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Local and Landscape Correlates of Spider Activity Density and Species Richness in Urban Gardens

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ABSTRACT Urbanization is a major threat to arthropod biodiversity and abundance due to reduction and loss of suitable natural habitat. Green spaces and small-scale agricultural areas may provide habitat and resources for arthropods within densely developed cities. We studied spider activity density (a measure of both abundance and degree of movement) and diversity in urban gardens in Santa Cruz, Santa Clara, and Monterey counties in central California, USA. We sampled for spiders with pitfall traps and sampled 38 local site characteristics for 5 mo in 19 garden sites to determine the relative importance of individual local factors. We also analyzed 16 landscape variables at 500-m and 1-km buffers surrounding each garden to determine the significance of landscape factors. We identified individuals from the most common families to species and identified individuals from other families to morphospecies. Species from the families Lycosidae and Gnaphosidae composed 81% of total adult spider individuals. Most of the significant factors that correlated with spider activity density and richness were local rather than landscape factors. Spider activity density and richness increased with mulch cover and flowering plant species, and decreased with bare soil. Thus, changes in local garden management have the potential to promote diversity of functionally important spiders in urban environments.

KEY WORDS Araneae, biodiversity, garden, habitat characteristic, urbanization

Urbanization is a serious threat to biodiversity and is a leading cause of declines in animal populations (Czech et al. 2000, McIntyre 2000, McKinney 2002). Urban development results in the conversion of natural space to buildings and pavement, resulting in loss of habitat and fragmentation of habitats suitable for wildlife, changes in local climate change and hydrology, and pollution (McIntyre et al. 2001). Unlike many other forms of human activity, urbanization is often a more permanent form of habitat loss. For example, habitats loss from farming or logging can be restored through ecological succession, but most urban areas continue to grow and expand into other local ecosystems (McKinney 2002). As human populations have increased, so has the number of people living in urban areas. The human population increased from 600 million in 1700 to 7 billion in 2011 (Bloom 2011, United States Census Bureau [USCB] 2014). In 1800, about 2% of people lived in cities; by 1900, the number had increased to 12%, and as of 2014, >50% of people live in cities (United Nations Population Division [UNPD] 2014). As a result of these increases, additional habitat loss in urban areas is expected. Yet, urban green space exists and can cover relatively large fractions of cities (Nowak et al. 1996, Savard et al. 2000).

Although urbanization tends to negatively impact biodiversity, some characteristics of urban areas may promote biodiversity (McKinney 2002). For example, across gradients of urban development, arthropod species richness may directly correlate with plant diversity, richness, and density (Raupp et al. 2009). Some urban areas have very high spatial habitat heterogeneity at small spatial scales due to land use and implementation of gardens (McIntyre et al. 2000, McKinney 2008, Savard et al. 2000). Urban gardens can have higher primary productivity than surrounding areas due to irrigation, fertilizers, and other factors, leading to increases in arthropod populations, species richness, and biodiversity (McIntyre 2000, McKinney 2008).

Arthropods are optimal for studying ecological effects of urbanization on the environment for several reasons. They reproduce relatively quickly and usually have high rates of fecundity, meaning they may respond rapidly to small-scale changes such as differences in soil or vegetation. They are abundant, allowing for large sample size, and are relatively easy to sample in comparison to larger organisms (McIntyre 2000, McIntyre et al. 2001). Arthropod predators also provide a variety of ecosystem services in agricultural landscapes such as pest control and nutrient cycling (McIntyre et al. 2001, Isaacs et al. 2009). Green spaces within urban ecosystems can benefit from these services, and provide habitat and resources for arthropods within densely developed cities (Thompson et al. 2003, Mc-Kinney 2008). Urban gardens differ from other green spaces in urban environments. They are generally designed, built, and managed by people who use them,

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Table 1. Names, locations, ages, and sizes of all urban gardens included in the research

Site	Size (acres)	Age (yr)	County	Latitude (decimal degrees)	Longitude (decimal degrees)	Garden type
Alan Chadwick Garden	2	46	Santa Cruz	36.99881	122.05222	School
U. of California, Santa Cruz Farm Garden	2	41	Santa Cruz	36.98357	122.05569	School
Trescony Community Garden	1	31	Santa Cruz	36.96848	122.04159	City
Homeless Garden Project	0.5	21	Santa Cruz	36.95713	122.06194	Private
Beach Flats Community Garden	0.5	9	Santa Cruz	36.96713	122.01741	City
Live Oak Grange Community Garden	0.5	16	Santa Cruz	36.97834	121.98157	Private
Aptos Community Garden	0.5	4	Santa Cruz	36.97013	121.87122	Church
Mi Jardin Verde Community Garden	0.65	4	Santa Cruz	36.92793	121.75636	Church
The Forge, Santa Clara U. Student Garden	0.5	5	Santa Clara	37.35241	121.93932	School
Berryessa Community Garden	2	10	Santa Clara	37.37531	121.86291	City
El Jardin Community Garden	2	32	Santa Clara	37.34173	121.84586	City
Coyote Creek Community Garden	1	20	Santa Clara	37.31228	121.84319	City
La Colina Community Garden	2	36	Santa Clara	37.23492	121.81355	City
Laguna Seca Community Garden	0.65	33	Santa Clara	37.217	121.76387	City
Community Garden of Salinas	1	4	Monterey	36.706	121.64327	Church
Salinas Chinatown Community Garden	0.5	7	Monterey	36.67952	121.65237	Private
Seaside Giving Garden	0.25	4	Monterey	36.60165	121.8339	Church
MEarth Garden & Kitchen	1	9	Monterey	36.54182	121.89426	School
Our Green Thumb Community Garden (Monterey Institute of International Studies)	0.25	5	Monterey	36.60031	121.89792	School

