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Denisha M. Parker[1] · Katherine J. Turo[1] · Yvan A. Delgado de la flor[1] · Mary M. Gardiner[1]

Abstract

Urban insect communities are structured by hierarchical filters including regional processes, human facilitation, and species interactions. We sought to inform future urban conservation endeavors by identifying how landscape composition and configuration as well as the management of vacant lot greenspaces affect native lady beetle (Coccinellidae) community structure within the city of Cleveland, Ohio, USA. We found no effect of habitat treatment on native lady beetle abundance when comparing vacant lots seeded with native wildflowers and those with naturally occurring weedy vegetation mown monthly or annually. Nonetheless, establishing conservation plantings that vary in plant height, biomass, and bloom abundance could aid in supporting a greater richness of coccinellid species, as these variables had differential effects on the abundance of fungivorous and aphidophagous feeding guilds. Further, we found that vacant lots embedded within landscapes with increased impervious surface and a high degree of greenspace isolation contained fewer aphidophagous native and exotic lady beetles. Our findings suggest that landscape context is a critical consideration when aiming to utilize vacant land as conservation habitat for coccinellids. Given their large holdings of vacant land, shrinking cities offer a unique opportunity to incorporate landscape-scale planning into future sustainable development initiatives. For instance, with over 27,000 vacant lots, the city of Cleveland could aid lady beetle conservation by electing to maintain vacant lots that promote greenspace connectivity while targeting isolated lots within intact neighborhoods for new residential development.

Keywords Shrinking city · Invasive species · Urban greenspace · Habitat management · Urbanization · Coccinellidae · Filters

Introduction

Changes in landscape heterogeneity associated with urbanization can alter the composition of regional species able to inhabit remaining fragmented habitat patches, generally causing a decrease in native species abundance and richness (McIntyre 2000; Shochat et al. 2010; Pickett et al. 2011; Geslin et al. 2013). In an urbanizing world, native species are threatened by changes in habitat quality, quantity, and configuration coupled with additional stressors such as pollution and increased competition for prey from urban-adapted exotic taxa (Crooks et al. 2004; Hung et al. 2017; McKinney 2006).

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Despite the documented challenges of life in cities, urban greenspaces often support a high abundance and richness of arthropod species (Delgado de la Flor et al. 2017; Sivakoff et al. 2018; Uno et al. 2010; Matteson et al. 2008) and have begun to be recognized as undervalued conservation resources (Hall et al. 2017; Turo and Gardiner 2019; Riley et al. 2018). This is particularly true for "shrinking cities", where economic decline and population loss result in an overabundance of infrastructure that continues to be demolished creating vacant land. Not only are vacant lots potentially valuable for arthropod conservation in their current form, but opportunities exist to transform them into greenspaces such as rain gardens, native pocket prairies, and urban farms (Alonso-Blanco et al. 2009; Chaffin et al. 2016). However, key questions remain regarding how the design and management of vacant lot greenspaces, as well as their landscape context, might influence their conservation value for native species.

Ecological theory suggests that urban communities are influenced by hierarchical environmental filters (i.e. local and landscape components) coupled with human interventions (McIntyre 2000; Jones and Leather 2012; Aronson et al.

2016). Empirical evidence supports this framework and has shown that insect communities are influenced by landscape-scale process (Sivakoff et al. 2018), local-scale habitat design (Egerer et al. 2017b), and trophic interactions (Nelson and Forbes 2014). At a landscape-scale, composition, configuration, and a legacy of heavy metal contamination initially filter insect species pools. Factors such as loss of greenspace connectivity, reduction of habitat size, and habitat degradation can all cause declines in abundance and richness of insect species at this scale (Lindborg and Eriksson 2004; Tscharntke et al. 2012; Gardiner and Harwood 2017). In contrast, if the spatial pattern of urban greenspaces across a landscape enable focal taxa to disperse, these habitats can be considered as corridors or stepping-stones (Beninde et al. 2015; Colding 2007; Lepczyk et al. 2017) and may support increased richness at landscape scales (Tscharntke et al. 2012; Fahrig 2017). Local-scale habitat factors such as vegetation structure (i.e. vegetation height, bloom abundance) are contingent upon human design and management and are also known to influence urban insect biodiversity (Hahs et al. 2009; Aronson et al. 2014; Threlfall et al. 2017). For instance, increased habitat disturbance (i.e. herbicide use, tillage, mowing, etc.) in agricultural and urban settings results in decreased beneficial insect abundances (Grez et al. 2013). Conversely, adding native wildflowers to agricultural production sites can enhance beneficial insect populations, through the provisioning of pollen, nectar, and increased prey resources (Blaauw and Isaacs 2015).

Lady beetles (Coleoptera: Coccinellidae) are charismatic, flagship species (Tumminello et al. 2015) that provide a vital ecosystem service as biological control agents of common plant pests such as aphids (Hemiptera: Aphididae), scales (Hemiptera: Coccoidea), and powdery mildews (Ascomycota: Erysiphales) (Gordon 1985; Caltagirone and Doutt 1989). Unfortunately, multicids are declining in abundance across the US and Europe (Alyokhin and Sewell 2004; Harmon et al. 2007; Roy and Migeon 2010; Roy et al. 2012; Gardiner et al. 2012; Bahlai et al. 2015). For instance, the nine-spotted lady beetle (*Coccinella novemnotata* Herbst) is now exceedingly rare across the US (Losey et al. 2007; Gardiner et al. 2012) and the two spotted lady beetle (*Adalia bipunctata* L.) has exhibited dramatic declines in abundance across the US and Europe (Roy et al. 2012). Moreover, the introduction of aphid-feeding exotic coccinellids coincides with these declines, and increased direct and indirect competition from these species has been implicated as a principal driver (Alyokhin and Sewell 2004; Evans 2004; Majerus et al. 2006; Harmon et al. 2007; Gardiner et al. 2012; Bahlai et al. 2015; Roy et al. 2016; Honek et al. 2016; Grez et al. 2019). Exotic lady beetles are documented to compete directly with native species as intraguild predators (Cottrell 2004; Hoki et al. 2014; Smith and Gardiner 2013; Turnipseed et al. 2014). Likewise, exploitative competition with exotic species for shared aphid prey resources may also

