RESEARCH ARTICLE

Local and landscape-scale environmental filters drive the functional diversity and taxonomic composition of spiders across urban greenspaces

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Abstract

1. Urban patch colonization and species establishment within cities are restricted by the behavioural, life history and physiological attributes of colonizing species, in conjunction with environmental filtering processes at small and large spatial scales. To enhance the local biodiversity in urban greenspaces, these filtering processes need to be assessed so that greenspace design and management can guide establishment of local species pools.

2. We investigated the relative importance of local and landscape-scale features on spider community assembly using a functional and taxonomic approach. Within the city of Cleveland, Ohio, USA, we established a field experiment wherein control vacant lots, urban meadows, and low- and high-diversity pocket prairies were established across eight neighbourhoods ($N = 32$). Spiders were sampled during June–August of 2015 and 2016 using pitfall traps and vacuums. Spider functional diversity was assessed using null models, while local and landscape drivers were analysed via canonical partial least squares and clustered image maps.

3. Increased mowing was associated with lower-than-expected spider functional alpha and beta diversity in 2015. Patch isolation and percentage impervious surface increased the functional dissimilarity and taxonomic diversity of spiders in 2016, resulting in higher-than-expected overall functional alpha diversity. We also found that increasing plant height and biomass favoured spiders with large body size and decreased the abundance of small web weavers.

4. *Synthesis and applications*. Our findings suggest that increasing the amount of impervious surface in cities will act as a strong environmental filter, producing more spatially distinct spider communities at a landscape scale. Additionally, while periodic mowing in vacant lots benefits some spider taxa, it has a negative impact on the establishment of several species, mainly larger spiders and those most sensitive to disturbance. To conserve spiders and the biota depended upon them, investment in managed greenspaces such as pocket prairies that require infrequent mowing is warranted. In doing so, cities can enhance urban biodiversity and beautify local neighbourhoods.

1 | INTRODUCTION

Wildlife conservation research in cities has received considerable attention in the last decade due to the number of studies reporting that urban greenspaces can support diverse local communities, including rare and endangered species (Ives et al., 2016; Mckinney, 2002). Invertebrates have been a major focus of this research, and speciose arthropod assemblages have been reported in urban areas world-wide (Jones & Leather, 2012; McIntyre, 2000). In some cities, greenspaces are increasing due to local conservation efforts or newly available parcels resulting from prolonged economic and population decline (Blanco et al., 2009; Gardiner, Burkman, & Prajzner, 2013). However, managing this influx of green infrastructure to support biodiversity is challenging as species have different resource requirements. To achieve the conservation potential of urban greenspaces, a multiscale spatial approach is needed to elucidate the hierarchical filters involved in the distribution and establishment of species within cities (Aronson et al., 2016; Pickett et al., 2011).

There is substantial evidence demonstrating that environmental filters (local habitat characteristics and landscape composition and configuration) influence the species composition and spatial distribution of arthropod communities in cities (Aronson et al., 2016; Tscharntke et al., 2012). At the local scale, insects have been associated with plant diversity and vegetation complexity (Eckert, Möller, & Buchholz, 2017; Randlkofer, Obermaier, Hilker, & Meiners, 2010), whereas landscape-scale features such as the amount of impervious surface and greenspace connectivity have been implicated as important environmental predictors (Braaker, Obrist, Ghazoul, & Moretti, 2017; Davis, Debinski, & Danielson, 2007), especially for species with limited dispersal capabilities (Sivakoff, Prajzner, & Gardiner, 2018). To date, many studies have described how environmental filters shape local species pools, yet it is still challenging to determine the spatial scale responsible for assembling species communities, as the relative importance of local and landscape drivers varies by taxa (Jones & Leather, 2012; Lepczyk et al., 2017; McIntyre, 2000). This has led to the application of ecological theory to identify the mechanisms driving arthropod communities within cities (Fattorini, Mantoni, De Simoni, & Galassi, 2018; Tscharntke et al., 2012). Deriving from the 'single large or several small' dilemma in ecology, one hypothesis suggests that fragmented habitats increase biodiversity due to species turnover across several small patches (Fahrig, 2017; Tscharntke et al., 2012). This hypothesis has been criticized due to the well-documented detrimental effects of fragmentation on local species (Fletcher et al., 2018; Pfeifer et al., 2017); yet to draw definitive conclusions, more research is needed examining the response of arthropods to habitat fragmentation (Fattorini et al., 2018; Gibb & Hochuli, 2002), especially within cities.