sometimes resulting in strict rules regarding pesticide and herbicide usage. Gardens greatly benefit from biological pest control that natural predators can provide (Francis 1989, McIntyre et al. 2001).

Spiders, in particular, are among the most common and abundant arthropod predators in terrestrial ecosystems (Turnbull 1973). They are polyphagous, obligate carnivores, and feed primarily on insects and other spiders (Bristowe 1941, Nentwig 1987, Nyffeler 1999, Turnbull 1973). Differences in prey preference, hunting methods, and timing of predation are complementary and allow for effective pest control (Sunderland and Samu 2000). Different spider species utilize a variety of hunting techniques, including ambush or sitand-wait, nocturnal or diurnal wandering, and web spinning (Marc et al. 1999, Riechert 1999). Several European, Asian, and American studies have demonstrated the effectiveness of using spiders as biological control agents as an alternative to high pesticide use (Mansour et al. 1980, Riechert and Lockley 1984, Nyffeler and Benz 1987, Nyffeler 2000). Not all spider species may be effective against a specific pest, but preserving spider diversity may help control many types of pests (Marc and Canard 1997).

Previous research shows not only local factors influence local diversity and abundance, but landscape factors can also have a large impact on organisms (Kareiva and Wennergren 1995, Duelli and Obrist 2003, Clough et al. 2005). Interactions between local and landscape conservation strategies are important but can affect different taxonomic groups in different ways, implying that other mechanisms such as dispersal ability, range size, or response to disturbance are also important (Tscharntke et al. 2005, Batáry et al. 2012, Gonthier et al. 2014). Both local and landscape factors may also have significant effects on biological control in agricultural areas (Schmidt et al. 2004). Specifically, for spiders, apparent variation in the extent to which local factors influence abundance and diversity could actually be due to differences at the landscape scale (Booij and Noorlander 1992, Feber et al. 1998, Clough et al. 2005, Schmidt et al. 2005). Therefore, testing for the influences of both local and landscape factors at multiple scales is essential.

We surveyed spiders in urban gardens in three counties of California to examine the changes in spider communities with changes in local and landscape characteristics. We sought to answer the following questions: 1) How many spider species are supported by urban gardens and which are common families and species in urban gardens? 2) Which local habitat characteristics and landscape factors correlate with spider activity density (a measure of both abundance and degree of movement) and richness? and 3) Are local or landscape factors stronger correlates of spider activity density and richness?

Materials and Methods

Study Design and Site Characteristics. We conducted research in 19 urban garden sites in three California counties: Santa Cruz, Santa Clara, and Monterey (Table 1). The gardens ranged in size from 444 to 15,525 m². All gardens had been in production for at least 4, but up to 46 yr. The gardens were chosen for their perceived differences in terms of local factors (e.g. vegetation, ground cover, canopy cover) based on site visits, as well as landscape factors (e.g. percent of agriculture, forest, developed land surrounding gardens) as initially assessed using Google Earth images. Approximately one-third of the sites were surrounded by high percentages of developed land, one-third of the sites surrounded by relatively large amounts of extensive agriculture, and one-third of the sites were surrounded by forests or natural land cover types (Table 2). Each garden was separated by a minimum of 2 km.

Table 2. Range of local and landscape characteristics measured in the gardens

x 14 1 C .	2.0	
Local/landscape factors	Min.	Max
	value	value
% Cover bare soil (1 by 1 m)	2.75	78.75
% Cover grass (1 by 1 m)	0	32.50
% Cover herbaceous plants (1 by 1 m)	0	95.75
% Cover rocks (1 by 1 m)	0	9.50
% Cover leaf litter (1 by 1 m)	0	39.25
% Cover mulch (1 by 1 m)	0	85.75
% Cover concrete (1 by 1 m)	0	25
Height of tallest herbaceous vegetation (1 by 1 m)	17.25	178.25
No. of flowers (1 by 1 m)	0	9200
No. of crop species (1 by 1 m)	0	12
No. of ornamental species (1 by 1 m)	0	6
No. of weed species (1 by 1 m)	0	10
No. of grass species (1 by 1 m)	0	4
No. of herbaceous plant species (1 by 1 m)	2	27
% Canopy cover (20 by 20 m)	0	69.2
No. trees (20 by 20 m)	0	11
Mean tree height (m; 20 by 20 m)	0	6.09
No. shrubs (20 by 20 m)	0	21
Mean shrub height (cm; 20 by 20 m)	0	22.69
No. trees or shrubs in flower (20 by 20 m)	0	18
No. woody plant species (20 by 20 m)	0	11
% Cover concrete (100 by 100 m)	0.25	41.25
% Cover woody plants (100 by 100 m)	2.5	50.25
% Cover mulch (100 by 100 m)	1.25	33
% Cover buildings (100 by 100 m)	0.25	37
% Cover bare soil (100 by 100 m)	3	29
% Cover weeds (100 by 100 m)	2.5	44.75
% Cover lawn (100 by 100 m)	0.75	18
% Cover nonwoody plants (100 by 100 m)	4.25	35.75
No. trees (100 by 100 m)	5	199
% Open space (500 m radius)	1.03	75.29
% Urban area (500 m radius)	3.55	98.97
% Natural area (500 m radius)	0	52.63
% Agricultural area (500 m radius)	0	23.74
% Open space (1 km radius)	2.63	57.24
% Urban area (1 km radius)	9.30	97.37
% Natural area (1 km radius)	0	66.96
% Agricultural area (1 km radius)	0	28.51

