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RESEARCH ARTICLE*

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Land use history and seed dispersal drive divergent plant community assembly patterns in urban vacant lots

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Abstract

1. Despite high levels of disturbance and habitat modification, urban ecosystems still host substantial levels of biodiversity. The processes that maintain existing levels of diversity, however, remain understudied. Identifying the links between urban ecological processes and patterns has, therefore, become a fundamental research goal to support urban biodiversity and ecosystem functioning.
2. We conducted a study to determine how the diversity and composition of urban plant communities is affected by spatially and temporally variable land use legacies. We constructed a chronosequence of vacant lot properties covering a range of 3–22 years since demolition, in an urban neighbourhood in Baltimore, Maryland (USA). Surveys of herbaceous plant species abundance were conducted during the summers of 2012 and 2013 in sections of each vacant lot where the building previously stood (the “building footprint”) and sections of the lot that was previously a backyard or garden (the “remnant garden”).
3. We found divergent patterns in plant community composition between areas of vacant lots with varying land use histories. This includes significant shifts in the functional composition of biotically vectored seed dispersal strategies, as well as an increase in seed mass and terminal velocity trait values of plant communities in building footprints over time. In addition, we found that plant communities in different sections of the same vacant lot tended to become more functionally dissimilar in seed dispersal strategies over time. In contrast, we found no significant changes in taxonomic diversity over time for any of our measures.
4. *Policy implications*. Our study suggests that regional-scale patterns of seed dispersal interact with diverse land use legacies to structure the plant communities of urban vacant lots. Although it has been suggested that highly altered local environmental conditions and competition from introduced species limit native plant diversity in urban environments, we find seed dispersal to be a more significant driver of urban plant community assembly patterns. Implementing management strategies that focus on habitat connectivity and enhancing species pools via seeding may present an effective strategy for promoting more successful establishment of diverse plant communities in urban environments.

KEYWORDS
Baltimore, community assembly, land use history, plant diversity, plant traits, seed dispersal, urban ecology, urban green space, USA, vacant lots

1 | INTRODUCTION

The rapidly increasing and urbanising human population poses a substantial threat to biodiversity around the world (Hoekstra, Boucher, Ricketts, & Roberts, 2004). Urbanisation not only destroys or severely alters pre-existing habitat patches, it also creates new habitats captured within the urban landscape, resulting from the abandonment of previous human uses. The area of abandoned, vacant urban habitat is substantial in many cities, sometimes greater than 20% of the city area (Kremer, Hamstead, & McPhearson, 2013; Martinez-Fernandez, Audirac, Fol, & Cunningham-Sabot, 2012). Although it has been suggested that vacant land could serve as valuable space for conservation in urban areas (Klaus, 2013; Rudolph, Velbert, Schwenzfeier, Kleinebecker, & Klaus, 2017), supporting diverse and functional plant communities requires an initial understanding of community assembly processes.

There is reason to expect that assembly patterns in urban grasslands, such as those found in vacant lots, may be fundamentally different than those observed in non-urban grasslands (Lundholm & Richardson, 2010). Urban grasslands experience a novel combination of management pressures, environmental and biotic drivers, and structural differences (e.g. high levels of fragmentation) compared to similar non-urban habitat patches (Aronson et al., 2016). Collectively, these factors influence local patch conditions and dispersal potential, which can lead to differential successional trajectories and compositional divergence between habitat patches (beta diversity) within cities over time (e.g. Lososová et al., 2011; Swan, Johnson, & Nowak, 2017). Heterogeneity in urban conditions, disturbance patterns and community assembly drivers among studies (Lososová et al., 2016) has, subsequently, led to difficulties in making generalisations about the impact of urbanisation on plant communities. For example, a recent review of studies considering the response of plant functional traits to urbanisation (Williams, Hahs, & Vesk, 2015) found few consistent or linear shifts in functional community composition with increasing urbanisation.

In spite of the expected variability in urban plant community structure, a number of potentially important drivers of urban grassland community assembly have begun to emerge. A review and synthesis of the European literature on urban brownfield and wasteland diversity (Bonthoux, Brun, di Pietro, Greulich, & Bouché-Pillon, 2014) found that successional age of urban wastelands was consistently an important factor in determining plant community diversity and structure. Multiple studies have also found evidence to suggest that plant assemblages are selectively filtered with respect to dispersal vectors along urban connectivity gradients (Concepción, Moretti, Altermatt, Nobis, & Obrist, 2015; Schleicher, Biedermann, & Kleyer, 2011), as well as by local environmental constraints or land use legacies (Aronson et al., 2016; Johnson, Tauzer, & Swan, 2015).