To better understand how environmental filters affect species assemblages in urban ecosystems, we need to shift our focus from biodiversity assessments to the mechanistic processes behind these patterns (Cadotte, Carscadden, & Mirotchnick, 2011; Schwarz et al., 2017). Despite the important contributions of taxonomic metrics (e.g. abundance and richness) to conservation biology, functional diversity, wherein ecologists group species by traits and quantify the diversity of traits and functions, has shown to more accurately link biodiversity and ecosystem processes at different spatial scales (Cadotte et al., 2011; Díaz & Cabido, 2001; Gagic et al., 2015). Trait-based analyses have elucidated the mechanisms by which functional groups respond to habitat alteration, changes in temperature and urban greenspace management (Delgado de la flor, Burkman, Eldredge, & Gardiner, 2017; Magura, Nagy, & Tóthmérész, 2013; Venn, 2007). Additionally, trait-based approaches are particularly useful in monitoring arthropod communities because practitioners can target specific functional groups and achieve desired management or conservation goals. For example, studies have shown that urban greenspace management intensity is a determinant to the colonization and establishment of beetle and spider functional groups (Braaker et al., 2017; Delgado de la flor et al., 2017).

Consequently, we employed both a functional and taxonomic approach to investigate the local and landscape drivers of spider community assembly. To do so, we established the Cleveland Pocket Prairie Project, a large-scale field experiment where four habitat treatments were replicated on individual vacant lots across eight inner-city neighbourhoods (Figure 1). Cleveland, Ohio, USA has experienced steady human population decline and infrastructure loss over the last 60 years resulting in 27,000+ vacant lots spread across the city (Western Reserve Land Conservancy, 2018). These reclaimed greenspaces represent an opportunity to examine the impact of urban greenspace management on biodiversity across a large landscape scale (Blanco et al., 2009; Gardiner et al., 2013). We focused on spiders as they are among the most abundant and diverse predatory groups in urban ecosystems and are considered biological indicators of habitat alteration due to their sensitivity to environmental changes (Langellotto & Denno, 2004; Sarthou, Badoz, Vaissière, Chevallier, & Rusch, 2014). Within an urban landscape, a single patch may not have the capacity to sustain spider communities long term; nonetheless their spatial configuration may enable greenspaces to act as stepping stones, facilitating interactions among distant populations (Colding, 2007; Lepczyk et al., 2017). Following the premise that heterogenous, fragmented landscapes determine biodiversity patterns (see Hypothesis 2 in Tscharntke et al., 2012), we hypothesized that landscape-scale features would drive the functional dissimilarity of spider communities and determine the functional diversity of spiders occupying
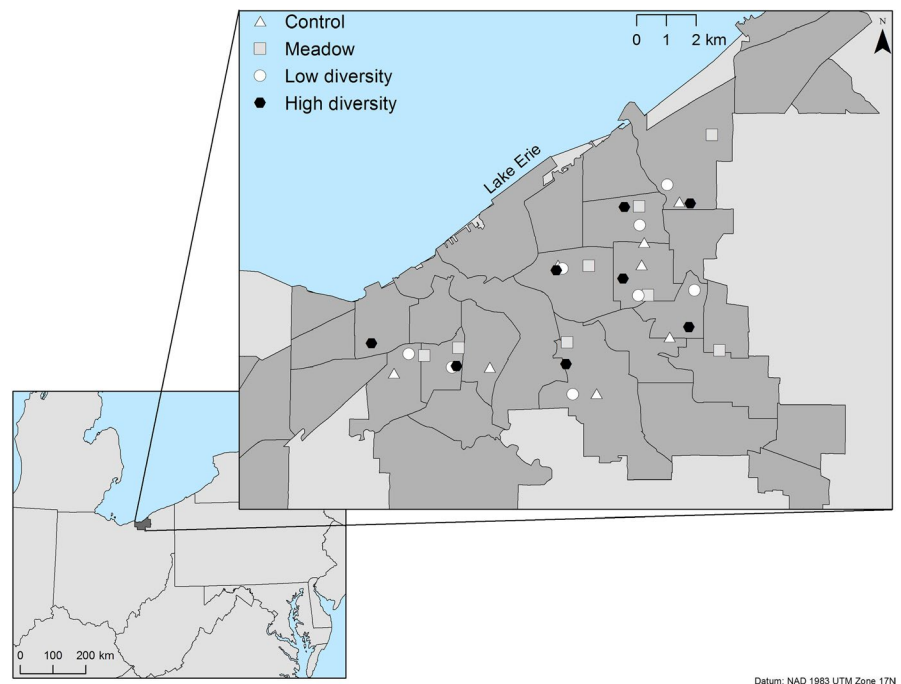
a patch, overriding local habitat characteristics. We predicted that spider functional beta diversity (dissimilarity) would increase with impervious surface, as variation in dispersal capabilities and adaptation to disturbance are demonstrated to aid successful spider community colonization (Argañaraz, Rubio, & Gleiser, 2018; Braaker et al., 2017). We also predicted that spider functional alpha diversity would be higher than expected at random, resulting from variation in successful colonization and establishment of spider functional groups within patches that vary in vegetation community composition, management and landscape context (Cattin, Blandenier, Banašek-Richter, & Bersier, 2003; Lowe, Threlfall, Wilder, & Hochuli, 2018).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in the city of Cleveland, Ohio, USA. Since the 1950s, Cleveland has experienced prolonged population decline and infrastructure loss, leading to the overabundance of vacant lots that are seeded with turf grass and mown monthly by the city. In 2014, we established the Cleveland Pocket Prairie Project across eight inner-city neighbourhoods and selected 32 vacant lots (15 × 30 m on average) wherein the following four experimental treatments were established (Figures 1 and 2): control vacant lots, urban meadows, low-diversity pocket prairies and high-diversity pocket prairies (Figure 2; Table S1). Pocket prairies were mown to a height of 20 cm monthly in 2015 to reduce weed competition and facilitate the establishment of flowering species. All data collection occurred within a 7 × 15 m grid of 105 quadrats (1 m² each), placed within the centre of each site.