contribute to the decline of native species (Evans 2004). The intensity of these forms of competition are likely to vary among urban greenspaces that differ in landscape context, vegetation composition, management, and shared prey availability. Rich coccinellid communities have been documented in cities (Gardiner et al. 2014; Grez et al. 2019), yet for urban greenspaces to play a role in conserving native lady beetles, it is essential to identify the urban distribution patterns and habitat preferences of these species.

Post-industrial cities offer an opportunity to develop and test management plans to promote the conservation of urban biodiversity due to their extensive holdings of vacant land. These cities have lost substantial proportions of their populations; for example, Cleveland was once the 5th largest US city and has lost nearly 50% of its residents (Beauregard 2009). Protracted population loss in Cleveland has resulted in the demolition of unoccupied residential and commercial buildings, creating 27,000+ vacant lots (Western Reserve Land Conservancy 2015). These habitats are managed as early successional, weedy greenspaces mowed approximately monthly throughout the growing season. Vacant lots have been targeted as opportunities to implement conservation-focused habitats within the city (Turo and Gardiner 2019). Towards this end, we established the Cleveland Pocket Prairie Project to examine how vacant land management regimes ranging from successional weedy habitats with reduced mowing frequency to "pocket prairies" consisting of native grasses and forbs, influenced insect communities. Within this network of vacant lots, we measured how both native and exotic Coccinellidae were influenced by local and landscape-scale filters. We hypothesized that due to coccinellid's high dispersal capacity (Honek 1985), landscape variables would act as weak filters of lady beetle distributions whereas local-scale variables, such as vegetation height, bloom abundance, and aphid prey availability would prove to be strong filters of lady beetle abundance and richness. We predicted that seeding vacant lots with native Ohio wildflowers would support a higher abundance of native coccinellids than frequently mown vacant lots composed of turf grass, by providing a greater richness and abundance of food and shelter resources. By testing our hypotheses, we aimed to inform the development of vacant lot greening initiatives for supporting native coccinellid biodiversity in the city.

Methods

Study Sites

This study focused on 32 vacant lots within eight neighborhoods included in the Cleveland Pocket Prairie Project (Fig. 1). Within each neighborhood, four vacant lots (each approximately 12 × 30 m) were assigned to four habitat

Fig. 1 The Cleveland Pocket Prairie Project included 32 vacant lot habitats arrayed across eight inner-city neighborhoods of Cleveland, OH. We established four habitat treatments: *Control, Meadow, Low Diversity* and *High Diversity* (Supplementary Table 1) in each neighborhood and sampled for lady beetles monthly (June–August) in 2016 and 2017
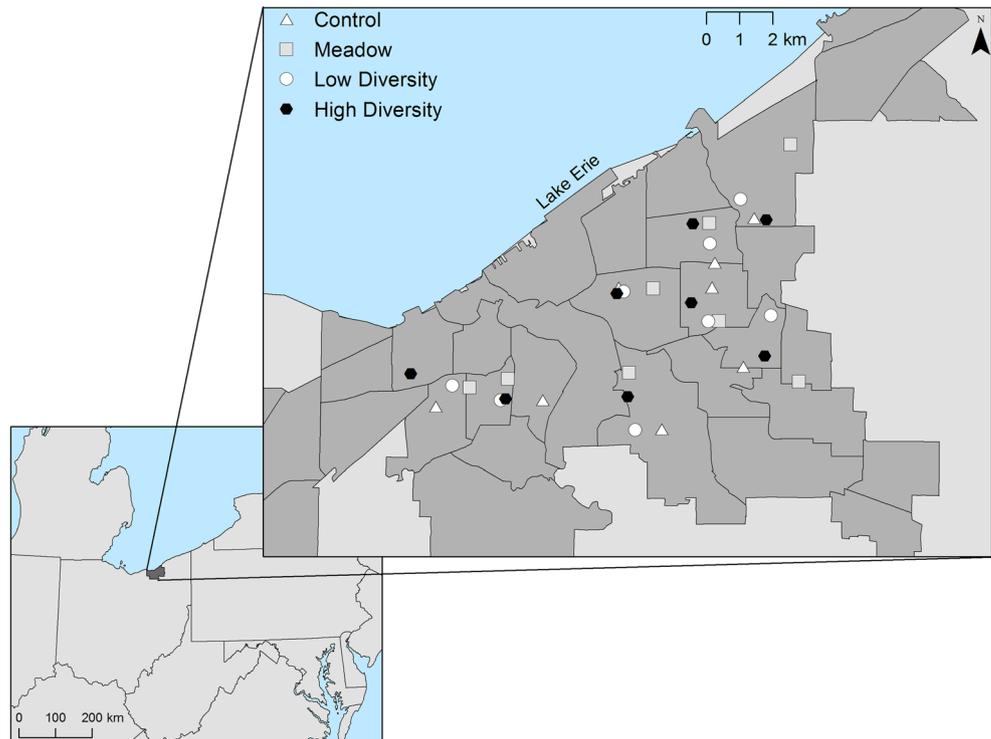
treatments: *Control, Meadow, Low-Diversity Prairie*, and *High-Diversity Prairie* (Table S1). *Control* sites consisted of a turf grass seed mixture established by the City of Cleveland following house demolition and were mowed monthly per standard city management guidelines. These sites also contained weedy, primarily non-native flowering plants from the existing seed bank. *Meadow* sites were also seeded with turf grass but were managed as a successional meadow and only mowed annually in October of 2016 and 2017. Prairie treatments were seeded in 2014. Sites were prepared by Ohio Prairie Nursery (Hiram, Ohio) with two treatments (May 28–30, 2014; June 23–25, 2014) of glyphosate herbicide, followed by seeding in November 2014 with a broadcast application of three prairie grasses and either four (*Low Diversity*) or sixteen (*High Diversity*) native prairie forbs (Table S1). These pocket prairies were mown annually in October of 2016 and 2017. Prior to data collection, we established a 7 × 15 m plot within the center of each site. The plot was divided into 1 m² quadrats, and all vegetation and lady beetle data were collected from within this grid.