This study investigates the degree to which plant communities converge or diverge in composition and diversity over time in vacant lots, an urban habitat type commonly targeted for conservation, restoration or greening activities (Rudolph et al., 2017). We asked three key questions: (1) How does species diversity change in vacant lots over time? (2) Do functional traits and species identities shift predictably over time? (3) Does fine-scale spatial variation in land use legacies within vacant lots drive divergent community composition over time?

We addressed these questions in a network of fragmented urban vacant lots with distinct land use histories nested within each individual lot. We compared patterns of community composition and diversity within each vacant lot between the section where buildings previously stood (the building footprint) and the section that was previously a garden or backyard (remnant garden). In building footprints—where communities assemble from the regional species pool onto introduced fill material over relatively short periods of time after buildings are demolished—we expected that regional-scale dispersal limitation would be the primary driver of species assembly and lead to increases in diversity over time, as well as shifts in community-level patterns of traits related to seed dispersal. Conversely, because remnant gardens retain their original (i.e. prior to demolition) soil profile, seed bank, and components of their plant community, we predicted that local effects driven by competition and/or environmental filtering would play a dominant role in driving species assembly trajectories. This would result in the convergence of traits related to establishment and persistence in remnant gardens over time, and a reduction in diversity over time. In addition, we expected to find compositional differences between sections of the same vacant lot to increase over time, as different assembly processes and different compositional and environmental starting points lead to divergent successional trajectories.

2 | MATERIALS AND METHODS

2.1 | Study system and data collection

Vegetation was surveyed in 29 lots in Baltimore, MD, USA during the summers of 2012 and 2013. Surveyed lots were not actively managed, apart from periodic mowing that occurred several times per growing season. All lots were located within a *c.* 20-ha area in the densely urban neighbourhood of Harlem Park, in West Baltimore, at least 2 km from the nearest large green space. This neighbourhood consists primarily of three-story brick row houses built directly adjacent to the sidewalk, each with a small backyard that opens onto a shared inner block park (Figure 1). These parks contain open space for parking and recreation and the vegetation rarely contains species that are not also present in the vacant lots (A.L. Johnson pers. observ.).

As historical records of vegetation diversity and composition were not available, we took a space-for-time, or chronosequence, approach to analysing successional patterns (e.g., Dornelas et al., 2012). Lot age for each surveyed site was determined based on a combination of demolition records obtained from the Baltimore City Housing Department and visual interpretation from historical aerial photographs. We supplemented scanned paper copies of demolition records made available for 20 properties by the Baltimore City Housing Department with estimates of time since demolition made for nine properties from a series of historical aerial photographs. Photographs were collected from

FIGURE 1 Typical arrangement of vacant lots in Baltimore study sites. Each block (a) features a central "inner block park," which is a mix of paved or green space areas. Row homes (b–d) are standard widths and built directly adjacent to the sidewalk, with backyard spaces that face the central inner block park. Images all taken from Google Earth [Colour figure can be viewed at wileyonlinelibrary.com]

USGS (earthexplorer.usgs.gov) and were available at a resolution high enough to identify individual housing parcels for the study region from 1972, 1981, 1994, 2002, 2004, 2006 and 2007. The date of demolition was estimated as the mean of the range of years during which the house could have been demolished. For example, if the house was visible in the photograph from 1994 but no longer present in 2002, then the demolition date was set as 1998.

Lot age was not spatially autocorrelated (Mantel test between matrix of site coordinates and matrix of site ages, $r = -.1$, $p = 1$, permutations = 999), so we did not incorporate geographic distances between sites into our models. Because changes in soil environmental conditions over time can influence community assembly patterns, we additionally used soil data collected from a subset of our sites during a previous study (for collection methods, see Johnson et al., 2015) to test whether shifts in soil abiotic characteristics were correlated with the composition of plant communities. We found, however, no significant relationship between soil characteristics and species in either remnant garden or building footprint soils (analysis methods and results in Appendix S1, soil data available in: Johnson, Swan & Borowy 2017).

To assess plant community diversity at each site, we visually estimated per cent cover of each plant species in stratified randomly placed 1 m^2 quadrats along transects lined perpendicular to the street. Plots were assigned proportionally by area to the larger building footprint vs the smaller remnant garden sections such that three plots per transect were located in the building footprint and one plot was located in the remnant garden. Two transects per lot were surveyed (for a total of 8, 1 m^2 plots per site) for the majority of sites. For narrower, single-parcel wide sites, only one transect was established, to prevent plots from being surveyed within 1 m of site boundaries.