2.2 | Spider sampling and identification

To account for both active and less mobile spiders, specimens were collected in each site using four pitfall traps and four vacuum samples three times per year in 2015 (12–22 June, 8–20 July and 11–18 August) and in 2016 (1–9 June, 6–14 July and 3–11 August). Within each site, four quadrats were randomly selected, and pitfall traps were set up for seven consecutive days. Pitfall traps consisted of 1 L plastic cups (12 cm diameter × 14 cm depth) filled halfway with water containing a small amount of dish soap (Dawn® Ultra, original scent). While pitfall traps were active, we vacuumed an area of 0.25 m² (30–50 cm away from each trap in any direction) for 45 s using a modified leaf vacuum (12 cm diameter). Specimens were stored in 80% ethanol and transported to the laboratory for sorting and identification. Due to weather and issues with landscaping contractors, vacuum sampling did not occur in July 2015.

Lycosidae and Linyphiidae adult spiders were identified to species and other adult and subadult spiders were identified to genus. We used several identification resources including Spiders of North America: An Identification Manual (Ubick, Paquin, Cushing, & Roth, 2017), Guide d'identification des Araignées (Araneae) du Québec (Paquin & Dupérré, 2003) and taxon-specific keys available at the World Spider Catalog (2018). Spider functional traits and groups (Table S2) were classified following Cardoso, Pekár, Jocqué, and Coddington (2011). Functional traits comprised foraging activity (web type or hunting method), prey range (stenophagous or euryphagous), vertical stratification (ground or vegetation), circadian activity (diurnal or nocturnal) and mean body size measured as the community-weighted mean (Cardoso et al., 2011; Uetz, Halaj, & Cady, 1999). Voucher specimens were deposited in the Museum of Biological Diversity at The Ohio State University.

FIGURE 2 Four treatments were established in 2014 across 32 vacant lots in Cleveland, Ohio: (a) Control vacant lots (seeded fescue grass and weedy flowering plant species, mowed monthly in 2015 and 2016 reflecting the city's management practices), (b) urban meadows (seeded fescue grass and weedy flowering plans, mowed annually in October 2015 and 2016), (c) low-diversity prairies and (d) high-diversity prairies (mowed monthly in 2015 and annually in October 2016). Prairies were seeded with a mixture of native grasses and flowing plants (Table S1)

2.3 | Local habitat variables and landscape cover

Local habitat variables were measured within 20 randomly selected quadrats. Using a 0.5 m^2 subquadrat, vegetation was sampled twice in 2015 (16 June–3 July and 22 July–13 August) and three times in 2016 (13–24 June, 11–22 July and 4–16 August). We recorded the three most dominant plant species per quadrat and diversity was calculated per site using the Shannon–Wiener index (Shannon, 1948). Plant biomass was estimated with a comparative yield method and the dry-weight-rank method from the 20 selected quadrats (Haydock & Shaw, 1975; Mannetje & Haydock, 1963). First, five quadrats were ranked (1 = lowest biomass density, 5 = highest biomass density and 2–4 in between) and established as the 'standard yields' reflecting the range of biomass within each site. In each of our 20 quadrats, we estimated the biomass yield, on a scale of 1 to 5, in comparison to our five standard yields. Only the five standard yields were harvested, oven-dried at 75°C for 48 hr and weighted. Finally, we plotted our standard yields, obtained an equation from the trendline and inserted our 20 ranked comparative yields from each site into this equation to estimate biomass in each quadrat. Average site-wide biomass was then calculated as the mean of these 20 comparative yield estimates.