Lady Beetle and Prey Collection and Identification

Monthly sampling took place three times in 2016 (June 2–9, July 7–14, August 4–11) and in 2017 (June 1–8, June 29–July 6, July 27–August 3). Lady beetles and aphid (Aphididae) prey were collected using 14 × 24 cm no-bait yellow sticky card traps (Great Lakes IPM, Vestaburg MI). Five traps were deployed in each site, with one trap placed into the center and each corner quadrat of our 7 × 15 m plot. Cards were attached to stakes at vegetation height, and remained in the field for seven days, after which they were brought into the laboratory and stored at 4 °C. All lady beetles were later counted and identified to species. We estimated aphid abundance by counting the number of individual aphids present on one side (selected at random) of the folded yellow sticky card trap.

Landscape Data

Cuyahoga County Planning Commission provided 1 m resolution landscape data at 500 m and 1500 m buffers surrounding each of our 32 vacant lot research sites. We chose these scales as lady beetles are capable of both long dispersal flight (Jeffries et al. 2013) and are known to respond to local habitat features (Hemptinne et al. 1992). Land cover was classified from 2011 aerial imagery as the percentage of grass/shrubs, bare soil, water, buildings, roads/railroads, other paved surfaces, tree canopy (TC) over vegetation, TC over buildings, TC over roads/railroads, and TC over other paved surfaces present. For our analysis of landscape composition, we focused on the proportion of impervious surface present, which we calculated by pooling the land cover classes roads/railroads, buildings, and other paved surfaces within each buffer. Landscape configuration was calculated with ArcGIS spatial Analysts 10.3 (ESRI 2014) wherein we reclassified landscape categories into 'greenspace' (grass/shrubs and TC over vegetation) or 'other' (all other land cover categories). Next, we used Fragstats version 4.2 (McGarigal et al. 2002) to compute

the *class*-metrics (1) average greenspace patch size (m²) and (2) average greenspace patch isolation (m) or Euclidean Nearest Neighborhood distance (ENN).

Vegetation Data Collection

Vegetation sampling was conducted monthly in the summers of 2016 (June 13–24, July 11–22, August 4–16) and 2017 (June 5–16, July 10–21, August 1–11). We selected 20 quadrats (1 m²) at random from our grid in order to measure the biomass. Six additional quadrats within the grid (1 m²) were also randomly selected to measure plant height and bloom abundance.

We used the comparative yield method to estimate vegetative biomass in each of our sites (Haydock and Shaw 1975). Five standards were selected to represent biomass within a lot and then 20 randomly selected quadrats were compared to these standards. When selecting standards, we used a 0.5 m² area and created a scale ranging from 1 (lowest biomass) to 5 (highest biomass). We then estimated biomass in each of the 20 randomly selected quadrats using our 1–5 comparative scale and allowing for quarter-step increments (e.g. 2.25). All vegetation within the five standards was harvested and transported to the laboratory where dry weight was recorded, and comparative yield scores were estimated. The five dry weights were used to form a linear regression equation and the 20 estimated yield scores were inserted into this equation to calculate biomass per quadrat. The biomass from each equation was then averaged and used to represent the average site biomass (g/m²).

Plant height was measured in six randomly selected quadrats within each site. This was done by placing a 0.5 m² PVC square in the center of each quadrat and recording three plant heights (cm), one located in the center and two from opposite corners of the square. The average height and standard error were calculated from a total of 18 plants at each site. Similar to measuring plant heights, *bloom abundance* was measured by placing a 0.5 m² PVC square in the center of each quadrat and counting all blooms within the square.

Statistical Analysis

To quantify and compare distribution patterns of native and exotic lady beetles within our treatments, we conducted three separate generalized linear mixed models (GLMM) in R (R Core Team 2019). The abundance of all native coccinellids, aphidophagous native coccinellids, and exotic coccinellids were compared, using treatment (*Control, Meadow, Low Diversity, High Diversity*) and month (June, July, August) as a random effect. We included an analysis of aphidophagous native species individually as they compete with exotics for a shared food resource and a subset of native aphidophagous taxa have exhibited dramatic declines. Therefore, we were particularly interested in whether the abundance of these

coccinellids varied among vacant lot treatments, as this could indicate habitat's conservation potential. Each year was analyzed separately and due to over-dispersion, we refitted our models using a negative binomial distribution with function 'glmer.nb' from the "lme4" package (Bates et al. 2015). The 'Anova' function in the "car" package (Fox and Weisberg 2018) was then used to perform a Type II analysis of variance that generated analysis of deviance tables from which likelihood-ratio test statistics were obtained. Pairwise comparisons were examined with Tukey's test in the 'multcomp' package (Hothorn et al. 2008). An alpha level of 0.05 was specified for all statistical tests.