2.2 | Functional data

We collected functional trait data from online databases (USDA PLANTS Database, plants.usda.gov; USDA FEIS Invasive Plants, USDA, Forest Service, feis-crs.org; LEDA Traitbase, Kleyer et al., 2008; KEW SID, the Royal Botanic Gardens Kew Seed Information Database, data.kew.org/sid/) to describe species establishment and persistence strategies (Table 1). We described species dispersal characteristics based on data from online databases and primary source literature compiled by D. Borowy and C. M. Swan (unpubl. data; Table 2). Although online databases that collate sampled trait data have provided a powerful tool for addressing mechanistic questions about multispecies assemblages (e.g. Fischer, von der Lippe, & Kowarik, 2012; Knapp, Kühn, Wittig, Ozinga, & Poschlod, 2008), they may not represent urban populations exposed to unique selection pressures (Alberti et al., 2017). To mitigate this concern, the majority of the traits we focused on for this study were categorical and, thus, unlikely to shift substantially across populations.

The establishment and persistence traits included in this study were specific leaf area (SLA), height, vegetative spread, life history (annual, biennial or perennial). SLA correlates to species relative growth rates, palatability and response to nutrient and moisture gradients, plant height relates to competitive ability (particularly for light) and vegetative spread and life history correlate to the ability to occupy space over time (Weiher et al., 1999). Selected dispersal traits included seed mass, seed terminal velocity, and primary dispersal vector (nine categories). Seed mass relates to dispersal distance, seedling germination, and growth rates, whereas terminal velocity is associated with dispersal distance (Weiher et al., 1999). When multiple values were provided for a species' trait in the databases used, we reported the mean across each species. We tested for correlation between traits using a Pearson correlation coefficient; no traits were correlated above .70, and all traits were retained for analyses (Table S1).

2.3 | Statistical analyses

We carried out all analyses using R (version 2.14.1; R Foundation for Statistical Computing, Vienna, AT, 2014). To measure local, or

TABLE 1 Functional traits collected from the literature for this study, with survival strategy group interpretations based on the review of Weiher et al. (1999). Continuous traits' unit of measurement provided in parentheses following trait name. Strategy group refers to how traits were divided for analysis, and % Missing Data refers to the number of species lacking available trait information in databases

Trait	Strategy group	Values	Data source	% Missing data
Specific leaf area (m)	Establishment, persistence	Continuous	LEDA	28
Height (m)	Establishment, persistence	Continuous	LEDA, USDA PLANTS, USDA FEIS	3
Vegetative spread	Establishment, persistence	Categorical (present/absent)	LEDA	13
Life history	Establishment, persistence	Categorical (perennial, biennial, annual)	USDA PLANTS	0
Seed mass (g per 1,000 seeds)	Dispersal	Continuous	KEW SID	3
Terminal velocity (m/s)	Dispersal	Continuous	LEDA	31
Dispersal vector	Dispersal	Categorical (anemochory, anthropochory, ballistic, barochory, endozoochory, epizoochory, hydrochory, myrmecochory and synzoochory)	D. Borowy and C. M. Swan unpubl. data	1

TABLE 2 Compositional divergence over time, as determined by permutational multivariate analysis of variances (PERMANOVA) tests, in building footprints and remnant gardens for taxonomic and functional composition. Bold indicates statistically significant value ($p < 0.05$).

Diversity metric	Legacy group	*df*	*F*	R^2	*p*
Taxonomic	Building footprint	1,27	1.6023	.06	.108
	Remnant garden	1,27	0.98	.04	.457
Dispersal traits	Building footprint	1,27	1.78	.06	**.001**
	Remnant garden	1,27	0.66	.02	.86
Establishment and persistence traits	Building footprint	1,27	0.94	.03	.54
	Remnant garden	1,27	1.41	.05	.11

alpha, taxonomic diversity at each site, we calculated the Shannon diversity index (*H*), an abundance-weighted measure, separately for the building footprint and remnant garden in each lot. To estimate local functional diversity, we range-standardised functional traits after $\log_{10}$ transforming both seed mass and canopy height. We then calculated functional dispersion (FDis), which is an index of functional diversity that weights the distribution of functional traits in a community by species abundances (Laliberté & Legendre, 2010). We used linear regression analyses, separately for building footprint and remnant garden sites, to assess the strength of the relationship between time since demolition and taxonomic and functional diversity. We assessed whether species composition and community weighted means (CWM) of functional traits shifted over time in vacant lots using permutational multivariate analysis of variances (PERMANOVA; Anderson, 2001) with the adonis function in the *vegan* package in R. In addition, we assessed changes in CWM values of individual functional traits over time, using linear regression, in both building footprint and remnant garden communities. To estimate changes in compositional similarity between building footprint and remnant garden sections of the same vacant lot, we computed pairwise similarity measures for taxonomic diversity using the Bray–Curtis dissimilarity index. We used Gower's distance (De Bello, Carmona, Mason, Sebastià, & Lepš, 2013), which handles both continuous and categorical traits, to estimate functional compositional dissimilarity separately for dispersal traits and for establishment and persistence traits and then used linear regression to assess dissimilarity changes over time.

