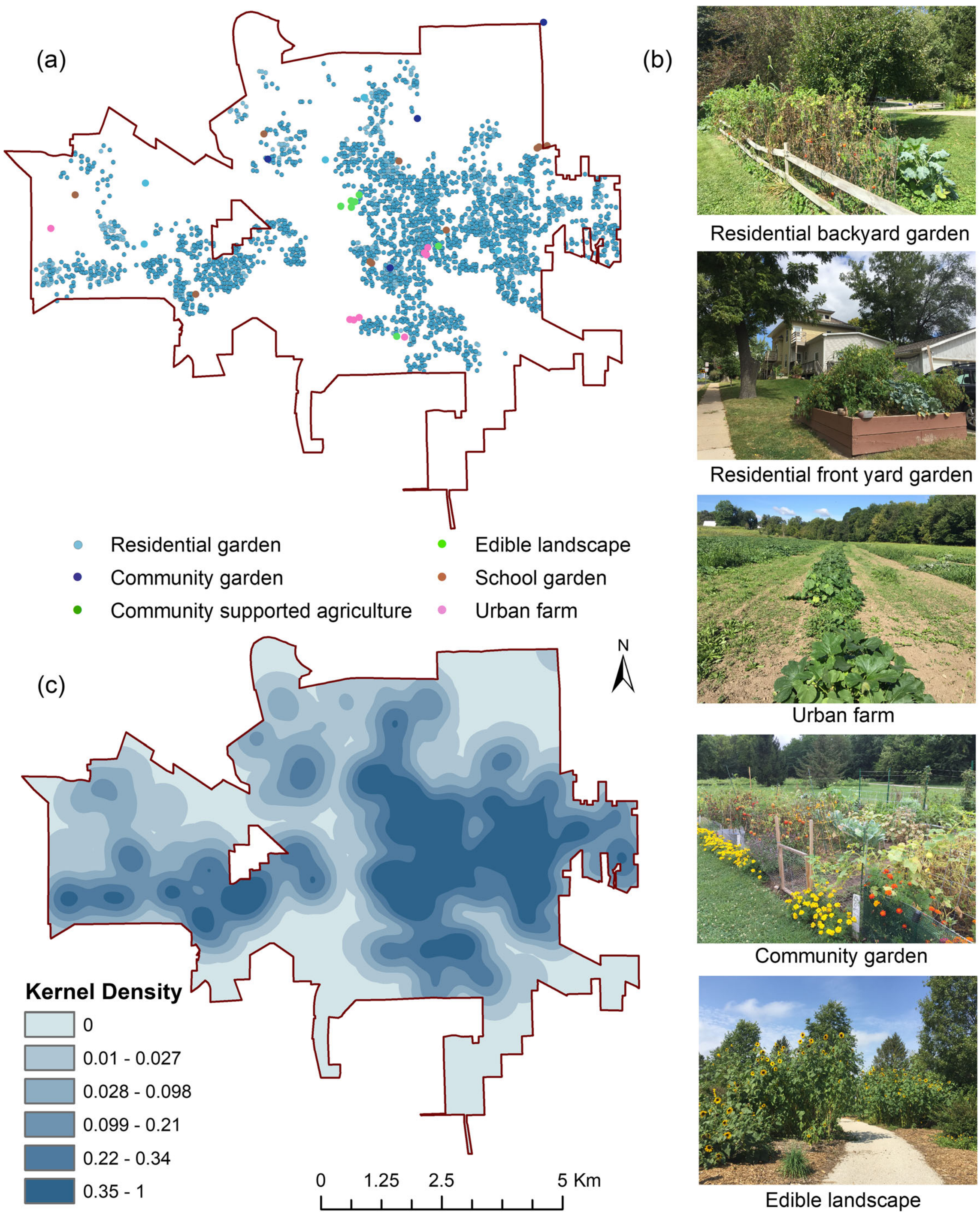


Fig. 5 Pollination demand maps. **a** Iowa City urban agriculture sites. **b** Examples of different types of urban agriculture, and **c** kernel-density smoothed map of urban agriculture, an indicator of social demand for pollination. Photographs were taken by the authors