Mean bloom abundance, bloom area and plant height were also calculated at each site from an additional six randomly selected quadrats. Average plant height was derived from three height measurements (cm) taken in each quadrat. Likewise, bloom abundances were counted per each flowering species present in the six quadrats. For each flowering species present, we recorded five bloom area measurements (mm^2) and then multiplied the average bloom size by the number of blooms present at a site to derive an average bloom area. Additionally, 20 soil cores were randomly sampled and pooled per site in April 2014 to measure the concentration of heavy metals. The contamination factor (Loska, Wiechuła, & Korus, 2004) of aluminium, antimony, arsenic, barium, cadmium, chromium, cobalt, copper, iron, lead, manganese, nickel, vanadium and zinc was calculated using regional background levels from eastern United States (US EPA, 2007), and from these values Pollution Load Indices were calculated per site (Tomlinson, Wilson, Harris, & Jeffrey, 1980; Weissmannová & Pavlovský, 2017).

Landscape information was obtained from the Cuyahoga County Planning Commission using remotely sensed images at 1–2 m resolution, captured in 2011. Following previous studies that reported spider community patterns across the landscape (Gardiner et al., 2010; Philpott et al., 2014), we selected buffer zones at 200 and 1,500 m radii from each site. Landscape cover was classified into percentage: 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. We limited the landscape covers to those directly affecting ground-dwelling spiders. To assess landscape composition, percentage grass/shrubs, percentage buildings, percentage flat impervious surface (roads/railroads and other paved) and Shannon landscape diversity were included in the analysis. For landscape configuration, we reclassified our categories into either 'greenspace' (grass/shrubs & TC over vegetation) or 'other' based on the importance of patch connectivity on our spider functional groups (Bonte, Baert, Lens, & Maelfait, 2004; Braaker et al., 2017), and calculated the *class*-metrics patch size (m^2) and patch isolation (m). Shannon landscape diversity, patch size and patch isolation were computed at 200 and 1,500 m radii using Fragstats v4.2 (McGarigal, Cushman, & Ene, 2012).

2.4 | Statistical analysis

To account for lost/stolen pitfall traps, catches were standardized to 84 trap days per site for each year (4 traps × 7 days × 3 months).

Samples were pooled per site per year to obtain a comprehensive representation of the spider community and a robust dataset suitable for functional diversity calculations (van der Plas, van Klink, Manning, Olff, & Fischer, 2017). Years were analysed separately and statistical analyses were performed in R v3.5.1 and RStudio v1.1.456 (R Core Team, 2019; RStudio Team, 2016).

2.4.1 | Functional diversity and null models

We calculated six functional diversity indices: the dendrogram-based functional alpha diversity (Petchey & Gaston, 2002) and functional beta diversity (Swenson, 2011) were computed using the PICANTE package (Kembel et al., 2010), while the distance-based functional divergence, functional richness, functional evenness and functional dispersion were calculated using the FD package (Laliberté & Legendre, 2010; Villéger, Mason, & Mouillot, 2008). Functional alpha and beta diversity were compared across treatments with analysis of deviance and type II Wald's chi-squared tests using the CAR package (Fox & Weisberg, 2019). Randomized null model communities (999) were generated using the trait-swap approach (Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Swenson, 2014), and standardized effect size (SES) was calculated for functional alpha and beta diversity. Observed SES functional diversity values were each compared to a null expectation using Wilcoxon signed-rank tests, where any significant deviation from zero represents a higher or lower value than would be expected by random chance (Chase, Kraft, Smith, Vellend, & Inouye, 2011).

2.4.2 | Multivariate pairwise correlation analysis

To examine patterns among spiders and environmental variables, we performed canonical partial least squares analyses (cPLS) using the MIXOMICS R package v6.8 (Rohart, Gautier, Singh, & Lê Cao, 2017). cPLS is a multivariate approach commonly used for analysing large datasets and maximizing the correlation between two datasets via two sets of latent variables (Krishnan, Williams, McIntosh, & Abdi, 2011; Tenenhaus, 1998). Our response dataset consisted of nine taxonomic metrics, 10 spider traits and six functional diversity indices. Taxonomic variables included the abundance, richness and diversity of Lycosidae and Linyphiidae species and of all spider genera. Spider functional traits comprised hunters, sheet/cob-web weavers, orb-web weavers, stenophagous, euryphagous, ground dwellers, plant dwellers, diurnal spiders, nocturnal spiders and spider body size. Functional diversity indices consisted of functional alpha and beta diversity, and functional divergence, richness, evenness and dispersion. Environmental predictor variables included seven local habitat variables and 12 landscape-scale variables (six variables at 200 m and six variables at 1,500 m). Local features included plant biomass, plant height, Shannon plant diversity, number of blooms, bloom area, pollution load index and mowing frequency. At each 200 and 1,500 m buffer zone, landscape composition

variables consisted of percentage buildings, percentage impervious surface and percentage grass/shrubs, while landscape configuration variables comprised landscape Shannon diversity, patch isolation and patch size. cPLS was performed between all 25 spider response variables and 19 environmental predictor variables, and pairwise correlations and clustered image maps were generated using Ward's hierarchical agglomerative clustering method (González, Cao, Davis, & Déjean, 2012).