We measured vegetation and other local habitat characteristics at two spatial scales five times between May and September 2013. First, at approximately the center of each site, we established a 20- by 20-m plot within which we measured various local characteristics. We measured canopy cover with a convex spherical densitometer at the center of the plot, and 10 m to the N, W, S, and E of the center. We measured the height and circumferences of all trees (at 1.37 m above ground) and shrubs (at 5 cm above ground), and noted if trees and shrubs were in flower. During each sampling period, we randomly sampled four 1- by 1-m plots within the 20- by 20-m plot. In each 1- by 1-m plot, we measured heights of the tallest non-woody vegetation, counted numbers of flowers by color (white, red, orange, yellow, green, blue, violet, and pink), and measured ground cover by noting the percent cover from bare soil, grass, herbaceous plants, rocks or concrete, leaf litter, and mulch or straw. All plants within the 1- by 1-m plots were identified to morphospecies, and classified into the following groups: crop, weed, grass, and ornamental plants. Second, we established a 100- by 100-m plot in which we counted all trees (>30 cm circumference at breast height) and quantified percent area with 1) concrete, 2) buildings, 3) mulch,

4) lawn, 5) woody vegetation, 6) weedy vegetation, 7) non-woody vegetation, and 8) bare ground. The 20- by 20- and 100- by 100-m plots together yielded 38 variables describing local habitat characteristics.

We also classified the landscape surrounding each garden. We obtained land cover data for the study counties from the 2006 National Land Cover Database (NLCD, 30-m resolution; Fry et al. 2011) and calculated the percentage of land cover types in buffers surrounding each study site. We used the NLCD land cover types to create four surrounding habitat categories: 1) natural habitat (including deciduous [NLCD] number 41], evergreen [42], and mixed forests [43], dwarf scrub [51], shrub-scrub [52], and grassland-herbaceous [71]), 2) open (including lawn grass, park, and golf courses [21]), 3) urban (including low- [22], medium- [23], and high-intensity developed land [24]), and 4) agriculture (including pasture-hay [81] and cultivated crop [82]). Other land cover types in the surrounding areas (open water [11], wetlands [90, 95], and barren land [31]) did not cover >5% of the total area in any buffer zone and were not included as correlates of spider data. We assessed the percent of each land cover type at 500-m and 1-km buffers around each garden with spatial statistics tools in ArcGIS v. 10.1. The 500-m buffer has been appropriate for analyzing landscape effects on species richness and activity density for many taxa (Concepción et al. 2007, Schmidt et al. 2007, Batáry et al. 2012). We also chose the 1-km buffer to account for variation in spider dispersal techniques, such as walking or ballooning. Because sites were separated by at least 2 km, no landscape buffers from different sites overlapped. This analysis yielded a total of 16 landscape variables.

Identification. We Spider Sampling and sampled spiders monthly from May to September 2013, for a total of five sampling periods at each site. We sampled spiders using pitfall traps placed level with the soil. The traps had a diameter of 11.5 cm and a height of 7.5 cm, and contained a saturated salt solution with drops of soap. At each site, we placed six traps in a rectangular arrangement, with each trap located 5 m from each other, within the 20- by 20-m vegetation plot. Because spiders must actively walk along the ground to fall into the traps, our surveys were a measure of spider activity density and not abundance. We collected the pitfall traps 72 h after placing them and kept all caught specimens for later identification. We identified individuals in the most common families to species, and identified individuals of other spider families to morphospecies with the identification manual by Ubick et al. (2005) and several American Museum Novitates (Barnes 1959; Platnick and Murphy 1984; Platnick and Shadab 1982, 1988).

Data Analysis. To determine the significance and relative importance of individual local and landscape factors for spider activity density and richness, we used regression trees with the "party" package in R (Hothorn et al. 2006). Regression trees examine which factors predict a dependent variable, and determine the relative importance of individual factors (Olden et al. 2008, Strobl et al. 2009). Specifically, regression trees

utilize an iterative, binary recursive data-partitioning algorithm to examine each variable, searching for the best predictor, splitting the data for the dependent variable into two distinct groups, and then repeating the variable selection until no more significant predictors are found (Hothorn et al. 2006).