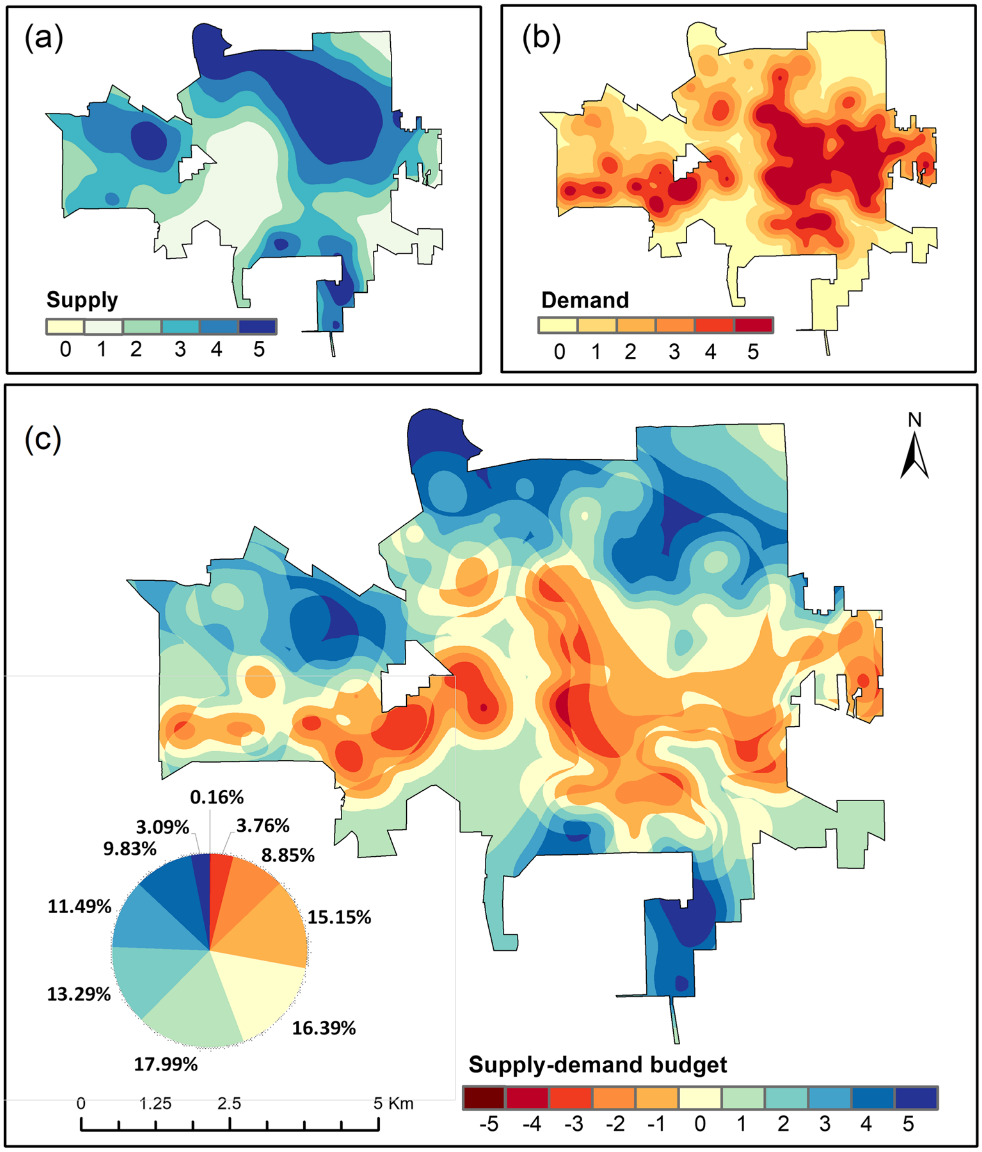


Fig. 6 Comparison between supply and demand. **a** Pollination supply on a scale of 0–5 based on quantile classification (0 = no supply, 1 = very low supply, 2 = low supply, 3 = medium supply, 4 = high supply, 5 = very high supply). **b** Pollination demand on a scale of 0–5 based on quantile classification (0 = no demand, 1 = very low demand, 2 = low demand, 3 = medium demand, 4 = high demand, 5 = very high demand). **c** Pollination supply-demand budget on a scale of −5 - 5 (−5 = highest budget deficit, 0 = neutral balance, 5 = highest budget surplus)

Discussion

Urban agriculture enhances the health and well-being of growing urban populations (Armar-Klemesu 2000). Ensuring the existence of wild bee communities to support urban agriculture requires an understanding of urban pollination services from both supply and demand perspectives. Existing studies typically identify only urban pollination supply, failing to identify pollination demand and supply-demand relationships and often oversimplifying highly heterogeneous urban environments. In this study, we sought to identify spatial patterns in urban pollination supply, demand and supply-demand balance, as well as scale and land-cover dependencies in estimating urban pollination services. We also explored indirect relationships between socio-economic variables and pollinator supply by identifying relationships between these variables and pollinator habitat quality and using them to refine existing land-cover data. By identifying these relationships and by quantifying and mapping pollinator supply and demand at ecologically-sensible and policy-relevant scales, this study adds to our understanding of pollination delivery in cities and ability to manage and support urban agriculture and the wild bees on which it depends.

Our results show that urban landscapes can generate high pollination supply, but that this ability varies with landscape composition. We find low supply in areas with high impervious surface coverage (e.g., industrial and commercial zones) and very high supply in natural areas and small, dispersed patches in moderately-urbanized settings (Fig. 4a). For example, we found the highest bee abundance in a small (1382 m^2) prairie patch surrounded by low-suitability habitat (i.e., site 5, Fig. 1, Appendix A: Table 5). This observation is consistent with past research that found isolated patches of high quality habitat exhibited high pollinator visitation rates in resource-poor areas (Davis et al. 2008; Olsson et al. 2015).