3 | RESULTS

A total of 16,549 adult and subadult spiders were identified during our 2-year study representing 21 spider families and 58 genera out of a possible 43 spider families and 254 genera recorded in Ohio. We sampled 7,943 spiders representing 17 families, 47 genera, 22 Linyphiidae species and seven Lycosidae species in 2015; and 8,606 spiders representing 20 families, 51 genera, 22 Linyphiidae and eight Lycosidae species in 2016 (Table S3). Lycosidae and Linyphiidae represented over 64% and 22% of all spiders collected respectively. *Pardosa milvina* (Hentz) was the most frequently trapped spider (45% of the total catch), followed by *Trochosa ruricola* (De Geer, 15%), *Xysticus* spp. (8%) and *Grammonota inornata* (Emerton, 6%).

3.1 | Functional diversity and null models

The overall functional alpha diversity was lower than expected by random chance in 2015 and higher than expected in 2016 (Figure 3a,b; Table 1). When functional alpha diversity was discriminated by treatment, we found that none of the treatments deviated significantly from null expectations during both sampling years (Figure 3a,b). Functional beta diversity was significantly lower than expected by random chance in 2015 for each individual habitat treatment and when all sites were examined together (Figure 3c). However, functional beta diversity did not differ from null expectations in 2016 (Figure 3d; Table 1). We also compared functional alpha and beta diversity across treatments, yet no differences were found in 2015 or 2016 (Figure S1).

3.2 | Multivariate pairwise correlation analysis

In 2015, functional beta diversity and taxonomic diversity of spiders were positively associated with plant height and biomass, and negatively correlated with mowing frequency. Conversely, total spider abundance, lycosid abundance, orb weavers, active hunters, ground dwellers, diurnal, nocturnal and spiders with broad diets were positively correlated with mowing and negatively associated with plant height and biomass (Figure 4; Table S4). Functional divergence was positively associated with landscape diversity and negatively correlated with percentage impervious surface, patch isolation, percentage buildings at 1,500 m; whereas linyphiid abundance and plant-dwelling
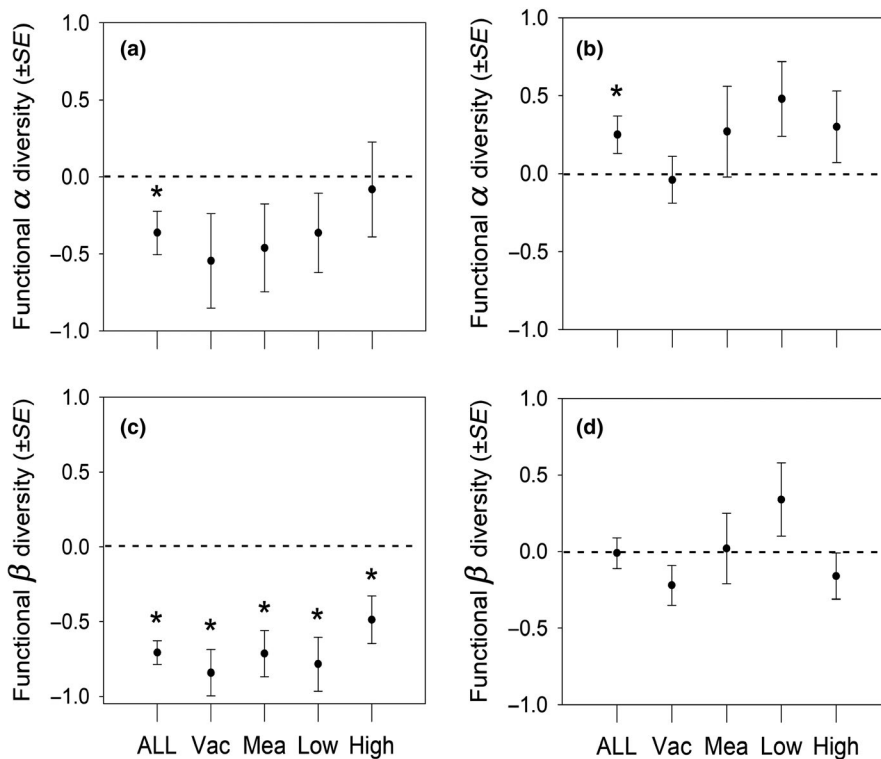
FIGURE 3 Functional diversity (standardized effect size, $M \pm SE$) versus null expectations (dash lines) in vacant Lots (Vac), urban meadows (Mea), low-diversity prairies (Low), high-diversity prairies (High) and across all sites (ALL): (a) Functional alpha diversity in 2015 and (b) 2016 and (c) functional beta diversity in 2015 and (d) 2016. Each diversity index was compared to zero using Wilcoxon's test and significance is denoted with asterisks when $p < 0.05$