3 | RESULTS

We identified 96 species total across all the sites. Building footprints contained 73 species (19 unique) and remnant gardens contained 76 species (22 unique). Building footprint sites on average contained 16 species (min = 9, max = 23) while remnant gardens on average contained 12 species (min = 5, max = 22). Raw data with distribution of functional trait CWMs between site types are available in Johnson, Borowy, and Swan (2017).

3.1 | Local diversity over time

Local diversity developed differently over time in building footprints and remnant gardens (Figure 2). There was no change in taxonomic diversity or the diversity of establishment and persistence traits (SLA, plant height, vegetative spread, and life history) in building footprints

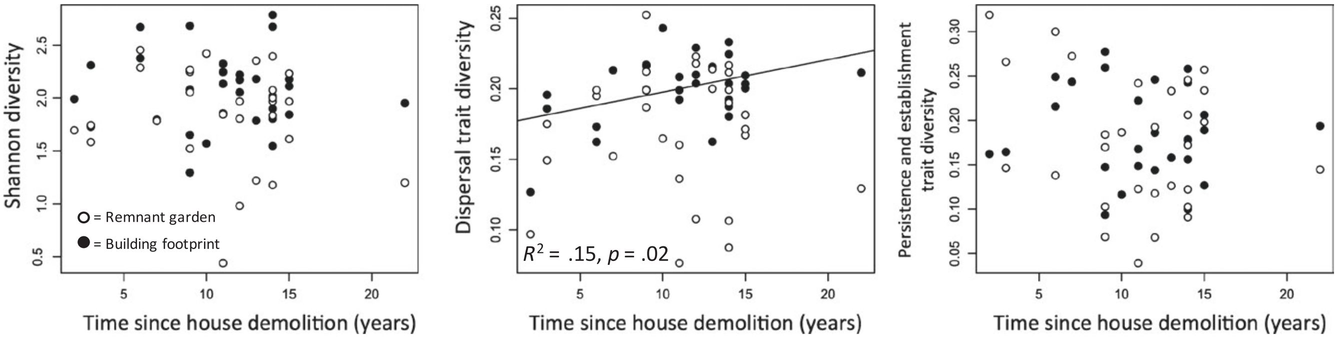

FIGURE 2 Change in alpha diversity over time in remnant gardens (open circles) and building footprints (filled circles). Regression lines were estimated separately for building footprint and remnant garden plant communities and are drawn only for significant relationships ($p \le .05$). When significant, black regression lines correspond to building footprints and grey regression lines would correspond to remnant gardens

or remnant gardens over time (Figure 2). There was also no significant change in dispersal trait diversity over time in remnant gardens. Dispersal trait diversity in building footprints, however, significantly increased over time (Figure 2).

3.2 | Compositional shifts over time

There was no evidence of compositional change over time in remnant gardens. In building footprints, however, dispersal trait composition shifted significantly over time (Table 2). The CWMs of individual functional traits also shifted significantly with time since demolition in building footprints (Figures 3 and 4). In particular, terminal velocity, seed mass and most traits related to biotic dispersal vectors (anthropochory, endozoochory, epizoochory) increased over time in building footprints (Figure 4). Myrmecochory, however, decreased over time. Synzoochory was the only biotic dispersal vector that showed no significant changes over time. All traits associated with abiotic dispersal vectors (anemochory, ballistic dispersal, barochory, hydrochory) were non-significant.

3.3 | Changing similarity between sections of vacant lots over time

Remnant garden and building footprint sections of the same vacant lot did not become more taxonomically convergent or divergent over time (Figure 5, Table S2). Dispersal trait composition of plant communities growing in remnant gardens and building footprints of the same site, however, was less similar (i.e. more divergent) in older lots, suggesting that over time communities with different land use legacies favored a different suite of plant species colonists. There were no compositional changes in establishment and persistence traits between remnant gardens and building footprints in the same lot over time, although there was a weak, non-significant trend towards increasing similarity (R^2 = .01, p = .25).