We examined patterns for activity density and richness of all spiders, and species richness for families composing >15% of total spiders with >3 species. We tested six dependent variables: 1) activity density of adult spiders, 2) activity density of Gnaphosidae spiders, 3) activity density of Lycosidae spiders, 4) spider family richness, 5) spider morphospecies richness, and 6) Gnaphosidae species richness. We included 54 predictor variables (38 local factors and 16 landscape factors) in regression trees. We considered the pooled sample of six traps per site on a single sample date as a replicate, and the minimum criterion was set to 0.95 (P = 0.05). We justify using the samples from different months as independent samples because 1) the vegetation characteristics were also measured each month, and significantly differed, and 2) including mean or total activity density and richness as dependent variables and means in the site characteristics would homogenize the data, reducing the detectability of ranges of variables collected across the field season. All analyses pertain to only adult spiders.

Results

We collected a total of 2,904 spider individuals, and 1,549 (53%) of these were adults. For adult spiders only, we found 22 families and 46 morphospecies. The most abundant spider family was Lycosidae (64% of individuals captured), followed by Gnaphosidae (17%) that together represented the vast majority of individuals collected. Within Lycosidae, we found two species: *Pardosa sierra* Banks (988 adults) and *Schizocosa mccooki* Montgomery (8 adults). Within Gnaphosidae, we found four species: *Trachyzelotes barbatus* L. Koch (81 adults), *Urozelotes rusticus* L. Koch (67 adults), *Drassyllus saphes* Chamberlin (66 adults), and *Micaria utahna* Gertsch (35 adults). Theridiidae had the highest species richness, with 7 morphospecies.

Spider activity density was correlated with several local habitat characteristics and two landscape factors. Adult spider activity density was positively correlated with agriculture within 1 km, flowering tree and shrub abundance, mulch cover within 100 m, and ornamental plant species presence (Fig. 1a). Gnaphosid activity density increased in sites without concrete cover in 100-m plots. Further, Gnaphosidae activity density decreased in sites with higher percentages of bare soil cover within 100 m and higher percentages of leaf litter cover within 1 m (Fig. 1b). Lycosid activity density was positively correlated with agriculture within 500 km, flowering tree-shrub abundance, and mulch cover within 100 m (Fig. 1c). We tested for differences in factors that correlated with activity density of male and female Lycosidae spiders (by far the most common spider group), and the same factors were significant drivers of both sexes.

Spider family richness was higher in sites with ornamental species presence and higher crop species richness (Fig. 1d). Morphospecies richness was higher in sites with more mulch cover within 100 m, in sites with taller trees within 20 m, and in sites with more than one ornamental plant species (Fig. 1e). Gnaphosid species richness was positively correlated with mulch cover within 100 m, but declined with large amounts of bare soil cover within 1 m (Fig. 1f).

Discussion

Our first research question was directed at understanding how many spider species inhabit urban gardens in the California central coast, and which are the most common families and species. Our family richness and morphospecies richness are similar to other spider studies that were performed in central California, or that had similar methods. In past non-California urban habitat studies that used pitfall traps, family richness averaged at 18 spider families and 64 morphospecies (Moorhead and Philpott 2013, Gardiner et al. 2014, Philpott et al. 2014). Fraser and Frankie (1986) compared spider communities in urban and natural habitats in Berkeley, CA, and found a total of 20 families and 75 morphospecies, with Gnaphosidae and Lycosidae dominant in pitfall traps for both habitat types. Further, Hogg and Daane (2011) found an average of 15 families and 40 species in both natural and agricultural habitats in California. Our morphospecies richness of 46 seems in line with other research, and is relatively high especially considering that we only sampled from one habitat type. Many of these past studies with >50 species or morphospecies collected from urban gardens and natural or less disturbed habitats that thus increased the likelihood of capturing a higher number of species.

Our second and third research questions aimed to understand which local and landscape factors correlate with spider activity density and species richness in urban gardens, and whether local or landscape factors appear to be more important for spiders. Several different local factors, and a few landscape factors, correlated with changes in spider activity density and species richness, and most of the significant factors that correlated with spider activity density and richness were local, rather than landscape-scale factors. This is consistent with ideas that spiders tend to not relocate habitats or webs often due to risk of predation while moving between habitat sites, or the energy expenditure associated with patch choice (Vollrath and Houston 1986, Uetz 1992). The factors that influenced activity density and richness of spiders fall into three general categories: ground cover factors, vegetation factors, and amount of agricultural land in the landscape. In the paragraphs below, we discuss the mechanisms by which these different groups of factors may influence spider communities.

