

Diversity in flowering plants and their characteristics: integrating humans as a driver of urban floral resources

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Abstract Urban neighborhoods vary in development intensity and in the life style and demographics of their residents. Decisions made by urban residents affect plant communities, their functional characteristics, and the floral resources they provide. We recorded flowers in front-facing yards in 58 neighborhoods in Chicago, IL (USA) and examined patterns in community composition and species turnover between neighborhoods. We investigated how species richness and plant characteristics, including origin, cultivation intent, and life cycle, are affected by neighborhood socioeconomic factors. Urban plant species tended to be perennial, ornamental, and non-native. White clover had the broadest distribution and the highest floral abundance but was not present in several of the highest-income neighborhoods. Although we found 144 morpho-species across neighborhoods, most occurred infrequently. Species turnover was highest for ornamental species and lowest for weedy species, suggesting that intentional plantings are driving beta diversity across the landscape. We found the highest species richness in neighborhoods with intermediate numbers of Hispanic and white residents and with intermediate number of residential lots; neighborhoods with racially or ethnically homogenous populations had fewer plant species. The high frequency of weeds in low-income neighborhoods, the occurrence of certain ornamental plant species in whiter, wealthier communities, and high turnover of species from one neighborhood to another, all suggest a disparity in plant-related ecosystem services across cities. Complexity in urban plantings may be influenced by the suite of perspectives that residents bring towards habitat management. Cultivation sustains a diversity of plants and creates a disparity in plant traits by neighborhood socioeconomics.

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Introduction

As the percentage of global population residing in cities continues to increase, there is a need for healthy and sustainable urban areas. Urban ecosystems potentially provide many important resources to residents. For example, local plants deliver a number of economic and social benefits, including fresh produce, aesthetics (Goddard et al. 2013), and connection to nature (Fuller et al. 2007; Luck et al. 2011). However, the fine-scale heterogeneity of cities (Cadenasso et al. 2007), and the patchwork of small, private parcels of land, creates patchy plant communities that may not provide benefits equally across a city.

Residential yards and gardens play an important role in urban plant biodiversity (Gaston et al. 2005; Bertoncini et al. 2012; Knapp et al. 2012). Making up between 25 and 47 % of urban green space (Loram et al. 2007; Mathieu et al. 2007), yards reflect a managed ecosystem that contributes to plant, invertebrate, and bird diversity (Loram et al. 2007; Lerman and Warren 2011; Belaïre, et al. 2014). Front yards are diverse and can include food gardens, flower gardens, and turf grass. Some yards are actively managed for wildlife (Goddard et al. 2013), and many are tended carefully for cultural or social purposes (Grove et al. 2006). Rather than soil type or other environmental characteristics, behavioral decisions of urban residents have a strong effect on urban vegetation. Humans further influence yard vegetation by modifying canopy cover, adding nutrients and water, and using herbicides. As a result, many yards are dominated by non-native, cultivated plants sourced from garden centers (Pyšek 1998; Cook et al. 2012; Aronson et al. 2015). Since many of these plants are flowering species, the decision of what to plant or remove has profound consequences for animals that use floral resources.

As a managed ecosystem, urban vegetation cover and diversity are influenced by demographic and socioeconomic factors. Income (Hope et al. 2003; Mennis 2006), ethnicity (Minor et al. 2016), family life stage and education (Grove et al. 2006), housing age (Smith et al. 2005), human population density (Lowenstein et al. 2014), and housing density (Knapp et al. 2012) are associated with plant community patterns in residential yards. Although cities have been drastically altered from their natural habitats, environmental pressures such as nighttime lighting and altered soil chemistry still select for and against plants (Williams et al. 2009). Human behavior may act independently or concurrently with abiotic drivers to influence plant traits in yards (Kendal et al. 2012; Goddard et al. 2013). Many questions remain about how humans influence plant traits. A meta-analysis suggested that urbanization may favor taller species with larger seeds, although this trend did not hold true for all cities (Duncan et al. 2011). Other studies conflict on whether native (La Sorte et al. 2014; Bertoncini et al. 2012) or non-native flora (Knapp et al. 2012; Aronson et al. 2015) are dominant in cities. It is not known how traits such as life cycle (e.g., annual vs. perennial) or native status may change between different neighborhoods within a city.