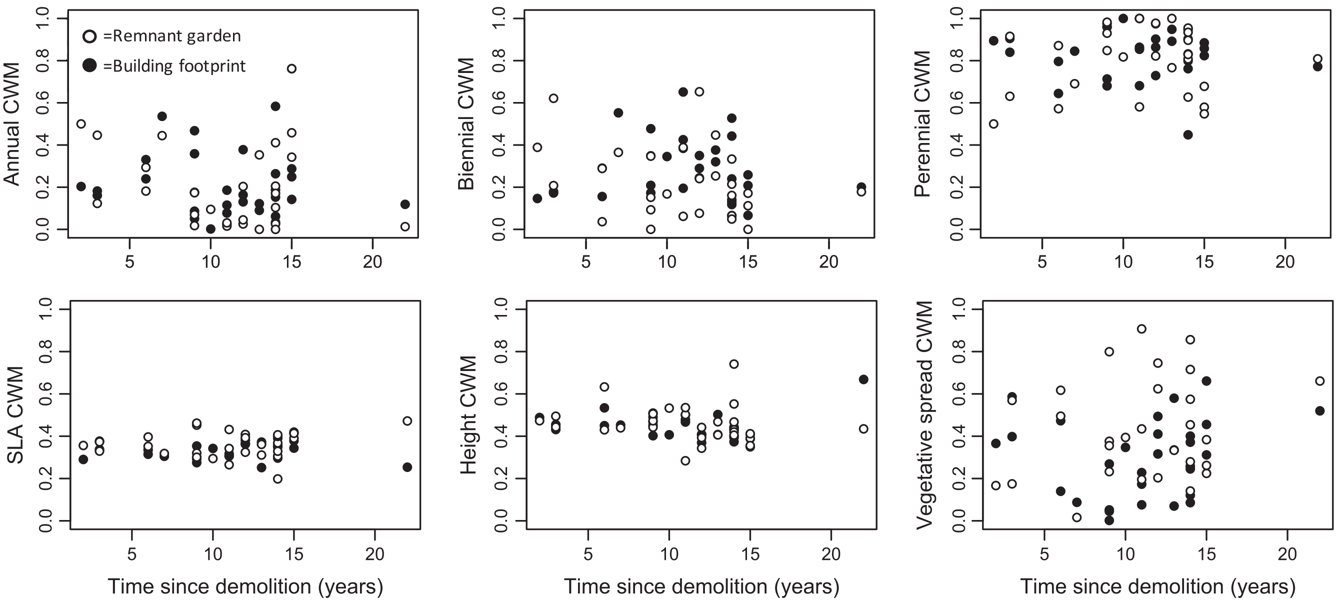

FIGURE 3 Regression results for change in the CWMs of establishment and persistence traits over time in building footprint (filled circles) and remnant garden (open circles) communities. There were no significant changes in establishment and persistence traits over time