Several ground cover variables were correlated with increases or decreases in spider activity density and richness including mulch, bare soil, concrete, and leaf litter. Mulch cover within 100 m correlated with (a)

(b)

10

Agriculture within 1 km p < 0.001

> 20,54%

≤ 20.54%

Number of

flowering trees/shrubs within 20 m

< 0.001

> 3

n = 18

o

150

150

Mulch cov

Number of

within 1 m p = 0.003

150

>0

36

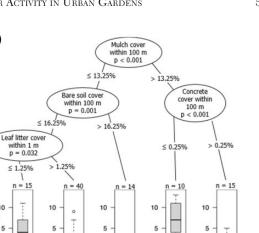
150

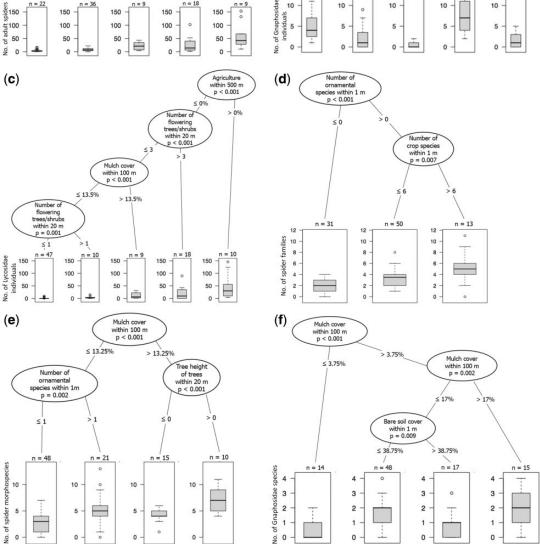
≤ 0

= 22

supplet

within 100 m p < 0.001





Regression trees showing the relationship between the overall (a) spider activity density, (b) Gnaphosidae activity Fig. 1. density, (c) Lycosidae activity density, (d) spider family richness, (e) spider morphospecies richness, and (f) Gnaphosidae species richness, with significant predictors selected from 38 local and 16 landscape characteristics measured in urban gardens in the California central coast. Significant predictors are circled and ranked (top, highest correlation with dependent variable). P-values indicate the significance of the relationship being tested. Threshold values for each characteristic, listed below the respective circle, divide the data into subgroups until no more significant predictors are found. n indicates the number of garden sites that fall into a subgroup. Box plots include the inner quartiles (grey box), the median values (solid black line), and $1.5 \times$ the inner quartiles (error bars) of spider activity density or richness associated with each significant predictor.

increased Lycosidae activity density, Gnaphosidae activity density, overall spider activity density, and increased Gnaphosidae species richness and overall morphospecies richness. Individuals in the Lycosidae and Gnaphofamilies, representing 81% sidae of captured individuals, are ground spiders. Ground spiders do not rely on webs for capturing prey, but instead move actively over the ground and chase or pounce on their prey (Uetz and Unzicker 1976). Spiders are sensitive to both microclimate and habitat structure, and mulch may provide suitable burrowing habitat for groundhunting spiders that need specific humidity and temperature conditions (Riechert and Bishop 1990, Uetz 1991, Bell et al. 2001). Covering the surface of bare soil with mulch reduces soil water evaporation by decreasing soil temperature, preventing vapor diffusion, absorbing water vapor into the mulch, and reducing wind speed gradients at the soil-atmosphere level (Hatfield et al. 2001). The negative correlation of Gnaphosidae activity density with concrete cover and bare soil may be related to the inefficiency of humidity and temperature regulation on these types of ground cover.

It is interesting that Gnaphosidae activity density negatively correlates with leaf litter at the 1- by 1-m range, when there are lower percentages of mulch within the 100- by 100-m plot. Considering past studies that looked at spider activity density and species richness across gradients of leaf litter on the forest floor, we would have expected a positive correlation with percentage of leaf litter with spider activity density or species richness (Uetz 1979, Bultman and Uetz 1982). Perhaps leaf litter cover in urban gardens differs from leaf litter in forests and less disturbed habitats. Leaf litter cover from crop species might reduce the ability for ground hunters to adequately locate and chase down prey in urban settings. Evidence from other arthropod natural enemy studies show that additional habitat structure can inhibit foraging capabilities (Andow and Prokrym 1990, Clark et al. 1999, Legrand and Barbosa 2003, Schmidt and Rypstra 2010).

Several vegetation characteristics, including number of flowering plants and trees, ornamental and crop plant richness, and tree height correlated with changes in activity density and richness. Flowering tree and shrub abundance was correlated with lycosid and overall activity density. Ornamental and crop plant richness correlated with family and morphospecies richness. Increased abundance and diversity of flowering trees, shrubs, and ornamental or crop species that are often associated with agricultural habitats may attract many potential prey items (Rebek et al. 2005). An increase in prey abundance or richness would also encourage an increase in activity density and diversity of spiders (Sunderland and Samu 2000). Alternatively, studies have shown that spiders are more abundant in habitats with higher structural complexity (Langellotto and Denno 2004, Shrewsbury and Raupp 2006). An increase in plant abundance and diversity could increase habitat complexity, thus driving increases in spider activity densities and diversity.

The positive correlation between morphospecies richness and tree height of trees within 20 m may be

related to bird habitat or canopy cover for spiders. It is possible that the food webs of these gardens rely on birds as a keystone species, and increased tree height would provide perching or nesting sites for birds as predators. Birds may prey on the spiders and might help control arthropod populations and maintain ecological stability in each garden (Gruner 2005). Species richness may help maintain ecological resilience and function after disturbances (Folke et al. 1996, Naeem and Li 1997, Sattler et al. 2010). Single species have limited functions they perform for ecosystems they inhabit. Ecosystems with more species are usually more stable when experiencing disturbances, allowing the system to resist drastic changes (Tilman 1996). Alternatively, increased tree height may provide more canopy cover to spiders. Canopy cover and mulch can provide temperature and humidity regulation for species-specific habitat requirements (Riechert and Bishop 1990, Hatfield et al. 2001, Lin 2010).