Our pollination supply map also shows high service provisioning in medium-density residential neighborhoods. We attribute this higher pollination supply primarily to human production of hybrid landscapes that exhibit fine-scale interspersion of built areas with fruit trees, ornamental flowers and small urban greenspaces (e.g., road ditches, nature trails, playing fields, vacant lots), providing high-quality floral resources and nesting substrates for pollinators. As our floral resources model indicates, these landscapes are at least partially tied to socio-economic attributes of urban populations (i.e., wealth, education) and to the age of urban environments, indicating urban land-use history interacts with the characteristics of urban land managers to produce pollinator habitat of varying quality at the scale of individual parcels. This fine-grained, variation in habitat quality in turn influences pollinator supply for urban agriculture. The actions of individual humans in managing their seemingly miniscule portions of urban landscapes, thus, in aggregate shape urban systems and the provision of pollinators in those systems.

Our pollination model validation suggests that accurate mapping of pollination supply requires high thematic resolution land-cover datasets that reflect urban habitat quality in more detail than existing land-cover datasets (e.g., NLCD, HRLC) provide (Fig. 4a and b). Through field surveys and statistical inference, we identified substantial heterogeneity in the distribution of plant genus richness within and across urban residential neighborhoods that existing land-cover data did not capture. Different land-management practices produce residential yard land covers that differ widely in their ability to provide foraging resources for wild bees, but that are typically classified into only one or two land-cover classes in existing datasets. Given that land-cover data of sufficiently high thematic resolution for ES modeling are rarely readily available, this finding stresses the importance of refining these datasets to ensure an ecologically-relevant thematic resolution and the quality of pollination supply predictions.