A recent editorial (Hahs and Evans 2015) called for more research on functional ecology in urban ecosystems. Here, we respond to that call by examining plant characteristics and functional traits, distribution, and composition of floral resources in residential, front-facing yards in a highly developed U.S. city. We use the term ‘yard’ to refer to the open vegetated space in front of a residence; it is synonymous with ‘front garden’. By surveying flowering plants across neighborhoods of different socioeconomic status, we aim to understand how

plant traits vary at a fine scale within urban areas. We classify plants according to their life cycle (annual versus perennial), region of origin (native versus non-native), and intent of cultivation (ornamental versus weedy), and ask how income, race, and other socioeconomic factors affect floral resources with respect to these traits. We identify drivers of 1) plant species richness, 2) community composition, 3) turnover, and 4) several plant characteristics in urban neighborhoods. As flowering plants provide important resources for numerous animal species, our work contributes to an understanding of how humans affect biotic interactions and ecosystem function.

Methods

We recorded all open flowers on herbaceous plants and shrubs on 58 urban residential neighborhood blocks (called “neighborhoods” from here forward) in and around Chicago, Illinois (see map of study sites in Figure S1). Site selection was non-random to include neighborhoods across a gradient of socioeconomic conditions (Table 1), enabling a comprehensive assessment of urban floral community composition. Neighborhoods included multi-story apartment dwellings, single family homes, and multi-family two- or three-flats.

We visited each neighborhood twice in summer 2013: a first time between 10 June and 19 July, and a second time approximately 25–30 days later between 25 July and 21 August. Consequently, our methods do not account for plants that bloom during the spring or fall months. We recorded both taxonomic richness of flowers and floral abundance along a 150 m transect that centered on the sidewalk. We counted flowers in a 5 m buffer on either side of the transect and identified flowers to the species level when possible, or to genus level if species identification was not possible (e.g. for genera with many hybrid varieties). We refer to all identified plants, including those identified only to the genus level, as ‘species’ from here forward. To quantify floral abundance, we counted the number of floral units for each species. A floral unit consisted of a raceme, umbel, spike, capitulum, or a single flower, depending on the morphology of the plant (see Baldock et al. 2015; Lowenstein et al. 2015). We pooled flower abundance and species presence at each neighborhood over both sample dates for all analyses.

Classifying plants

All recorded plants were classified by three traits. First we categorized plants by their life cycle in USDA Plant Hardiness Zone 6A, corresponding to Chicago, IL, as surviving for multiple

Table 1 Summary statistics of socioeconomic variables as measured at the block group encompassing each study neighborhood ($n = 58$)

Variable (Unit)	Mean	SD	Range
Human population density (persons/km ²)	17,930	1256	4594–39,583
Median household income (USD)	56,024	3914	11,029–138,188
Renter occupied (%)	50	2	12–78
Hispanic residents (%)	24	4	0–95
White residents (%)	47	4	0–100
Number of residential lots on the block	11	4	3–18

years (biennial or perennial) or surviving for a single year (annual). Second, we classified plants as native or non-native, defining 'native' as plants that evolved in the area east of the Rocky Mountains of the United States. We used taxonomic guides and the Missouri Botanical Garden plant finder when characterizing plant life cycle and origin. Finally, we classified plants by their intent of cultivation as ornamental or weedy species. A plant was classified as ornamental if available for purchase in a garden center or nursery and usually planted intentionally. Weedy plants included species such as *Trifolium repens* L. (white clover) and *Taraxacum officinale* F.H. Wigg (dandelion) that tend to be regularly mowed by homeowners or removed by landscaping companies and also included species that are listed as weedy by turfgrass companies. In a small number of cases, we could not easily classify a plant into one group or another; these species were excluded from the relevant analyses and are noted in Table S1.