Finally, the amount of agricultural habitat within 500 m and 1 km correlated with changes in spider activity density. Adult spider and lycosid activity density were positively correlated with the amount of the landscape in agriculture. This is likely due to prey density and polyphagous eating habits of spiders. Agricultural areas generally attract high numbers and a variety of arthropods, which in turn may attract spiders as predators (Sunderland and Samu 2000). Additionally, ballooning (aerial dispersal) is the most efficient dispersal technique at the landscape scale and allows spider individuals to survey separated, varying habitats in a short span of time to find mates or resources, reduce competition, or avoid cannibalism (Weyman 1993). Destinations of ballooning individuals are determined by meteorological factors, such as wind speed, humidity, and temperature. Thus, ballooning is a high-risk activity through which individuals may land in unfavorable habitats and will not be able to reproduce (Samu et al. 1999). Juvenile spiders are more likely to exhibit ballooning behavior, but adults have also been observed ballooning (Bristowe 1929). Species of Lycosidae are not observed ballooning as often as other spider families, but lycosids are commonly among the first spiders to colonize agroecosystems (Dean and Sterling 1985, Pearce et al. 2005).

One caveat of our study is that pitfall traps, as a sampling method, are limited to collecting primarily ground-dwelling spiders and spider activity. Over 80% of the captured spiders were wandering spiders that spend most of their time either along the ground or just beneath the surface. Thus, the captured spiders may not be a complete representation of spider abundance, activity density, diversity, and species richness in these urban gardens. Further diversity studies could use pitfalls in addition to visual observations, sweep netting, or sticky traps to accurately capture many webdwelling species that rarely travel along the ground. Pitfall traps may also be a better indicator of spider activity as opposed to abundance. Spiders must be actively walking to fall into traps, and some species are generally more active than others.

In sum, we find that urban gardens support a high diversity and activity of spiders, that spiders in urban gardens primarily respond to local scale changes in garden management associated with ground cover and plant communities, and that the amount of agriculture nearby to the gardens is also associated with spider community changes. As garden habitats support relatively high activity density, and relatively high richness of spiders within urban areas, understanding the mechanisms behind these correlations may be important for promoting conservation of spider biodiversity. In addition, spiders, including the very abundant ground spiders, potentially provide pest control services within urban gardens. Spiders appear to be more affected by local factors rather than landscape-scale factors, meaning that gardeners may be able to manipulate their garden environments to promote these beneficial arthropods. Mulch may maintain proper temperature and humidity requirements for several species of ground spiders, and increased abundance and diversity of flowering or crop plant species may attract potential prey items. Urban gardens, managed with these features, may promote spider activity density, richness, and biodiversity. Thus, as urban areas continue to expand, it is important to preserve and maintain green space within cities to provide adequate habitat for spider conservation.

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References Cited

- Andow, D. A., and D. R. Prokrym. 1990. Plant structural complexity and host finding by a parasitoid. Oecologia 82: 162–165.
- Barnes, R. D. 1959. The lapidicina group of the wolf spider genus *Pardosa* (Araneae, Lycosidae). Am. Mus. Novit. 1960: 1–20.
- Batáry, P., A. Holzschuh, K. M. Orci, F. Samu, and T. Tscharntke. 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. Agric. Ecosyst. Environ. 146: 130–136.
- Bell, J. R., C. P. Wheater, and W. R. Cullen. 2001. The implications of grassland and heathland management for the conservation of spider communities: A review. J. Zool. 255: 377–387.
- Bloom, D. E. 2011. 7 Billion and counting. Science 333: 562–569.
- Booij, C. J. H., and J. Noorlander. 1992. Farming systems and insect predators. Agric. Ecosyst. Environ. 40: 125–135.