The vast majority of past studies of urban pollinator supply relied solely on existing land-cover data to estimate the quantity and location of habitat resources for pollinators. We found that readily available socio-economic data could be used to refine these datasets to improve their representation of pollinator habitat. These results highlight the ability of socio-economic data to act as indicators of urban land-use decision-making and thereby to capture variation in urban land-use practices that influence urban pollination supply. Our method, which predicts parcel-level heterogeneity in habitat resource availability based on nationally-available census data, treats residential gardens not as independent units, but instead as interconnected habitat patches whose quality is shaped by socio-economic attributes at the neighborhood/landscape scales. This approach could be applied in studies of additional cities to improve the ecological relevance of existing land-cover data, thus improving ES mapping in cities where human activities related to socio-economic status exert dominant impacts on landscape characteristics.

Our results support previous work that found that social stratification (e.g., income, education, housing age, home ownership) and lifestyle factors (e.g., average family size, ethnicity) influence residential land management (Hope et al. 2003; Kinzig et al. 2005; Grove et al. 2006; Mennis 2006; Troy et al. 2007; Luck et al. 2009; Kendal et al. 2012). Through such land management, these attributes of urban households influence the resources available to pollinators. In this study, education level exhibited a significant, positive relationship with plant richness, possibly due to increased knowledge of residential landscape design and sufficient wealth to support it among highly educated populations. Such knowledge may increase the likelihood of undertaking activities such as planting ornamental or native flowers (Luck et al. 2009). Neighborhood age also showed a strong positive correlation with plant richness, with higher richness in older neighborhoods, likely reflecting the lifestyle choices, landscape preferences and cultural values of populations living in older housing districts in the study area (Hope et al. 2003; Grove et al. 2006). The time elapsed since construction may also allow sufficient time for the development of mature gardens.

Our pollination demand map indicates that most of the study area exhibits high urban agricultural pollination demand. Such widespread high demand is due to the prevalence of home gardens. Iowa City is largely suburban. Residential areas occupy approximately a quarter of the study area and have a total of 2.6 km^2 (4%) productive yard space that could support home gardening, as opposed to larger-scale community-based gardens, urban farms, and publicly-owned edible landscapes that constitute a small portion of the landscape. Thus, spatial patterns of pollination demand largely resemble patterns of residential housing in the study area with high demand in medium-density housing districts with detached, single-family homes, and low demand in uninhabited areas (e.g., forests, grasslands, monoculture agriculture). While we only quantified demand from the perspective of urban agriculture, the vast majority of flowering plants, including wild and ornamental garden plants not considered in this study, require insect-mediated pollination. Thus, the true demand for pollination services in our study area landscape is likely to be higher than our estimates.

Our supply-demand analysis identifies interesting relationships and patterns between pollinator sources and urban agriculture. The majority of the study area exhibits a positive or relatively balanced supply-demand budget, indicating an adequate pollination supply for urban agricultural activities. High supply and demand values typically cancel each other out in the vegetated residential neighborhoods adjacent to natural areas. Many such neighborhoods are historic conservation districts, which have dense canopy and herbaceous plant coverage, as well as private vegetable gardens. Areas of high impervious surface coverage also exhibit balanced service delivery due to coincident low supply and demand. Natural areas show high pollination supply, but low urban agricultural demand, resulting in high pollination surplus.

High pollination deficits, however, occur in renter-occupied neighborhoods, high-poverty neighborhoods and new housing developments characterized by heavily-managed urban lawns. In the case of new housing developments, the timing of development may play a key role in determining resource availability such that on such sites sufficient time has not elapsed to allow planting and garden establishment to build floral resources. The situation in high-poverty, renter-occupied neighborhoods suggests interesting feedbacks within urban social-ecological systems whereby poorer, less educated populations manage land in ways that produce lower quality pollinator habitat, leading to low supply of pollinators in their neighborhoods. Wealthy, highly educated populations, conversely, are more likely to enhance pollinator habitat and supply. Urban agricultural developments such as community gardens are frequently touted as means for improving the wellbeing of poorer populations, but may thus be doomed to lower success given the limited ability of pollinator habitat and correspondingly lower pollinator supply in poor neighborhoods. However, as even small patches with high floral richness appeared to enhance pollinator resources in our study, this suggests that simply including a variety of flowering plant species on and around community gardens could enhance their success.