Seasonal variation of native and exotic lady beetles in both 2016 and 2017 were also examined with GLMMs in R with function 'glmer' from the "lme4" package (Bates et al. 2015). Models utilized a Poisson distribution and examined how lady beetle capture rates (all native species, aphidophagous native species, exotic species) were predicted by month (June, July, August) and a random effect, neighborhood (1–8). Finally, pairwise comparisons across months were examined for each response variable with Tukey's test.

Partial least squares canonical analysis (PLSCA) was used to examine how vegetation variables, surrounding landscape composition and configuration at 500 and 1500 m, and aphid abundance influenced the abundance and richness of lady beetles in R using the library "plsdepot" (Sanchez 2013). PLSCA is a multivariate analysis used to display the relationship between a large set of colinear response and predictor variables while accommodating small sample sizes relative to the number of dependent variables (Abdi and Williams 2013). PLSCA analyzes the linear relationships between variables in two matrices by deriving a latent variable from each matrix to maximize the covariance explained between them (Abdi and Williams 2013).

To verify the strength and determine the significant relationships between all variables included in the PLSCA, we conducted pairwise correlations using the library 'mixOmics' (Rohart et al. 2017) in R, which are displayed in a relevance network. Within the relevance network plot, we consider significant associations among variables as ±0.5. We examined each year individually, pooling the sticky traps placed at each site and the sampling months. We included five response variables: exotic (abundance of exotic coccinellids), native fungivorous (abundance of *Psyllobora vigintimaculata* Say), native non-myrmecophile aphidophagous (abundance of all native aphid feeding species that do not live in association with ants) and native myrmecophile (abundance of *Brachiacantha ursina* Fabricius). We elected to examine coccinellids by feeding guild as we expected that diet might influence landscape-scale dispersal patterns and local habitat preferences. Exotic coccinellid species were not further separated by diet as all four species captured in our study (*Coccinella septempunctata* L., *Harmonia axyridis*

Pallas, *Hippodamia variegata* Goeze and *Propylea quatuordecimpunctata* L.) are aphidophagous. *Brachiacantha ursina* was the most common native coccinellid collected and is a myrmecophile whose larvae feed on aphids within ant nests (Smith 2002). Given this unique life cycle we included variables to examine the response of *B. ursina* (native myrmecophile) and other aphidophagous natives individually. We did not include native coccidophagous species in our analysis due to their low abundance. Our PLSCA predictor variable data set included the local features: average plant height, bloom abundance, plant biomass, and aphid abundance. At the landscape scale, we included percentage impervious surface, average greenspace patch size, and greenspace patch isolation at 500 m and 1500 m.

Results

Lady Beetle Abundance and Distribution Patterns

A total of 1598 and 1339 lady beetles were collected from our 32 vacant lot habitats during 2016 and 2017, respectively. We collected four exotic and 12 native species (Table 1). Exotic species dominated the community, representing 74% of total lady beetles captured. The majority of these specimens were the exotic *P. quatuordecimpunctata* (69% of all captured lady beetles). Native aphidophagous species represented 24% of the total coccinellid abundance collected, with *B. ursina* being the most abundant species, followed by fungivorous (~2%) and coccidophagous (>1%) coccinellids (Table 1). In both sampling years, the abundance of lady beetles per yellow sticky card trap varied by month with increased captures

occurring in July for all native species (2016: $z = 8.58$, $p < 0.001$; 2017: $z = 8.30$, $p < 0.001$), aphidophagous native species (2016: $z = -6.03$ $p < 0.001$; 2017: $z = -3.52$, $p < 0.001$) and exotic lady beetles (2016: $z = 18.27$, $p < 0.001$; 2017: $z = 15.11$, $p < 0.001$) (Fig. 2a-c).

In 2016, exotic lady beetle abundance was similar within the *Control* and *Meadow* treatments ($z = -0.078$, $p = 0.99$, Fig. 3a). However, there was a greater abundance of exotic lady beetle species in *Low-Diversity* ($z = 2.882$, $p = 0.023$) and *High-Diversity* ($z = 2.75$, $p = 0.030$) treatments versus the *Control* (Fig. 3a). Likewise, exotic abundance was also significantly greater within *Low-Diversity* ($z = 0.21$, $p = 0.021$) and *High-Diversity* treatments ($z = 2.800$, $p = 0.026$) than in *Meadow* treatments (Fig. 3a). However, exotic lady beetle trends were not consistent from year to year, and we did not detect treatment effects in 2017 ($p > 0.05$, Fig. 3b). Habitat treatments also had no effect on total native lady beetle abundance or aphidophagous lady beetle abundance in 2016 or 2017 ($p > 0.05$, Fig. 3c-d).

Landscape Variables Influence on Lady Beetle Trap Captures

During 2016 and 2017 we found that both exotic and native lady beetles were influenced by surrounding landscape composition and configuration (Fig. 4a-b). Increased percentage of impervious surface at the 500 m landscape scale was a negative driver of exotic (2016 and 2017), native non-myrmecophile aphidophagous (2016), and fungivorous (2016) lady beetle abundance. Increased percentages of impervious surface at the 1500 m landscape scale was also

Table 1 Abundance, origin, and primary diet of lady beetle specimens collected from yellow sticky card traps placed at vegetation height within *Control*, *Meadow*, *Low Diversity*, and *High Diversity* vacant lot treatments within Cleveland, Ohio from June–August 2016 and 2017