Socioeconomic variables

To assess the relationship between socioeconomic factors and floral communities, we measured several socioeconomic variables from each neighborhood, using block group data from the U.S. Census 5 year American Community Survey 2008-2012. These variables, which were selected based on prior studies of neighborhoods in Chicago (Minor et al. 2016) and other cities (e.g., Grove et al. 2006; Knapp et al. 2012; Goddard et al. 2013), included percentage of renter-occupied households, percentage of residents identifying as Hispanic, percentage of residents identifying as white, human population density, and median household income (Table 1). The percent of residents identifying as black or African-American was not included, as this variable is highly correlated with income and with the percent of residents identifying as white. Additionally, we summed the total number of residential lots per neighborhood as a measure of development density. Two sets of socioeconomic variables were significantly correlated: percent renter occupied and income ($r=-0.52$, $P<0.01$) and percent white and income ($r=0.59$, $P<0.001$).

Data analysis - univariate

We used independent t-tests to test for dominance in terms of life cycle, origin, and cultivation intent of plants. We also calculated species rank and abundance in two different ways to compare frequency of plant species in neighborhoods. First, we calculated rank and abundance based on geographic distribution, by counting the number of neighborhoods in which each species was observed. Second, we calculated rank and abundance based on the total floral abundance of each species over all neighborhoods.

We also investigated whether overall taxonomic richness, or richness of different plant groups (native, non-native, perennial, annual, weedy, ornamental), was influenced by neighborhood socioeconomic characteristics through best subsets regressions. We focused our modelling analyses on richness, as this type of presence/absence data is less prone to bias than our measure of floral abundance. We further divided ornamental plants into annual and perennial plants, as ornamental annuals may indicate greater resource allocation towards residential gardens. Species richness data met the assumptions of normality.

We used a model selection approach with multiple regression to test the effect of predictor variables on species richness. Upon inspecting model diagnostics, we identified several non-linear (quadratic) relationships between predictor variables and response variables. If a lower-

order predictor variable selected in the model selection procedure was determined to have a non-linear relationship with the response variable, we also included the quadratic predictor term in model selection. We compared the final best performing models, as identified by best subsets regression, using $\Delta AICc$. We examined the relative importance of each variable in explaining species richness by calculating the Akaike weight for each predictor variable. All modeling was performed using the leaps library in R 3.1 (Lumley 2009).

Multivariate analyses

To quantify change in the plant community from one neighborhood to another, we calculated two measures of beta diversity for each plant group. The first, “true beta diversity” (Whittaker 1960; Tuomisto 2010), was calculated by dividing the total number of species over all sites (i.e., gamma diversity) by the average number of species at a single site (i.e., alpha diversity). The second, Sorenson index, corrects for the increase in turnover as more sites are included through incorporating a pairwise comparison of the sites with the formula

$$Beta = (b + c) / (2a + b + c)$$

where a is the number of shared species in two sites, and b and c represent the number of species unique to each site. This index was averaged over all pairs of sites.

We used Nonmetric Multidimensional Scaling (NMDS) with Bray-Curtis distance to visualize patterns of association among plant species in different groups and used the final stress value of the ordination to evaluate the fit. We then overlaid the socioeconomic variables that were significantly ($P < 0.05$) correlated with plant community composition. Prior to analysis, we Hellinger-transformed the plant community matrices to reduce the weight of rarer species. All plants that could not be identified to genus as well as those appearing on only a single block (totaling 5 % of all plants) were excluded from community matrices. We used the vegan package in R 3.1 for all multivariate procedures.

Results

Plant characteristics

In total, we identified 119 plant species and an additional 25 genera for which we could not distinguish among species (Table S1). When considering all species recorded over all neighborhoods, 104 species were ornamental (72 % of classified species), 96 were perennial (69 % of classified species), and 104 were non-native (76 % of classified species). On average, each neighborhood contained 28 (± 1.2 SE) flowering species and 3407 (± 394 SE) floral units. The t-tests indicated that, at the neighborhood scale, most species were ornamental ($t = 7.25$, $P < 0.01$), perennial ($t = 9.49$, $P < 0.01$), and non-native to the region ($t = 17.54$, $P < 0.01$; Fig. 1). Similarly, at the neighborhood scale, perennial ($t = 5.31$, $P < 0.01$) and non-native ($t = 10.4$, $P < 0.01$) floral units were most abundant. The floral abundance of weedy and ornamental plants did not significantly differ ($t = 0.64$, $P = 0.52$).