TABLE 1 Functional alpha and beta diversity in 2015 and 2016 compared to null expectations using Wilcoxon signed-rank tests

Functional diversity	Treatment	V	Pseudo median	95% confidence intervals	p-Value
Alpha 2015	All sites	130	−0.400	−0.694, −0.090	**0.011**
	Vacant lots	5	−0.587	−1.285, 0.248	0.078
	Meadows	7	−0.393	−1.215, 0.421	0.148
	Low-diversity prairies	8	−0.479	−0.918, 0.288	0.195
	High-diversity prairies	13	−0.096	−0.717, 0.541	0.547
Beta 2015	All sites	6	−0.746	−0.910, −0.565	**<0.001**
	Vacant lots	0	−0.864	−1.246, −0.428	**0.008**
	Meadows	0	−0.725	−1.100, −0.315	**0.008**
	Low-diversity prairies	1	−0.793	−1.175, −0.269	**0.016**
	High-diversity prairies	2	−0.557	−0.867, −0.065	**0.023**
Alpha 2016	All sites	375	0.250	0.012, 0.505	**0.037**
	Vacant lots	17	−1.013	−0.437, 0.406	0.945
	Meadows	24	0.336	−0.480, 0.990	0.461
	Low-diversity prairies	30	0.433	−0.091, 1.013	0.109
	High-diversity prairies	27	0.387	−0.293, 0.816	0.250
Beta 2016	All sites	246	−0.039	−0.215, 0.157	0.747
	Vacant lots	7	−0.244	−0.540, 0.181	0.148
	Meadows	19	0.054	−0.660, 0.557	0.945
	Low-diversity prairies	28	0.197	−0.107, 1.049	0.195
	High-diversity prairies	9	−0.146	−0.526, 0.210	0.250

Significance was determined when $p < 0.05$ (in bold).

spiders showed the opposite pattern (Figure 4; Table S4). Percentage grass/shrubs at 1,500 m and patch size at 200 m were negatively correlated with plant dwellers and spider functional divergence respectively.

In 2016, patch isolation and percentage impervious surface at 1,500 m were positively correlated with functional beta diversity, spider genera diversity and lycosid diversity, but negatively correlated with the abundance of lycosids (Figure 4; Table S4). In contrast, total
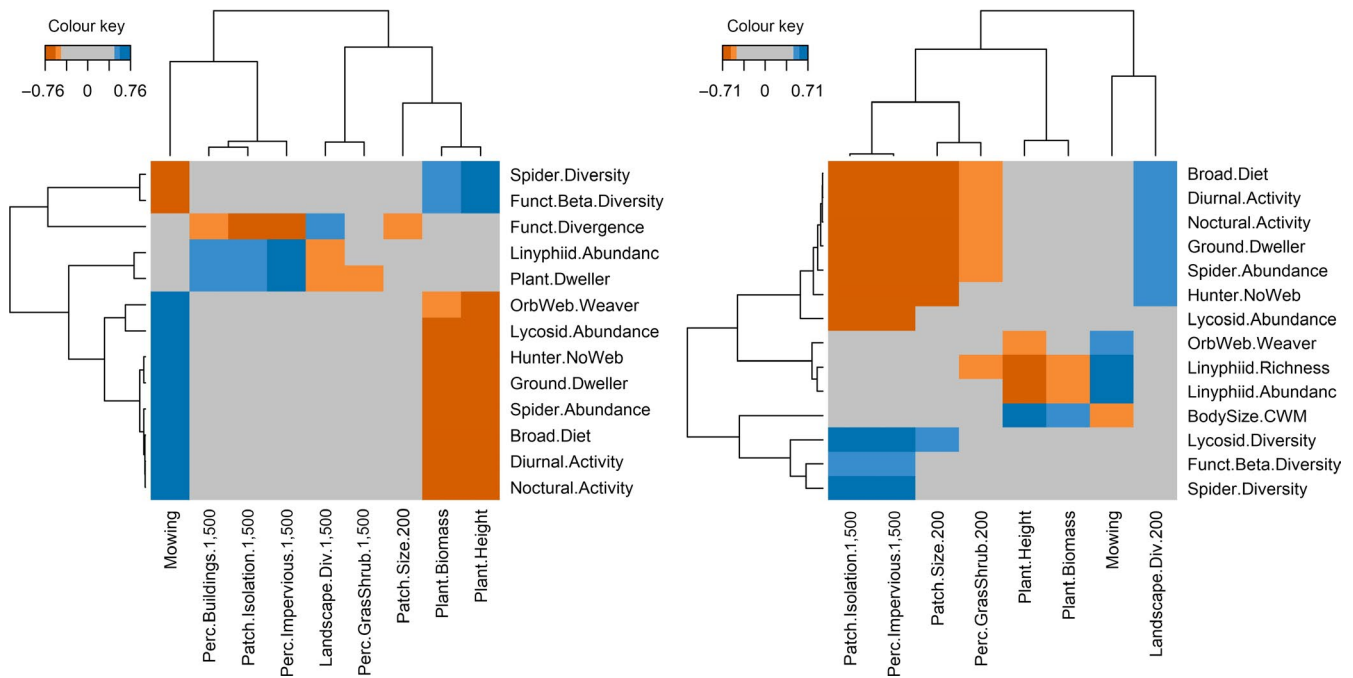
FIGURE 4 Clustered image map generated from canonical partial least squares. Spider response variables (*y*-axis) and environmental features (*x*-axis) in 2015 (left) and 2016 (right). Positive pairwise correlations are shown in blue and negative in orange. Light colour indicates correlation of 0.5–0.6 and dark colour indicates correlation of 0.6–0.75. Highly correlated variables (threshold set at ±0.5) are only shown here; all correlation coefficients and full image maps are available in Table S4 and Figure S2 respectively