- Bristowe, W. S. 1929. The distribution and dispersal of spiders. Proc. Zool. Soc. Lond. 99: 633–657.
- Bristowe, W. S. 1941. The comity of spiders. Ray Society, London, England.
- Bultman, T. L., and G. W. Uetz. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55: 34–41.
- Clark, M. E., T. G. Wolcott, D. L. Wolcott, and A. H. Hines. 1999. Intraspecific interference among foraging blue crabs *Callinectes sapidus*: Interactive effects of predator density and prey patch distribution. Mar. Ecol. Prog. Ser. 178: 69–78.
- Clough, Y., A. Kruess, D. Kleijin, and T. Tscharntke. 2005. Spider diversity in cereal fields: Comparing factors at local, landscape, and regional scales. J. Biogeogr. 32: 2007–2014.
- Concepción, E. D., M. Díaz, and R. A. Baquero. 2007. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. Landsc. Ecol. 23: 135–148.
- Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience 50: 593–601.
- Dean, D. A., and W. L. Sterling. 1985. Size and phenology of ballooning spiders at two locations in eastern Texas. J. Arachnol. 13: 111–120.
- Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat. Basic Appl. Ecol. 4: 129–138.
- Feber, R. E., J. Bell, P. J. Johnson, L. G. Firbank, and D. W. Macdonald. 1998. The effects of organic farming on surface-active spider (Araneae) assemblages in wheat in southern England, UK. J. Arachnol. 26: 190–202.
- Folke, C., C. S. Holling, and C. Perrings. 1996. Biological diversity, ecosystems, and the human scale. Ecol. Appl. 6: 1018–1024.
- Francis, M. 1989. Control as a dimension of public-space quality. Public Places Spaces 10: 147–172.
- Fraser, J. B., and G. W. Frankie. 1986. An ecological comparison of spiders from urban and natural habitats in California. Hilgardia 54: 1–28.
- Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States. Photogramm. Eng. Remote Sensing 77: 858–864.
- Gardiner, M. M., S. P. Praizner, C. E. Burkman, S. Albro, and P. S. Grewal. 2014. Vacant land conversion to community gardens: Influences on generalist arthropod predators and biocontrol services in urban greenspaces. Urban Ecosyst. 17: 101–122.
- Gonthier, D. J., K. K. Ennis, S. Farinas, H. Hsieh, A. L. Iverson, P. Batáry, J. Rudolphi, T. Tscharntke, B. J. Cardinale, and I. Perfecto. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. R. Soc. Biol. Sci. 281: 20141358.
- Gruner, D. S. 2005. Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai'i Island. Biol. Invasions 7: 541–546.
- Hatfield, J. L., T. J. Sauer, and J. H. Prueger. 2001. Managing soils to achieve greater water use efficiency. Agron. J. 93: 271–280.
- Hogg, B. N., and K. M. Daane. 2011. Ecosystem services in the face of invasion: The persistence of native and nonnative spiders in an agricultural landscape. Ecol. Appl. 21: 565–576.
- Hothorn, T., K. Hornik, and A. Zeileis. 2006. Unbiased recursive partitioning: A conditional inference framework. J. Comput. Graph. Stat. 15: 651–674.
- Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in

agricultural landscapes: The role of native plants. Front. Ecol. Environ. 7: 196–203.

- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373: 299–302.
- Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. Oecologia 139: 1–10.
- Legrand, A., and P. Barbosa. 2003. Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata L.* (Coleoptera: Coccinellidae). Environ. Entomol. 32: 1219–1226.
- Lin, B. B. 2010. The role of agroforestry in reducing water loss through soil evaporation and crop transpiration in coffee agroecosystems. Agric. For. Meteorol. 150: 510–518.
- Mansour, F., D. Rosen, and A. Shulov. 1980. A survey of spider populations (Araneae) in sprayed and unsprayed apple orchards in Israel and their ability to feed on larvae of *Spodoptera littoralis* (Boisd.). Acta Oecologica Oecologica Appl. 1: 189–197.
- Marc, P., and A. Canard. 1997. Maintaining spider biodiversity in agroecosystems as a tool in pest control. Agric. Ecosyst. Environ. 62: 229–235.
- Marc, P., A. Canard, and F. Ysnel. 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agric. Ecosyst. Environ. 74: 229–273.
- McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Ann. Entomol. Soc. Am. 93: 825–835.
- McIntyre, N. E., J. Rango, W. F. Fagan, and S. H. Faeth. 2001. Ground arthropod community structure in a heterogeneous urban environment. Landsc. Urban Plan. 52: 257–274.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52: 883–890.
- McKinney, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst. 11: 161– 176.
- Moorhead, L. C., and S. M. Philpott. 2013. Richness and composition of spiders in urban green spaces in Toledo, Ohio. J. Arachnol. 41: 356–363.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390: 507–509.
- Nentwig, W. 1987. The prey of spiders, pp. 249–263. In W. Nentwig (ed.). Ecophysiology of spiders. Springer, Berlin, Germany.
- Nowak, D. J., R. A. Rowntree, E. G. McPherson, S. M. Sisinni, E. R. Kerkmann, and J. C. Stevens. 1996. Measuring and analyzing urban tree cover. Landsc. Urban Plan. 36: 49–57.
- Nyffeler, M. 1999. Prey selection of spiders in the field. J. Arachnol. 27: 317–324.
- Nyffeler, M. 2000. Ecological impact of spider predation: A critical assessment of Bristowe's and Turnbull's estimates. Bull. Br. Arachnol. Soc. 11: 367–373.
- Nyffeler, M., and G. Benz. 1987. Spiders in natural pest control: A review. J. Appl. Entomol. 103: 321–339.
- Olden, J. D., J. J. Lawler, and N. L. Poff. 2008. Machine learning methods without tears: A primer for ecologists. Q. Rev. Biol. 83: 171–193.
- Pearce, S., M. P. Zalucki, and E. Hassan. 2005. Spider ballooning in soybean and non-crop areas of southeast Queensland. Agric. Ecosyst. Environ. 105: 273–281.
- Philpott, S. M., J. Cotton, P. Bichier, R. L. Friedrich, L. C. Moorhead, S. Uno, and M. Valdez. 2014. Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. Urban Ecosyst. 17: 513–532.
- Platnick, N. I., and J. A. Murphy. 1984. A revision of the spider genera *Trachyzelotes* and *Urozelotes* (Araneae, Gnaphosidae). Am. Mus. Novit. 2792: 1–30.