Species	Control	Meadow	Low-Diversity	High-Diversity	Origin	Primary diet
Brachiacantha ursina	104	118	69	62	native	Aphidoidea, Coccoidea
Coccinella septempunctata	4	3	4	1	exotic	Aphidoidea
Coleomegilla maculata	19	14	25	19	native	Aphidoidea, Pollen
Cycloneda munda	36	58	51	65	native	Aphidoidea
Harmonia axyridis	14	16	21	24	exotic	Aphidoidea
Hippodamia glacialis	1	0	0	0	native	Aphidoidea
Hippodamia parenthesis	0	0	0	2	native	Aphidoidea
Hippodamia variegata	16	9	36	3	exotic	Aphidoidea
Hyperaspis proba	0	0	1	0	native	Coccoidea
Hyperaspis undulata	2	3	2	2	native	Aphidoidea, Coccoidea
Propylea quatuordecimpunctata	495	394	574	551	exotic	Aphidoidea
Psyllobora vigintimaculata	10	10	32	17	native	Fungi (Erisyphaceae)
Scymnus americanus	16	12	9	13	native	Aphidoidea
Total	**717**	**637**	**824**	**759**		
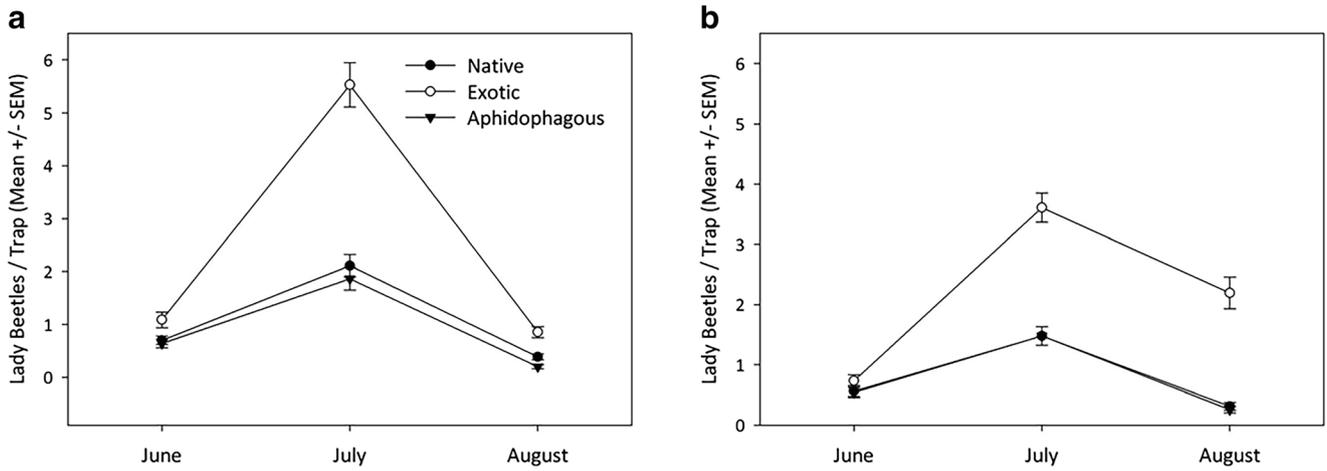
Fig. 2 Capture rate (Mean ± SEM) of exotic, native, and aphidophagous native coccinellids throughout the sampling periods of 2016 (a) and 2017 (b). We found that captures of native, exotic, and aphidophagous lady beetles varied significantly by month ($p < 0.05$) with the highest abundance found in July. Note that in 2017, all native lady beetles captured were aphidophagous with the exception of six fungivorous *Psyllobora vigintimaculata* individuals
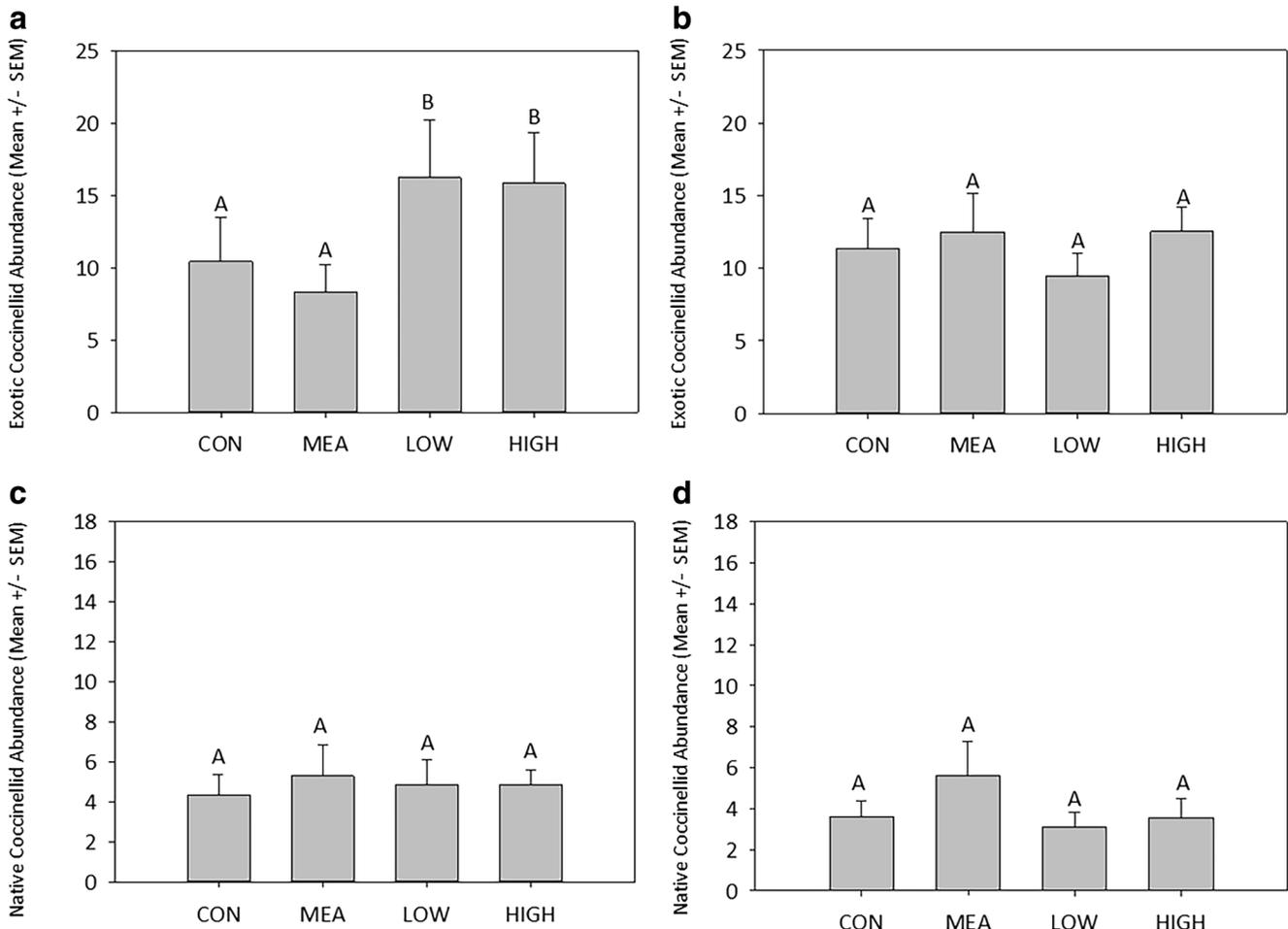
Fig. 3 Abundance (Mean ± SEM) of exotic (a: 2016 and b: 2017) and native (c: 2016 and d: 2017) coccinellids collected using yellow sticky card traps in *Control* (CON), *Meadow* (MEA), *Low Diversity* (LOW) and *High Diversity* (HIGH) vacant lot treatments. Letters indicate a significant difference in lady beetle abundance among treatments within a given year ($p < 0.05$)