On average, each species was observed in 11.6 neighborhoods. However, rank abundance diagrams indicated an uneven community, with a relatively small number of common species in terms of floral abundance and geographic distribution (Figs. 2, and S2). Only 15 % ($N = 21$)

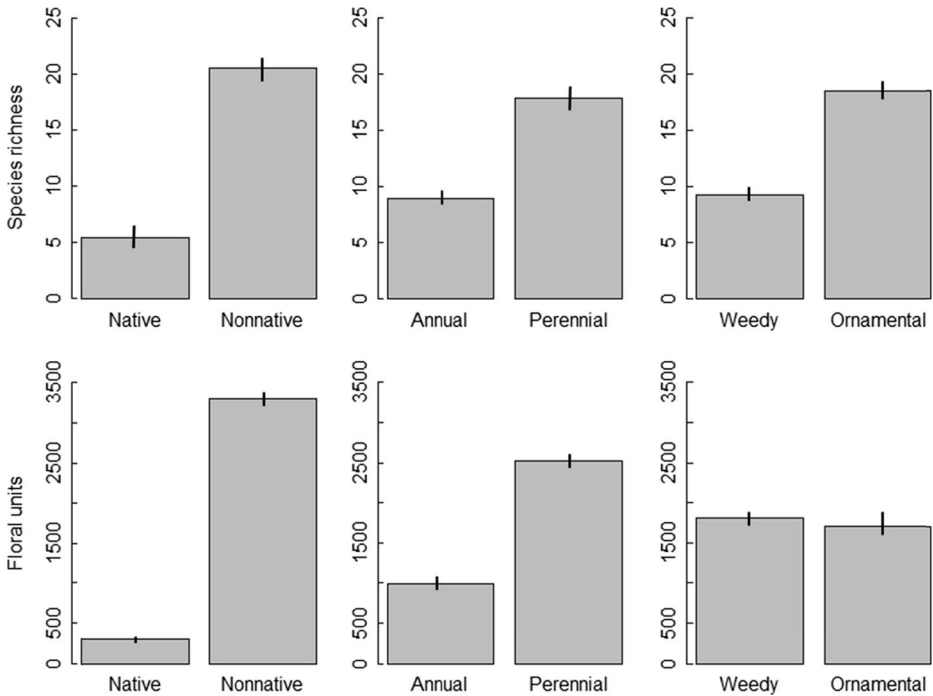


Fig. 1 Mean (\pm SE) species richness and floral units of plant traits per neighborhood

of species were present in > 50 % of neighborhoods, while nearly half were recorded in five or fewer neighborhoods. This disparity is magnified when considering floral abundance. *Trifolium repens*, the most abundant plant in terms of both geographic distribution and floral abundance, had more than twice the number of floral units than the second most abundant plant. Other common plants included *Plantago major* L., *Impatiens* spp., *Petunia* spp., and *Rosa* spp.

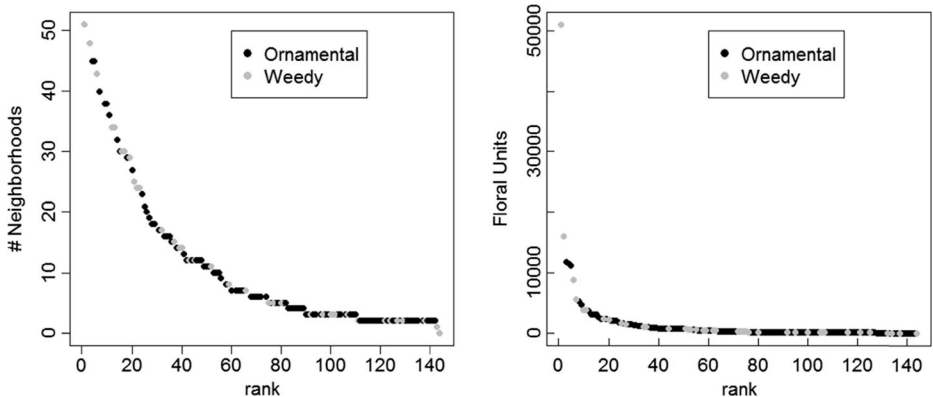


Fig. 2 Rank abundance diagrams for geographic distribution (*left*) and floral abundance (*right*), classified according to cultivation intent. Rank abundance diagrams for other plant characteristics are presented in Supplementary Material (Fig. S2)