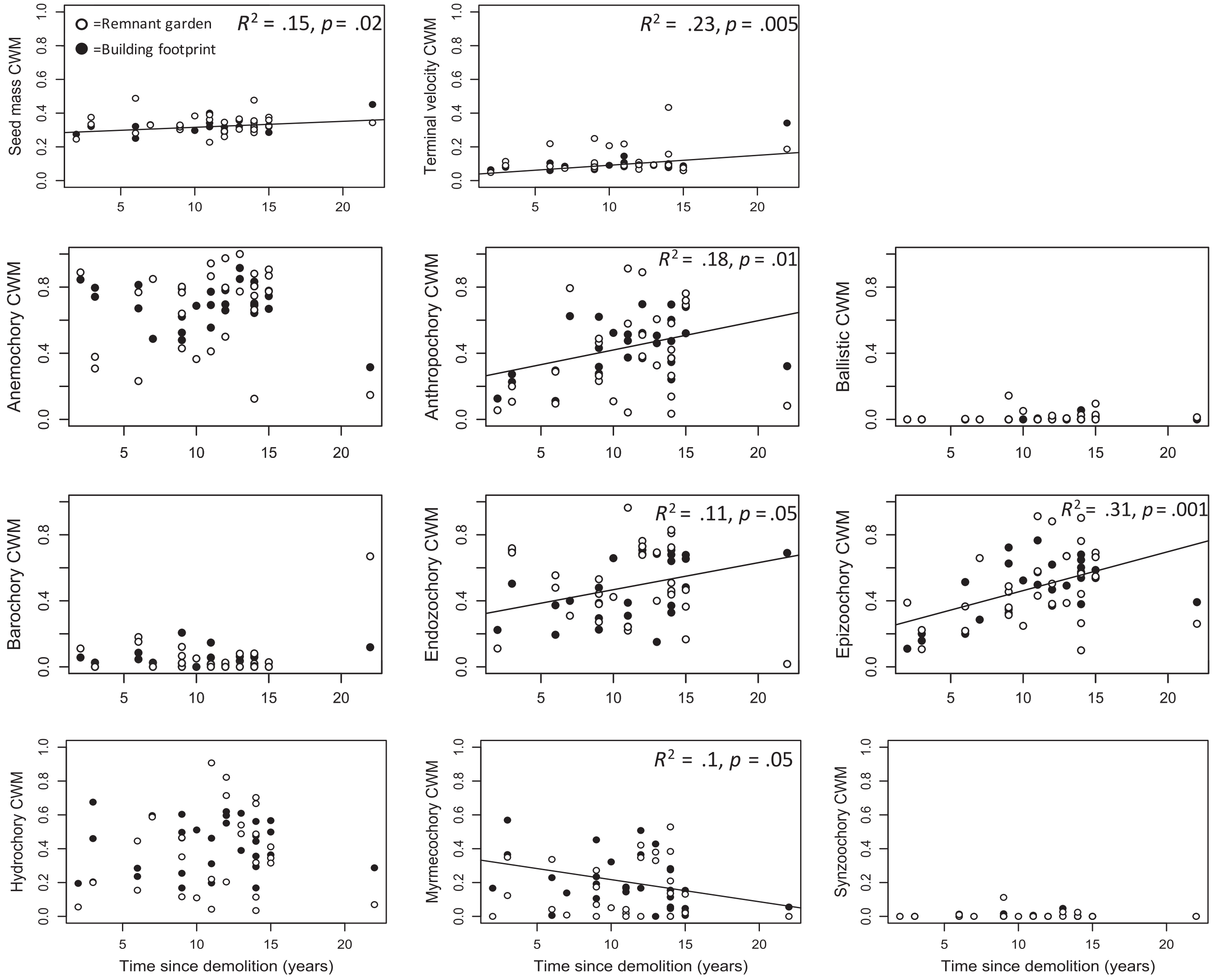

FIGURE 4 Regression results for change in the CWMs of dispersal traits over time in building footprint (filled circles) and remnant garden (open circles) communities. Black regression lines correspond to building footprints and grey regression lines correspond to remnant gardens. R^2 values and significance are reported within the plots for all significant regression relationships

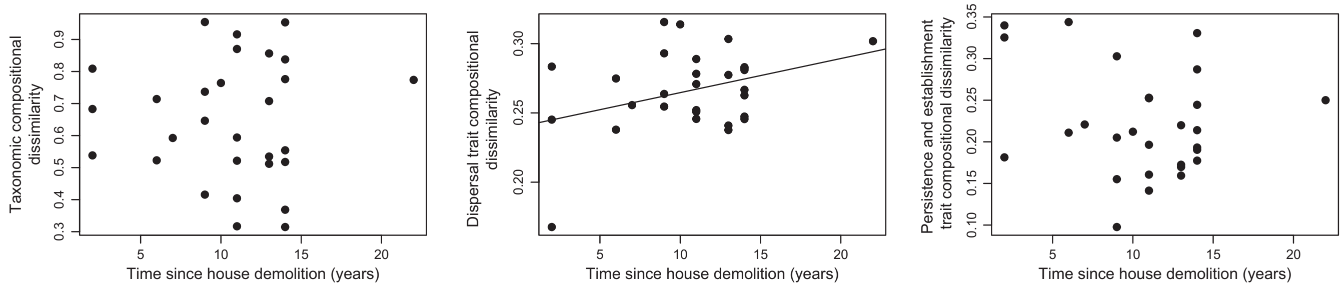

FIGURE 5 Regression results for changes in compositional dissimilarity between remnant gardens and building footprints. Each point represents the difference between the remnant garden and building footprint section of the same vacant lot. Solid lines represent significant relationships

4 | DISCUSSION

Urban plant communities are structured along complex environmental and anthropogenic gradients. Plant community diversity and composition drive many urban ecosystem functions and services of interest, including primary production, carbon sequestration, nutrient cycling, water infiltration and pollination (e.g. Gardiner, Burkman, & Prajzner, 2013; Gómez-Baggethun & Barton, 2013; Shuster, Dadio, Drohan, Losco, & Shaffer, 2014). While urban grasslands, such as those found in vacant lots, are often discussed as having potentially important roles in urban conservation and ecosystem service provision plans (Kattwinkel, Biedermann, & Kleyer, 2011; Klaus, 2013), the ability to make decisions that effectively conserve and restore functional ecosystems in cities is often constrained by a lack of understanding of the processes that assemble urban plant communities in these habitats.

Our study focuses on drivers of urban plant community assembly in vacant lot habitats that have been developing over 3–22 years. Assessing successional patterns in these "novel" urban ecosystems (Kowarik, 2011) and comparing them to well-documented successional patterns of old fields and other human-modified series is important for determining to what degree ecological theory and restoration or management approaches developed in other systems may be applied successfully to urban ecosystems.

4.1 | Changes in plant diversity and composition of vacant lots over time

We observed no change in the taxonomic diversity of vacant lots over time, contrary to our initial expectations. This is in contrast to other studies of successional changes in non-urban grassland ecosystems where management and human land uses have ceased, which often find substantial decreases in taxonomic diversity over time (e.g. Garnier et al., 2004; Hansen & Gibson, 2014; Sluis, 2002). One explanation for this is that urbanisation has been shown to result in regional species pools dominated by ruderal or generalist species, capable of rapidly colonising and establishing in open habitat patches and tolerant of a variety of common urban disturbances (McKinney, 2008; Prach, Pyšek, & Bastl, 2001).