Fig. 4 Relevance network plots for 2016 (A) and 2017 (B), illustrating relationships between lady beetle community metrics, local vegetation variables and landscape structure. Response variables in the PLSCA analysis included abundance of exotic lady beetles (Exotic), non-myrmecophile aphidophagous natives (Aphidophagous (NM)), the myrmecophile native *B. ursina* (Myrmecophile), fungivorous natives (Fungivorous), and native coccinellid species richness (Native Richness). Our predictor variables included the local factors: plant biomass (Biomass), bloom abundance (Bloom), plant height (Height), and aphid prey abundance (Aphid). We also included landscape variables: percentage impervious surface (IS), average patch size (Patch Size), and patch isolation (ENN) at 500 m and 1500 m. Only variables that exceeded a correlation threshold of ±0.5 are shown. Solid lines indicate positive associations, whereas dashed lines are negative associations. Thickness of the lines indicate the strength of the association between the two variables, with thicker lines having a stronger similarity value. Relevance network similarity values for lady beetle community metrics are provided in Table S2
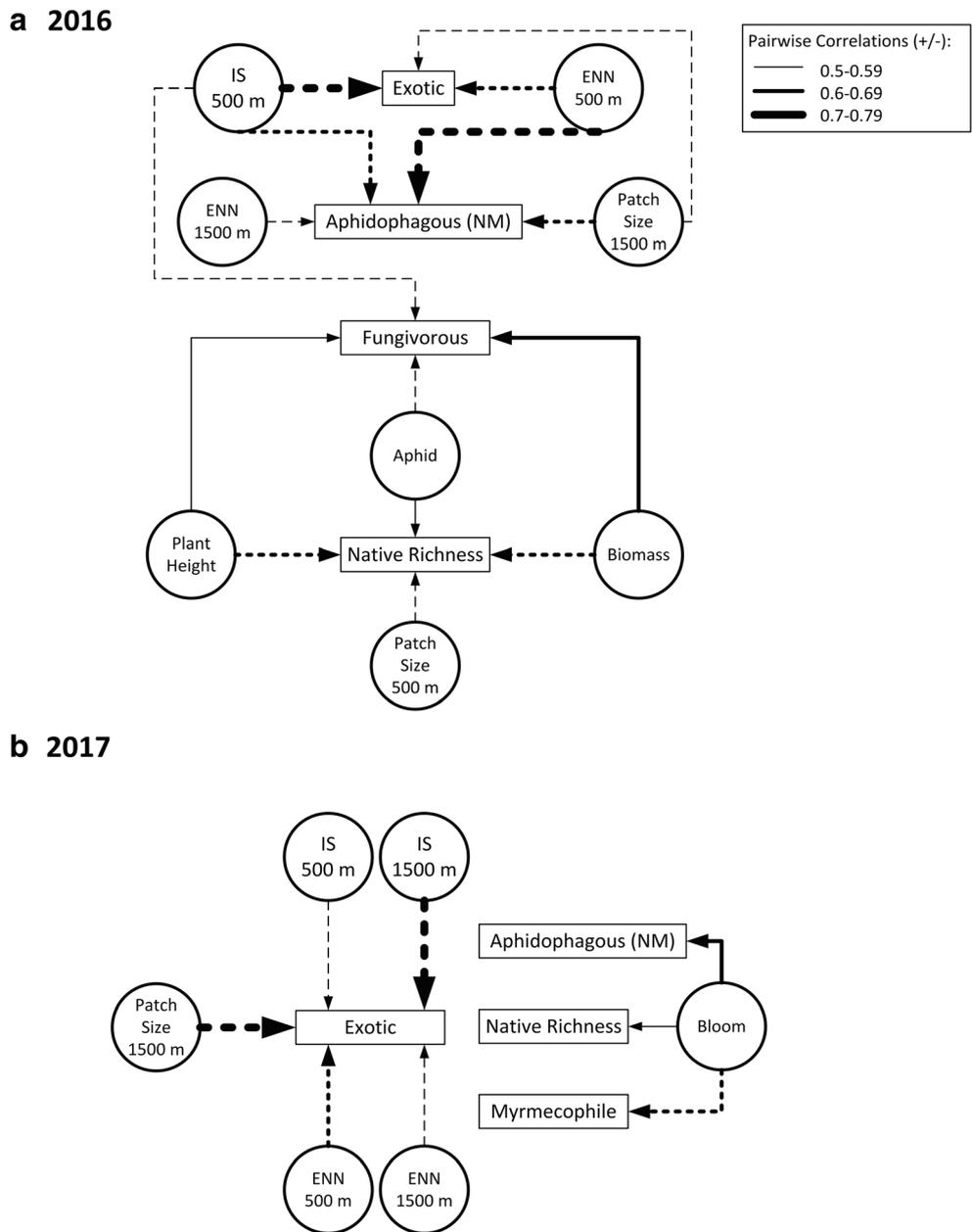
negatively associated with exotic species abundance in 2017. Greenspace patch isolation (ENN) was also a consistent negative predictor of lady beetle abundance in vacant lots. In 2016, captures of exotic lady beetles (500 m), and native non-myrmecophile aphidophagous beetles (500 m and 1500 m) decreased in more isolated landscapes (Fig. 4a). A similar pattern was found for exotics (500 and 1500 m) in 2017 (Fig. 4b). We found a negative relationship between average greenspace patch size at the 1500 m landscape scale and exotic (2016 and 2017) and non-myrmecophile aphidophagous natives (2016) (Fig. 4 a-b). Greenspace patch size was also negatively associated with native coccinellid richness at the 500 m landscape sale in 2017 (Fig. 4b).