Best subsets regression for species richness

We identified a moderate to strong relationship between socioeconomic variables ($0.40 > R^2 > 0.52$) and richness of all plant groups except for native plants. We detected nonlinear relationships between socioeconomic variables and total species richness, as well as richness of six other plant traits (Table 2). Total species richness was best explained by a nonlinear effect of number of residential lots, percent white residents, and percent Hispanic residents (Fig. 3). With the exception of weedy plants and annuals, richness of all plant groups showed a nonlinear relationship with number of residential lots, peaking at an intermediate development level. Weedy plant richness was unrelated to the number of lots, while annual plant richness was linearly and positively related. Other important predictor variables included the percent of white residents (selected for 6 plant groups), and percent of Hispanic residents (selected for 6 plant groups). Income appeared in one model, showing a significant negative linear relationship with weedy species richness (Fig. 4). Model selection identified several 'best' models with $\Delta AICc < 2$ for total species richness, weedy, native, and annual ornamental plants.

Beta diversity

Ornamental annual species had the greatest beta diversity, while weedy species had the lowest beta diversity (Table 3). Sorenson indices tended to be in agreement with beta diversity, suggesting an intermediate degree of turnover of all plant species between sites and the greatest turnover in ornamental plant species.

Multivariate analyses

A 3-dimensional NMDS ordination for total plant community composition shows an apparent geographic separation of weedy and ornamental plants along three axes (stress = 0.16; Fig. 5). All weedy plants are on the left side of the horizontal axis (NMDS1); a few species of interest are labeled. Household income ($r = 0.73$, $P < 0.01$), the percent of white residents ($r = 0.62$, $P < 0.01$), percent renter occupied households ($r = 0.44$, $P < 0.01$), and human population density ($r = 0.36$, $P = 0.03$) were related to plant community composition.

Discussion

Flowers in Chicago neighborhoods are predominantly on ornamental, non-native and perennial plants. Our results provide further evidence that non-native plants are common in densely populated regions (Pyšek 1998; Clemants and Moore 2001; Cook et al. 2012; Aronson et al. 2015) and particularly in yards, where they can comprise >50 % of total species in some cities (Smith et al. 2006; Knapp et al. 2012; but see Bertocini et al. 2012). While Chicago residents appear unconcerned about the origin of their ornamental plants, the trend to cultivate perennial plants, which have reduced yearly planting costs, was nearly identical in British gardens (Smith et al. 2006).

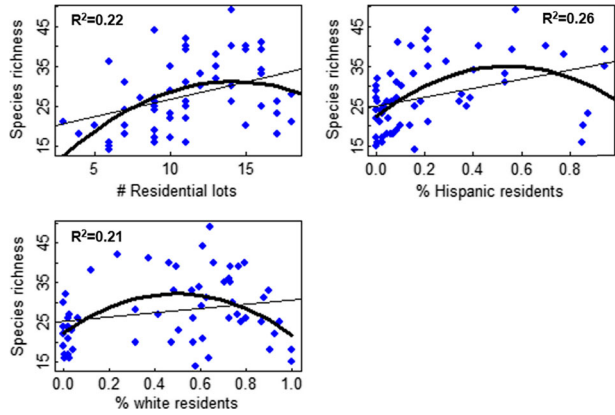
Floral resources were not uniform across neighborhoods. Rank abundance diagrams revealed that >50 % of species appeared in fewer than half of neighborhoods, and that these infrequently occurring species had 12x fewer floral units than more common plants. Some

Table 2 Multiple regression models for effect of socioeconomic variables on plant species richness