We also found no shift in the diversity of persistence or establishment traits over time, in contrast to many non-urban studies (e.g. Albert et al., 2014; Loranger et al., 2016; Roscher, Gerighausen, Schmid, & Schulze, 2015). This may suggest that establishment and persistence traits only differentiate over longer periods of time in vacant lot habitats. Kattwinkel et al. (2011), however, found that species diversity in vacant lots was maximised at 15 years' post-abandonment, suggesting our observed time frame of 3–22 years is appropriate for the majority of species to colonise and potentially establish at a site from the urban species pool. Nor did we observe significant compositional shifts in establishment and persistence traits over time, although there was a slight trend towards divergence in these traits in remnant gardens (Table 2). The urban plant species pool may already be strongly filtered with respect to the environment (e.g. Lososová et al., 2016), which would limit the role of local environmental filtering on community assembly over time within specific habitat patches embedded within the urban matrix. This is supported by an earlier study in this system that found soil characteristics did not have a significant effect on the spatial structure of plant communities in vacant lots (Johnson et al., 2015), as well as a successional study that found similar composition in urban sites of varying soil fertility levels (Prach et al., 2001).

Alternatively, disturbance regimes may play a key role in defining functional diversity patterns of plant communities in vacant lots over time. At our sites, semi-annual mowing conducted by the city to reduce "messiness" of appearance (Nassauer & Raskin, 2014) may serve as a disturbance that halts successional trajectories of the plant communities, by regularly opening niche space and reducing competition between species (Lososová et al., 2016). This is supported by other urban studies, which found that mowing frequency is negatively related to site floristic diversity (Politi Bertoncini, Machon, Pavoine, & Muratet, 2012; Rudolph et al., 2017).

Contrary to the lack of change in establishment and persistence traits, we found that dispersal trait diversity increased over time. This suggests that dispersal plays an important role in determining patterns of species assembly in our system, particularly in the more disturbed building footprints. This pattern was driven primarily by a strong increase in the relative abundance over time in species with biotically vectored seeds, which matches a number of studies of non-urban grassland habitats (Knapp, Stadler, Harpke, & Klotz, 2016; Neuenkamp, Lewis, Koorem, Zobel, & Zobel, 2016). While traits related to dispersal have been found to shift along urban connectivity gradients (Concepción et al., 2015; Schleicher et al., 2011) as well as along urban-rural gradients (Williams, Morgan, Mcdonnell, & Mccarthy, 2005), no other studies to our knowledge have demonstrated successional changes in dispersal trait diversity of plant communities located within highly urbanised habitats.

Plant species vectored primarily by epizoochory—adhesive seed dispersal—most strongly increased in abundance at our sites over time (Figure 4). Many native animal species that act as epizoochorous dispersal agents of native plants, however, are negatively impacted by habitat fragmentation and human-mediated disturbances associated with urbanisation (Chace & Walsh, 2006; Dickman & Doncaster, 1989). The loss of native disperser species from cities is often compensated by an influx of introduced, "urban exploiter" species (McKinney, 2006) and domestic animals such as cats and dogs (Knapp, Kuhn, Stolle, & Klotz, 2010). These species can maintain the service of epizoochory in heavily urbanised environments by acting as non-native dispersal surrogates, although they may be less specialised or efficient than co-evolved seed dispersal mutualists (Farwig & Berens, 2012). Similarly, non-native bird species which facilitate endozoochorous dispersal in urban areas may also be more generalised than co-evolved native partners and preferentially feed on invasive fruits (Aslan & Rejmanek, 2010). Species dispersed via human-mediated methods (anthropochory) also increased in abundance at our sites, as might be expected in a densely urban neighbourhood.

The abundance of myrmecochorous species (i.e. species dispersing via ants), however, diminished over time in building footprints. This may be explained by structural and compositional changes associated with urban environments. Studies have found that impervious surfaces can act as a strong dispersal barrier to ants, resulting in decreased ant species diversity in urban habitats (Thompson & McLachlan, 2007). In addition, urbanisation can induce compositional shifts in ant communities towards generalist species that are ineffective dispersal agents (Andersen & Morrison, 1998; Pudlo, Beattie, & Culver, 1980).

We also found a significant increase in the continuous dispersal traits of seed mass and seed terminal velocity, suggesting a trend towards competitive species with short-distance dispersal potentials over time. Seed mass is a trait strongly related to competition vs colonisation trade-offs in plant life strategies (Aicher, Larios, & Suding, 2011; Turnbull, Rees, & Crawley, 1999). Species with higher seed masses generally exhibit a competitive advantage through higher seedling germination and growth rates, but in exchange produce fewer seeds that only travel short distances (Turnbull, Coomes, Hector, & Rees, 2004). Seeds with higher terminal velocities fall to the ground more quickly and disperse shorter distances by wind. Conversely, all other dispersal modes (anemochory, ballistic, barochory, hydrochory and synzoochory) did not show any significant trends between lot types. Species relying on anemochory–wind dispersal—tend to be underrepresented in city environments (Williams et al., 2015), suggesting that some dispersal modes may filter species at broader spatial scales than our study. Alternatively, secondary dispersal may play a substantial role in our system. For example, secondary dispersal of seeds by wind and traffic along paved areas in cities can limit negative effects of habitat fragmentation on dispersal by maintaining connectivity between habitat patches (Kowarik & von der Lippe, 2011).