abundance of spiders, hunters, ground dwellers, diurnal, nocturnal and spiders with generalist feeding habits were positively correlated with landscape diversity at 200 m, yet negatively associated with patch size and percentage grass/shrubs at 200 m, and patch isolation and percentage impervious surface at 1,500 m. Linyphiidae richness also decreased with percentage grass/shrubs at 200 m. Lastly, spider body size increased with plant height and biomass and decreased with mowing frequency, whereas the abundance and richness of linyphiids and the abundance of orb-web weavers showed the opposite pattern (Figure 4; Table S4).

4 | DISCUSSION

To disentangle the environmental filters structuring spider communities, we examined the functional and taxonomic response of these predators to local greenspace management and landscape-scale features in four experimental vacant lot habitats in Cleveland, Ohio, USA. Our results illustrated that a combination of local and landscape processes influenced the assembly of spider communities, and that the relative importance of these assembly processes changed over time. Our study revealed that: (a) at the local patch scale, taxonomic and functional diversity were highest where mowing frequency was low and vegetation complexity was high; (b) at the landscape scale, patch isolation and the amount of surrounding impervious surface increased the taxonomic and functional diversity of spiders; (c) functional diversity was similar across vacant lot planting treatments and (d) *P. milvina*,

a ground-dwelling wolf spider, was the dominant species in urban greenspaces.

At the local patch scale, arthropod communities are influenced by environmental conditions associated with habitat quality such as plant diversity, vegetation complexity and disturbance frequency (Delgado de la flor et al., 2017; McIntyre, 2000; Randlkofer et al., 2010). Our results indicated that monthly mowing was a strong local environmental filter for spiders. We predicted that spider functional alpha diversity would be higher than expected by chance, since patches embedded in a fragmented urban landscape would vary in their habitat quality and accessibility for the urban spider species pool. However, we observed that functional alpha and beta diversity were lower than that expected in 2015 when control vacant lots, low- and high-diversity pocket prairies were mowed monthly to improve prairie establishment and growth. Additionally, we found that high functional similarity among greenspaces was driven by a few dominant disturbance-tolerant species. Spider communities were dominated (45% of sampled individuals) by the ground-hunter *P. milvina* (Lycosidae), which is known to respond positively to resource availability and is commonly found within disturbed habitats (Burkman & Gardiner, 2015; Marshall, Walker, & Rypstra, 2000). Orb-web weavers *Glenognatha* spp. (Tetragnathidae) were also abundant in control vacant lot sites. These small (3 mm) species build their webs close to the ground in low-lying vegetation where periodic mowing may not affect their populations. Although disturbance-tolerant arthropods may benefit, mowing regimes generally have negative impacts on arthropod communities (Garbuzov, Fensome, & Ratnieks, 2015; Unterweger,

Rieger, & Betz, 2017), and increased mowing likely impairs the establishment of spiders with unique habitat requirements and limited dispersal capabilities (Cattin et al., 2003).