Plant group	Socioeconomic predictor variables							# models AICc < 2	R ²	
	# lots	(# lots) ²	% white	(% white) ²	% Hispanic	(% Hispanic) ²	Pop. Density			Income
All plants	(+) 1	(-) 1	(+) 0.41	(-) 0.41	(+) 0.59	(-) 0.59			2	0.46**
Ornamental	(+) 1	(-) 1	(+) 1	(-) 1					1	0.50**
Weedy			(-) 0.37		(+) 0.18		(-) 0.13	(-) 1	4	0.43**
Perennial	(+) 1	(-) 1			(+) 1	(-) 1			1	0.40**
Annual	(+) 1				(+) 1				1	0.40**
Native	(+) 1	(-) 1	(+) 0.18	(-) 0.18	(+) 0.29	(-) 0.29			2	0.20*
Non-native	(+) 1	(-) 1			(+) 1	(-) 1			1	0.51**
Annual ornamental	(+) 0.77	(-) 0.55	(+) 1	(-) 0.55					2	0.52**
Perennial ornamental	(+) 1	(-) 1	(+) 1	(-) 1					1	0.40**

Only variables included in models with $\Delta AICc < 2$ are displayed. For each predictor variable, we show the direction of the coefficient (+ or -) and the variable importance, calculated by summing Akaike weights for the models in which the variable was included. A weight of 1 indicates this variable was included in all models with $\Delta AICc < 2$. We show R² for the model with lowest AICc. * indicates $P < 0.05$. ** indicates $P < 0.01$

Fig. 3 Fitted models for quadratic regression (*bolded line*) and linear regression (*lighter line*) for significant socioeconomic predictors of species richness for all plants. R^2 is shown for quadratic regression



ornamental plants can escape from cultivation to unmanaged spaces (Reichard and White 2001; Dehnen-Schmutz et al. 2007), further contributing to a plant community dominated by several commonly occurring and many infrequently appearing species. Both spontaneously-growing weeds and cultivated ornamentals were among the most common species. However, beta diversity was lower for weeds than for ornamental species, indicating that the same weeds are found almost everywhere and that human choices may be most responsible for large-scale (i.e., gamma) diversity across the city. On the other hand, beta diversity of weeds could have been higher if less-managed areas such as industrial areas or railroad rights-of-way were included in sampling.

Cultural preferences in ethnically diverse neighborhoods likely influence the characteristics of yard plantings and contribute to the high turnover in ornamental plants from one neighborhood to another. We observed that neighborhoods with intermediate percentages of Hispanic and white residents had greater species richness across multiple plant traits. The unimodal relationship suggests that yard management and/or preferences differ across ethnic and racial groups in Chicago neighborhoods. Other research indicates that ornamental flowers in pots or raised beds (Kent 1999) as well as floral density and vegetation other than herbaceous plants

Fig. 4 Fitted slope of median household income (USD) and weedy species richness indicating significant negative relationship

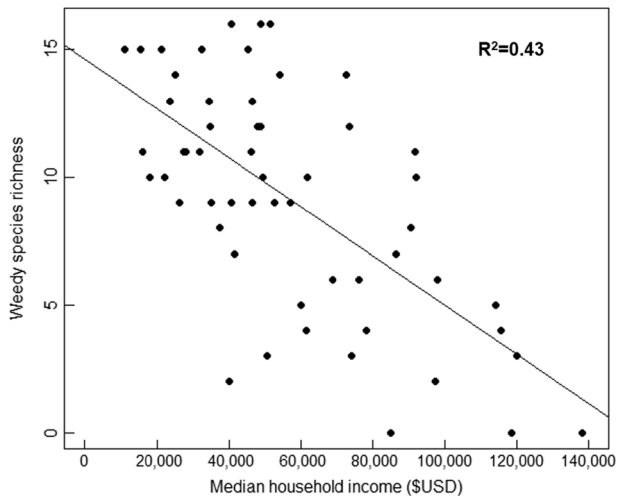


Table 3 Beta diversity values for plant characteristics

Characteristic	Beta diversity	Sorenson index
All	4.04	0.573
Ornamental	4.38	0.605
Weedy	3.00	0.503
Native	4.33	0.578
Non-native	3.84	0.539
Perennial	4.09	0.558
Annual	3.53	0.536
Ornamental perennial	4.14	0.591
Ornamental annual	4.53	0.517