Although trait-based techniques have been shown to provide a more conclusive link between biodiversity patterns and ecosystem processes (Díaz & Cabido, 2001) and have also shown stronger responses to urban environmental gradients than taxonomic metrics (Johnson et al., 2015), the success of trait-based methods is contingent upon selecting traits that reflect processes driving community assembly at relevant scales (McGill, Enquist, Weiher, & Westoby, 2006; Messier, McGill, & Lechowicz, 2010). Traits not captured in analyses, however, may drive competitive interactions and resource acquisition in our system, such as those related to water-use efficiency, interactions with mycorrhizal symbionts or rooting architecture. Continuing to refine hypotheses about trait-driven assembly in urban systems is a key to gaining a better mechanistic understanding of the environmental and anthropogenic forces that structure urban plant communities.

4.2 | Impacts of spatial variation in urban land use legacies on plant community compositional divergence over time

Dispersal traits in remnant gardens did not shift in composition and diversity over time, unlike in building footprints. This leads to increasing compositional divergence between building footprints and remnant gardens over time. This suggests that different land use legacies can act as historical contingencies that promote differential colonisation patterns (Fukami, 2015), altering the trajectory of community assembly.

Variation in land use legacies has also been found to consistently have an important structuring effect on non-urban semi-natural grasslands (e.g. Cramer, Hobbs, & Standish, 2008; Saar, de Bello, Pärtel, & Helm, 2017; Vandewalle et al., 2014). In urban areas, we have demonstrated that ecologically relevant variation in land use legacies may occur over even smaller spatial scales (meters rather than kilometers) than in non-urban areas. Just as the practice of researching land use history has been incorporated into policies for determining gardening and recreational potential of urban sites based on soil contamination with heavy metals (e.g. Schwarz, Pouyat, & Yesilonis, 2016), urban habitat patches meant for conservation or restoration could also benefit from taking into account site land use history. We have shown that this can be accomplished by relying on data sources such as city archival documents and historical aerial photographs.

5 | CONCLUSIONS

As urbanisation continues at an unprecedented rate, understanding how ecological dynamics respond to human actions is becoming increasingly important. Our results suggest that over a time frame of 3–22 years, the diversity of local plant communities does not change substantially in abandoned urban habitat patches. Much like other studies of disturbed grasslands, variation in land use legacies led to divergent compositional trajectories in vacant lots over time. This observed spatial and temporal variation in composition lends support to the use of networks of small, disaggregated patches of land within cities to maximise biodiversity conservation (e.g. Catalano, Marcenò, Laudicina, & Guarino, 2016; Goddard, Dougill, & Benton, 2010).

If vacant lots are to be managed as a network of sites for temporary conservation, a greater focus on the diversity of the surrounding regional species pool and maintaining habitat connectivity may be a key. This is increasingly presented in discussions of non-urban grassland conservation (Donald & Evans, 2006; Winsa, Bommarco, Lindborg, Marini, & Öckinger, 2015), yet relatively few empirical studies have considered the role of seed dispersal in the assembly of communities over time in fragmented urban habitat patches (but see spatial studies: Concepción et al., 2015; Lososová et al., 2016; Schleicher et al., 2011). Dispersal patterns are likely to interact with urban land use legacies, suggesting that site-specific history can influence a variety of community assembly processes. A combination of long-term seed addition experiments (e.g. Fischer, von der Lippe, Rillig, & Kowarik, 2013), studies of how habitat fragmentation influences regional seed dispersal patterns (e.g. Damschen et al., 2008), and a focus on potential mechanisms by which species diversity could be maintained locally over time (e.g. plant–soil feedbacks, Baxendale, Orwin, Poly, Pommier, & Bardgett, 2014) are likely to provide valuable insight into the interactive processes that structure communities in disturbed urban landscapes.

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AUTHORS' CONTRIBUTIONS

A.L.J. and C.M.S. conceived the ideas and designed methodology; A.L.J. and D.B. collected the data; A.L.J. and D.B. analysed the data; A.L.J. and D.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The following data are deposited in Dryad Digital Repository https://doi.org/10.5061/dryad.cb13r (Johnson et al., 2017): (1) Plant species by site matrix, (2) Demolition dates for individual vacant lots, (3) Plant species by functional traits matrix, (4) CWMs of functional traits in building footprints and remnant garden sites and (5) Raw soil data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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