- Platnick, N. I., and M. U. Shadab. 1982. A revision of the American spiders of the genus *Drassylus* (Araneae, Gnaphosidae). Bull. Am. Mus. Nat. Hist. 173: 1–97.
- Platnick, N. I., and M.U. Shadab. 1988. A revision of the American spiders of the genus *Micaria* (Araneae, Gnaphosidae). Am. Mus. Novit. 2916: 1–64.
- Raupp, M. J., P. M. Shrewsbury, and D. A. Herms. 2009. Ecology of herbivorous arthropods in urban landscapes. Annu. Rev. Entomol. 55: 19–38.
- Rebek, E. J., C. S. Sadof, and L. M. Hanks. 2005. Manipulating the abundance of natural enemies in ornamental landscapes with floral resource plants. Biol Control 33: 203–216.
- Riechert, S. E. 1999. The hows and whys of successful pest suppression by spiders: Insights from case studies. J. Arachnol. 27: 387–396.
- Riechert, S. E., and L. Bishop. 1990. Prey control by an assemblage of generalist predators: Spiders in garden test systems. Ecology 71: 1441–1450.
- Riechert, S. E., and T. Lockley. 1984. Spiders as biological control agents. Ann. Rev. Entomol. 29: 299–320.
- Samu, F., K. D. Sunderland, and C. Szinetár. 1999. Scaledependent dispersal and distribution patterns of spiders in agricultural systems: A review. J. Arachnol. 27: 325–332.
- Sattler, T., P. Duelli, M. K. Obrist, R. Arlettaz, and M. Moretti. 2010. Response of arthropod species richness and functional groups to urban habitat structure and management. Landsc. Ecol. 25: 941–954.
- Savard, J.-P. L., P. Clergeau, and G. Mennechez. 2000. Biodiversity concepts and urban ecosystems. Landsc. Urban Plan. 48: 131–142.
- Schmidt, J. M., and A. L. Rypstra. 2010. Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. Oecologia 164: 899–910.
- Schmidt, M. H., I. Roschewitz, C. Thies, and T Tscharntke. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. J. Appl. Ecol. 42: 281–287.
- Schmidt, M. H., C. Thies, W Nentwig, and T. Tscharntke. 2007. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. J Biogeogr 35: 157– 166.
- Schmidt, M. H., C. Thies, and T. Tscharntke. 2004. Landscape context of arthropod biological control, pp. 55–63. In G. M. Gurr, S. D. Wratten, and M. A. Altieri (eds.), Ecological engineering for pest management: Advances in habitat manipulation for arthropods. CSIRO Press, Collingwood, Australia.
- Shrewsbury, P. M., and M. J. Raupp. 2006. Do top-down or bottom-up forces determine *Stephanitis pyrioides* abundance in urban landscapes? Ecol. Appl. 16: 262–272.
- Strobl, C., J. Malley, and G. Tutz. 2009. An introduction to recursive partitioning: Rationale, application, and characteristics of classification and regression trees, bagging, and random forests. Psychol. Methods 14: 323–348.
- Sunderland, K., and F. Samu. 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: A review. Entomol. Exp. Appl. 95: 1–13.
- Thompson, K., K. C. Austin, R. M. Smith, P. H. Warren, P. G. Angold, and K. J. Gaston. 2003. Urban domestic gardens: Putting small-scale plant diversity in context. J. Veg. Sci. 14: 71–78.
- Tilman, D. 1996. Biodiversity: Population versus ecosystem stability. Ecology 77: 350–363.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8: 857–874.

- Turnbull, A. L. 1973. Ecology of the true spiders (Araneomorphae). Annu. Rev. Entomol. 18: 305–348.
- Ubick, D., P. Paquin, P. E. Cushing, and V. Roth. 2005. Spiders of North America: An identification manual. American Arachnological Society, Poughkeepsie, New York.
- Uetz, G. W., and J. D. Únzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. J. Arachnol. 3: 101–111.
- Uetz, G. W. 1979. The influence of variation in litter habitats on spider communities. Oecologia 40: 29–42.
- Uetz, G. W. 1991. Habitat structure and spider foraging. Habitat Struct. 8: 325–348.
- Uetz, G. W. 1992. Foraging strategies of spiders. Trends Ecol. Evol. 7: 155–159.

- (USCB) United States Census Bureau. 2014. Historical estimates of world population. USCB, Suitland, MD.
- (UNPD) United Nations Population Division. 2014. Our urbanizing world: Population Facts No. 2014/3, August 2014. UNPD, New York, NY.
- Vollrath, F., and A. Houston. 1986. Previous experience and site tenacity in the orb spider *Nephila* (Araneae, Araneidae). Oecologia 70: 305–308.
- Weyman, G. S. 1993. A review of the possible causative factors and significance of ballooning in spiders. Ethol. Ecol. Evol. 5: 279–291.

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