Beta diversity was calculated as total number of species recorded across all sites divided by the average richness per single site. Sorenson index uses of pairwise comparison of sites and accounts for number of shared genera between sites, with values ranging from all shared genera (0) to no shared genera (1)

are greater in majority Hispanic areas (Taylor and Lovell 2015; Minor et al. 2016). Compared to low and middle income white and African-American households, Hispanic residents' greater participation in outdoor water-gardening (Dennis and Behe 2007) and in food gardening in multifamily lots (Taylor and Lovell 2015) may also play a role. Residential yards offer an outlet for social and cultural expression that can lead to a greater diversity of plants in neighborhoods without a dominant ethnic or racial majority.

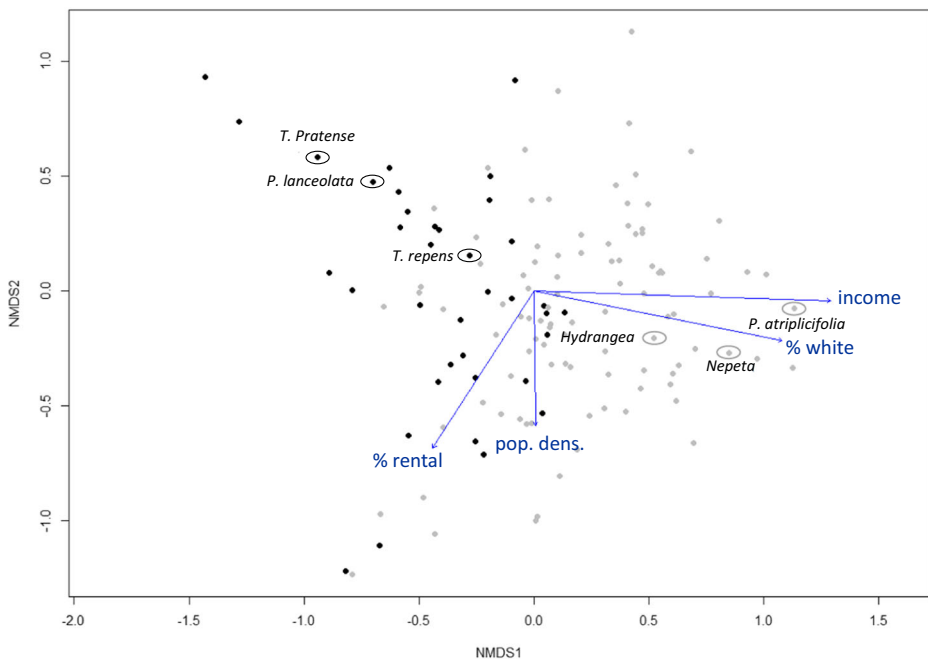


Fig. 5 NMDS ordination of all species with ornamental plants shown in *gray* and weedy plants shown in *black*. The ordination had a 3-dimensional solution but the two axes that explain the greatest amount of variation are shown. Socioeconomic variables that significantly ($P < 0.05$) explain community composition are overlaid as vectors. Several common plant species are labeled

With the exception of weedy species, richness across all traits was significantly related to number of residential lots. Most plant groups showed a non-linear relationship with number of lots, peaking in richness at intermediate-levels of development. The exception was annual species richness, which increased linearly with number of lots. However, several studies offer conflicting findings for positive (Knapp et al. 2012) and negative effects (Godefroid and Koedam 2007; Matteson et al. 2013) of building or development density on species richness. We offer four explanations for this discrepancy and for our novel finding of a peak in species richness at intermediate densities. First, the unit for measuring development is not standardized between studies. Building density, human population density, and number of lots all capture different aspects of the urban environment. Second, though linear relationships are documented for socioeconomic drivers of plants (Hope et al. 2003; Knapp et al. 2012; Grove et al. 2014), non-linear relationships may not have been explored due to an interest in obtaining a parsimonious result. In our study, linear relationships between number of lots and species richness were also significant although had less explanatory power than non-linear relationships. Third, other studies may not have spanned the density or socioeconomic gradient to the same extent that our study did. Finally, in a previous study (Lowenstein et al. 2014), we speculated that richness of flowering plants might be highest in urban neighborhoods with moderately high human population density. We hypothesized that people have diverse preferences for plants, which creates more diverse plant communities in neighborhoods with more people. However, taken to the extreme of very densely populated neighborhoods with many homes, the amount of non-impervious surface decreases and shade increases (Matteson and Langellotto 2010), reducing residents' ability to plant as many species as they might want to. The linear increase we observed here for annual species might be explained by flowers in small 'pot gardens' on porches and patios. This last argument is further supported by the fact that weedy species richness was not related to number of lots (i.e., weedy species richness is not driven by diverse human preferences).