Local Variables Influence on Lady Beetle Trap Captures

We found no relationships between local vegetation variables, aphid prey abundance, and the abundance of exotic coccinellids captured on yellow sticky card traps. However, local variables were predictive of native coccinellid distributions. In 2016, we found that vegetation biomass was negatively correlated with native coccinellid richness and positively correlated with the abundance of the fungivorous native *P. vigintimaculata* (Fig. 4a). Vegetation height was positively related to abundance of *P. vigintimaculata* and negatively associated with native richness in 2016 (Fig. 4a). Bloom

abundance was positively related to native coccinellid richness and native non-myrmecophile aphidophagous beetle abundance in 2017 and negatively correlated with the abundance of the myrmecophile *B. ursina* (Fig. 4b). Finally, aphid prey abundance was negatively associated with the fungivore *P. vigintimaculata* (2016) and positively associated with native lady beetle richness in 2016 (Fig. 4a).

Discussion

Urban greenspaces have noted potential for conservation, but their quality for native species, including coccinellids, is dependent on how species dispersal and habitat occupancy are influenced by urban filters such as landscape composition, configuration and greenspace management practices (Cameron and Blanuša 2016; Aronson et al. 2016). We established the Cleveland Pocket Prairie Project to determine if reducing mowing frequency of existing weedy vegetation or establishing native wildflowers within vacant lots would enhance native coccinellid abundance and richness. We were particularly interested in supporting populations of native aphidophagous lady beetles, a group of beneficial arthropods that includes multiple species documented as in decline. Our key finding was that vacant lots mown monthly, following current protocols employed by the city of Cleveland, OH, supported a similar richness and abundance of native and exotic lady beetles when compared with weedy meadows or native pocket prairies. However, across these treatments, vegetation features such as bloom abundance, height, and biomass influenced the abundance and richness of native coccinellids. We also found that landscape composition and configuration were strong drivers of exotic and native lady beetle distributions. Vacant lots embedded in landscapes dominated by impervious surface and with a high degree of habitat isolation were less suitable habitats.

The most commonly captured native lady beetles in this study were *B. ursina*, *Cycloneda munda* Say and *Coleomegilla maculata* Degeer. *Brachiacantha ursina* is found commonly in gardens and grassland habitats throughout the Midwest (Montgomery and Goodrich 2002; Gardiner et al. 2010a, 2012), where its larvae infiltrate the nests of *Lasius* ants (Smith 2002). *Lasius* are one of the most common genera of ants found in urban environments (Vepsäläinen et al. 2008; Slipinski et al. 2012), and the frequent capture of *B. ursina* within our vacant lots might reflect *Lasius* habitat preferences. Both *C. munda* and *C, maculata* are common aphidophagous species regionally in agroecosystems (Gardiner et al. 2009, 2010a) and residential gardens (Gardiner et al. 2012), illustrating that persisting species of native aphidophagous coccinellids are able to occupy urban vacant lot habitats. Unfortunately, we did not collect any specimens of several declining aphidophagous species including the nine-spotted lady beetle (*C. novemnotata*), two-spotted lady beetle

(*A. bipunctata*), three-banded lady beetle (*Coccinella transversoguttata* Mulsant), thirteen-spotted lady beetle (*Hippodamia tredecimpunctata* L.) or convergent lady beetle (*Hippodamia convergens* Guerin), providing further evidence of the rarity of these species within our region (Elliott et al. >1996; Alyokhin and Sewell 2004; Gardiner et al. 2012, 2014; Steffens and Lumen 2015; Egerer et al. 2017a). Exotic species dominated the community with *P. quatuordecimpunctata*, representing 69% of the total coccinellid captures. In contrast, *H. axyridis* was the dominant exotic lady beetle found statewide in residential gardens, where it was collected twice as frequently on yellow sticky card traps as *P. quatuordecimpunctata* (Gardiner et al. 2012). The dominance of *P. quatuordecimpunctata* within urban landscapes might be attributed to its generalist diet and habitat requirements (Honek 1985; Hagen et al. 1999; Pervez and Omkar 2011) faster reproduction (no latency in sperm transfer) (Pervez and Omkar 2011), and/or smaller size relative to other common exotic lady beetles, all traits shared by many urban-exploiters (Magura et al. 2006).