In addition to mowing, vegetation structural characteristics were important predictors of spider functional and taxonomic diversity. Plant height and biomass were positively correlated with functional beta and taxonomic diversity of spiders, implying that greenspace with complex vegetation enhanced the diversity and distinctiveness of spider communities. Studies have shown that managed habitats with complex vegetation structure create more microhabitats, enhancing natural enemy communities (Langellotto & Denno, 2004; Sarthou et al., 2014). Moreover, despite studies reporting that spider body size was not adversely affected by urbanization or landscape features (Alaruikka, Kotze, Matveinen, & Niemela, 2002; Kaltsas, Panayiotou, Chatzaki, & Mylonas, 2014), we provide evidence that spider body size is driven by local environmental conditions. Not only were small (<5 mm) linyphiids and tetragnathids more abundant in highly disturbed sites, but some large (>15 mm) agelenids and lycosids were only found in meadows and pocket prairies. This suggests that changes in vacant lot management, such as increasing vegetation structural complexity and reducing mowing frequency, facilitate the colonization of large and mobile spiders capable of consuming larger prey items.

At the landscape scale, the dominance of impervious surface and built structures, as well as the amount and connectivity of surrounding greenspaces can influence arthropod communities (Braaker et al., 2017; Davis et al., 2007; Sivakoff et al., 2018). We predicted that spider functional beta diversity (dissimilarity) will increase with impervious surface, due to variation in dispersal capabilities and adaptation to disturbance among species. In 2016, functional dissimilarity increased with impervious surface and the overall spider functional alpha diversity was higher than expected; consequently, our hypothesis was supported in the second year. Null model results indicated that spider functional beta diversity was neither higher nor lower than expected by chance, suggesting stochastic mechanisms of assembly. In 2016, monthly mowing only occurred in the control vacant lots, and once this strong local environmental pressure was relaxed, landscape processes were stronger drivers of spider community assembly. Functional similarity of spider communities decreased as vacant lots became increasingly isolated and surrounded by impervious surface, suggesting that outlying urban green patches contribute to the landscape-wide spider diversity. These isolated vacant lots supported more tiny ballooning spiders rather than larger generalist ground-hunter species. This compositional change in spider communities with increased patch isolation from urbanization likely represents an ecological barrier that hinders colonization of species that lack the traits to overcome dispersal challenges (Bonte et al., 2004; Braaker et al., 2017). Small web weavers are effective colonizers via ballooning than larger ground-hunter spiders that disperse by walking or running (Blandenier, 2009; Bonte et al., 2004). Moreover, the inherent stochasticity of successful colonization via ballooning could produce patterns of spider assembly in isolated vacant lots that appear random. Therefore, our findings suggest that in the absence of strong local environmental filters the permeability of the urban landscape, or the extent to which the matrix facilitates or limits dispersal, shapes the patterns of spider assembly based on key dispersal traits.

5 | CONCLUSIONS

This study provides evidence that habitat management, principally mowing frequency, determined the establishment of spider functional groups within distinct vacant habitats, whereas landscape composition and configuration restricted the colonization potential of spiders across the urban mosaic. The relative importance of these assembly processes changed over the 2-year study, with landscape processes becoming a major driver as mowing frequency was reduced within low-diversity and high-diversity pocket prairie treatments. We also demonstrated that the mechanisms behind spider community assembly were better understood when both functional and taxonomic approaches were investigated concurrently. Most importantly, our functional diversity approach revealed that current vacant lot management strategies favour the establishment of functionally redundant spider groups, suggesting that food–web interactions and ecological processes might be more dynamic and stable in habitats with reduced disturbance. Therefore, to promote spiders and reliant conservation targets such as other predatory arthropods and insectivorous birds, shrinking city land use planners should incorporate vegetation plantings such as native grass and wildflower habitats that require reduced mowing. Importantly, to succeed in these endeavours it is imperative for the city to form a coalition with local community members and co-design these conservation themed greenspaces (Riley, Perry, Ard, & Gardiner, 2018; Turo & Gardiner, 2019). In summary, biodiversity and urban conservation depend on patch management and landscape design, as both drive species community assembly across the urban matrix, informing practitioners about the possible consequences of their management decisions.

AUTHORS' CONTRIBUTIONS

Y.A.D. and M.M.G. conceived the ideas and designed methodology; Y.A.D., K.J.T. and D.M.P. collected the data; Y.A.D. and J.L.T. identified spiders; Y.A.D. and K.I.P. analysed the data and interpreted results; Y.A.D. led the writing of the manuscript, with revisions from M.M.G. and other authors; K.I.P. contributed to the ecological framework of the manuscript; and all authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3tx95x6cf (Delgado de la flor, Perry, Turo, Parker, Thompson, & Gardiner, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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