Limitations related to our field surveys could impact our findings. First, we aggregated our bee surveys for the growing season, thus telling us little about seasonal changes in bee community structure. While our pollinator sampling sites were spatially dispersed and representative of different residential and agricultural land uses, they may not represent bee genera distributions across the full spectrum of urban intensities. For example, we lack pollinator surveys in downtown, urban fringe and forested areas. More systematic sampling along urbanization gradients in future studies would alleviate this issue. We also did not explicitly examine sampled bees for managed honeybees raised by urban beekeepers. However, only a small fraction (8.6%) of our sampled bees were of the genus *Apis* that includes these bees. It is also likely that we undercounted backyard plant genera in some neighborhoods where backyards could not be observed, resulting in lower sampling accuracy in these areas.

Given the small-scale, fragmented nature of urban agriculture, we could not obtain comprehensive, spatial pollination demand information related to individual farming and gardening practices. We particularly lack spatial data identifying home gardens on private property in our study area and thus based our assessment of residential pollination demand on site suitability analysis and extrapolation using home garden density estimates from field surveys. Although the geospatial analysis technique utilized here represents one of the most common approaches used to map urban agricultural potential (Kremer and DeLiberty 2011; Saha and Eckelman 2017), it omits many factors (e.g. soil properties, insolation, land ownership, sociocultural preferences) that may prohibit or facilitate residential food production, and could bias our demand map. As such, this demand map depicts realistic locations of residential vegetable gardens, but does not identify their true locations. Thus, while we consider the demand map to be representative, some deviations from true home garden locations could cause supply-demand relationships identified in the budget map to differ from reality. Future efforts could focus on conducting full censuses of residential agriculture through manual interpretation of high-resolution areal images (Taylor and Lovell 2012). Residential agricultural sites could also be identified using statistical models to link urban agriculture to the biophysical and socioeconomic characteristics of mapping units, for instance, based on surveys of a sample of residents. These surveys might also identify crops grown in urban gardens in more detail, thereby facilitating more accurate quantification based on the pollination mechanisms of particular crops (e.g., via insect pollinators, wind, self-pollination).

Conclusions

Mapping spatial relationships between urban pollinator supply and demand is important, but challenging given that the habitats that influence the persistence and distribution of wild bee pollinators are highly fragmented, and that little spatial information exists to identify locations of urban agriculture. The mapping framework demonstrated here adds to our ability to detect spatial variation in the relationship between pollinator supply and demand across urban landscapes. We find that spatial datasets that fail to identify land cover in a manner that reflects habitat resource availability for bees do not accurately estimate pollination supply in heterogeneous urban areas. Our findings indicate, however, that socio-economic attributes can be used to indicate local land-management practices and refine existing land-cover datasets, thereby improving habitat suitability modeling and pollination supply estimates. Specifically, our work highlighted the effectiveness of using nationally-available census data to improve predictions of pollination supply at high spatial resolution.

The mapping framework we demonstrate in this study could support policy-making related to urban agriculture and pollinator conservation. In our study, the identification of specific neighborhoods with surpluses and deficits of pollinators could provide information to inform prioritization of critical areas for conservation or enhancement to support both healthy bee populations and urban agriculture.

Our work also stresses the important role of humans in shaping herbaceous plant richness and thus pollination potential. Human activities modify urban residential landscapes that thus exist as a nested hierarchy of garden management spanning household, neighborhood and landscape scales. Individual land-use decisions matter for the provision of pollination services, given that they collectively affect habitat quality and the distribution of pollinators at broader scales. To ensure coordinated landscape management for pollination services across scales, it is thus critical to integrate the design and management of private residential gardens into city-wide pollinator conservation strategies.

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