A principal aim of the Cleveland Pocket Prairie Project was to determine if practices such as reduced mowing of weedy vegetation or establishing native habitat plantings on vacant lots would increase use of these patches by native lady beetles. Certainly, reducing habitat disturbances such as mowing, and increasing vegetation variables such as bloom abundance and plant species richness, has been shown to support rich arthropod communities within rural landscapes (Siemann et al. 1998; Westphal et al. 2003; Lavandero et al. 2006; Gibson et al. 2006; Holzschuh et al. 2007; Gardiner et al. 2010b; Blaauw and Isaacs 2015). However, previous research by Egerer et al. (2018) and Matteson and Langellotto (2011) within cities found that the addition of floral resources to greenspaces had little effect on lady beetle, butterfly, bee or predatory wasp abundance or richness. Likewise, we did not find support for our prediction that seeding vacant lots with native Ohio wildflowers would result in a higher abundance of native coccinellids. Nevertheless, we did find that vegetation features influence native coccinellid abundance within vacant lots. For instance, the positive relationship between bloom abundance and non-myrmecophile aphidophagous species abundance in 2017 illustrates that the pollen and nectar provided by both seeded native and naturally occurring weedy plants can represent important forage for these species.

We did not find support for our hypothesis that a high dispersal capacity would minimize the influence of landscape variables in structuring lady beetle communities (Evans and Richards 1997). Instead, we found that landscape was a strong driver of exotic and native lady beetle abundance, which was reduced when vacant lots were surrounded by a high proportion of impervious surface, with a high degree of greenspace patch isolation. Urbanization has been previously identified as a strong, negative driver of lady beetle occupancy of urban agroecosystems of Michigan (Egerer et al. 2018) and the

abundance of coccinellids in parks within the metropolitan region of Santiago, Chile (Grez et al. 2019). Increased impervious surface might limit the success of lady beetle populations via several mechanisms. For instance, fragmentation can alter prey populations (Kareiva 1987; With et al. 2002), decrease overwintering habitats (Elliott et al. 2002) and aid the spread of exotic species (Gardiner et al. 2018; Lampinen et al. 2015). Likewise, while coccinellids are known to be strong dispersers (Evans and Richards 1997), roads and buildings are still thought to impose physical or behavioral constraints on lady beetle movement (Hanski 2011). It is possible that lady beetles respond similarly to bees, which are also mobile taxa capable of flying over roads, but which avoid doing so, and thus roads and railways still represent barriers to dispersal (Bhattacharya et al. 2003). At the same time, more abundant lady beetle populations have also been documented in landscapes with increasing impervious surface (Egerer et al. 2017b; Egerer et al. 2017a). This opposite pattern has been attributed to low availability of resources and habitats elsewhere (Egerer et al. 2017b). Such a concentration effect has been documented for other insect groups within the city of Cleveland, such as bees and mosquitoes (Sivakoff et al. 2018; Yang et al. 2019), where abundances are higher than expected in highly urbanized landscapes potentially because populations concentrate into a refuge habitat when other habitats are unavailable or inaccessible.

Finally, we predicted that aphid abundance would affect native aphidophagous abundance, as native species have been found to disperse from resource rich habitats to forage elsewhere when prey decline (Mack et al. 2000; Elliott et al. 2002; Evans 2004; Finlayson et al. 2008; Bahlai et al. 2015). For example, when prey abundance was artificially enhanced in alfalfa fields, Evans (2004) found that native lady beetle abundance increased, illustrating that these species were present in the surrounding landscape and able to recruit to this resource. However, when aphid populations were suppressed by exotic competitors, native species once again declined in abundance within the forage crop (Evans 2004). Given that the four exotic species found in our region are aphidophagous, we predicted that native aphidophagous species would be most abundant in patches with a high aphid abundance, where competition for prey would be relaxed. We found some support for this prediction as native species richness was positively associated with prey abundance in 2016. However, we did not document any relationships between prey abundance and aphidophagous species (both non-myrmecophiles and *B. ursina*) which could signal that prey abundance is not a limiting factor influencing urban patch occupancy.

Conclusion

Our study addresses ecological filters that structure communities of native lady beetle species within a post-industrial city.

Although exotic species dominated the community, we believe that urban focused conservation efforts are still warranted to support native lady beetle populations. While the degree of exotic dominance detected may seem high, exotic proportions found in this study are similar to those found in agricultural systems (Alyokhin and Sewell 2004; Gardiner et al. 2009; Bahlai et al. 2015) and habitats lacking a significant exotic presence are likely rare or nonexistent. In terms of conservation planning, our findings highlight that focus should be placed on the location of conservation habitats. Native lady beetles were less abundant in vacant lots embedded within highly developed landscapes where greenspace patches were isolated. Therefore, vacant lots surrounded by other greenspace patches (i.e. other vacant lots, parks, gardens) are priority sites for habitat development as they may facilitate greater connectivity across the landscape matrix. The type of vegetation established (native versus exotic) within a lot did not have a strong influence on native coccinellid distributions, however, the abundance of fungivorous and aphidophagous species differed in their relationships to vegetation variables such as plant height, density and bloom abundances. Therefore, maintaining a diversity of patches, including urban farms or pollinator plantings (Gardiner et al. 2013; Turo and Gardiner 2019), could enhance lady beetle richness, provided that these patches supported diverse vegetative communities and the landscape context was suitable.

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