The ordination of plant species suggests that income and race—but not number of residential lots—are linked with plant community composition. By symbolizing species according to their ornamental or weedy status, we confirmed that wealthier and whiter neighborhoods have fewer weeds. Weeds colonize rapidly, eventually reaching an equilibrium in species richness, in neighborhoods with unoccupied lots (Crowe 1979). Higher occupancy of lots as well as management in wealthier neighborhoods leads to their near absence, or complete absence in some cases, at sites with high median income. Another subset of plant species, including *Allium spp.*, *Nepeta spp.*, *Perovskia atriplicifolia* Benth., *Begonia*, and *Hydrangea*, are also closely linked with these neighborhoods. We hypothesize that this particular set of ornamental plants may be attributed to plantings from the commercial landscaping companies we observed working in high-income neighborhoods. These plants may be recommended by the landscaping companies or, alternatively, may simply reflect the status or desired status of neighborhood residents (Grove et al. 2006).

Effects of urban floral patterns on higher trophic levels

The dominance of non-native, cultivated and weedy species in certain neighborhoods has implications for nectarivorous insects and birds. In cities, weeds are a useful, if undervalued, pollinator resource (MacIvor et al. 2014; Larson et al. 2014). While we observed more ornamental species than weedy species overall, there was no difference in floral abundance of ornamental and weedy plants. Common cultivated species with higher floral abundance in

urban neighborhoods tend to produce little pollen and or low-quality nectar (Comba et al. 1999). These included species such as *Petunia* and *Impatiens*, which were present on most neighborhood blocks, but are visited by few pollinators (DML unpublished). However, other ornamental species found in approximately 1/3rd of Chicago neighborhoods, including *Hibiscus syriacus*, *Leucanthemum* and *Coreopsis*, have attractive floral stalks to pollinators, unique floral morphology, and long blooming periods. Furthermore, plants vary in attractiveness to insects within cultivars (Garbuzov and Ratnieks 2014).

Our finding of high turnover in plants suggests that while community composition varies between neighborhoods, there remains a diversity of nectar-rich plants with multiple traits. The co-occurrence of non-native and native plants enriches overall urban plant diversity and likely extends the flowering season, even though individual non-native species are often recorded at low frequencies (Cook et al. 2012). This diversity makes cities more beneficial than expected for pollinators (Leong et al. 2014; Lowenstein et al. 2015). However, it can come at the expense of phylogenetic diversity (Knapp et al. 2012) and could reduce the taxonomic diversity of plants to only a few common families.

Conclusion

We observed changing floral communities along an urban socioeconomic gradient. While most plants in our study area were perennial, non-native, and ornamental, species composition varied across the city and was related to income and race. Species richness was a function of number of residential lots and percent of white and Hispanic residents. We should emphasize that our measured socioeconomic factors are only a proxy for the multi-scalar drivers that affect residents' decisions about their yards (Cook et al. 2012). Future interdisciplinary work is needed to understand these drivers and make cities more livable and supportive for a diversity of plants and animals. Large-scale efforts to change planting habits across a city are a long-term goal. In the shorter term, collaboration with breeders to diversify the morphology of common cultivars could supplement efforts to encourage residents to increase plant biodiversity. Our previous work in the Chicago area (Belaire et al. 2014; Lowenstein et al. 2015) already indicates the success of its residents at providing resources for many birds and invertebrates.

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