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Genetic Diversity and Population Structure in Cities Is Not Consistent Among Cosmopolitan Plant Species

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ABSTRACT

Urbanisation has led to increasing homogenization of plant communities across cities. However, it is unclear whether these patterns extend to cosmopolitan plant species at the genetic level. We examined genome-wide genetic patterns in six widespread plant species (three Poaceae and three Asteraceae) across five cities in the USA (Boston, Baltimore, Minneapolis-St. Paul, Phoenix, and Los Angeles) using reduced-representation sequencing. We assessed genetic structure, differentiation, and patterns of isolation by distance (IBD) and environment (IBE) to determine if species were genetically homogeneous or differentiated by city, percentage of impervious surface, or both. Most species exhibited limited population structure overall, with *Poa annua* (annual bluegrass), *Taraxacum officinale* (dandelion), and *Cynodon dactylon* (Bermuda grass) showing no significant genetic differentiation among cities, a pattern consistent with high gene flow mediated by human activity. Notable exceptions included city-level differences in *Erigeron canadensis* (horseweed) and *Lactuca serriola* (prickly lettuce), especially in Phoenix. We also observed low genetic diversity in *Digitaria sanguinalis* (crabgrass) from Phoenix, suggesting recent founder effects or selection via environmental filtering. *Erigeron canadensis,* the only native species studied, displayed stronger differentiation by city, along with significant isolation by temperature and distance. Among all species, we found no evidence for population structure by impervious surface. Our findings indicate that widespread population genetic structure patterns of cosmopolitan plants are likely to depend more on species attributes (e.g., self-compatibility) and human-mediated dispersal than on urbanisation per se.

1 | Introduction

Global ecosystems have been transformed by human activity. Urban environments in particular have been dramatically altered, with a greater presence of impervious surfaces, higher temperatures, and novel combinations of species (Ruas et al. 2022). For example, in the USA regional policy, residential income, as well as personal aesthetic values, have led to the homogenization of urban plant communities (Groffman et al. 2014; Wheeler et al. 2017). This pattern is reinforced by the presence of cosmopolitan plant species, which are widespread and distributed globally across many cities

(Aronson et al. 2014; Del Tredici 2020). These species are often historically associated with agricultural or ruderal areas (La Sorte et al. 2007) and are likely to be introduced (non-native) and spontaneous (not planted by humans) in urban environments (Cavender-Bares et al. 2020; Huang et al. 2025; Knapp et al. 2012; Padullés Cubino et al. 2019; Wittig and Becker 2010). However, despite the clear presence of common plants that contribute to homogenization across urban environments, less is known about genetic patterns within these species, which ultimately limits our understanding of their origin and spread.

Humans modify plant dispersal, which directly impacts the degree to which plant populations are related to one another. Specifically, relatedness can change through gene flow (exchange of alleles) and founder effects (populations established by a limited number of individuals). When human activity increases rates of plant dispersal, higher gene flow can result in high genetic similarity among populations. For example, historical trade routes are thought to be pathways through which urban genotypes of *Plantago* (Plantains) species dispersed, maintaining genetic homogeneity among populations (Iwanycki Ahlstrand et al. 2022; Smith et al. 2020). For introduced plant species, including most North American cosmopolitan species which are native to Eurasia, colonisation history also impacts how populations are related to one another. Plant species that are dispersed outside their native range can be subjected to founder effects or genetic bottlenecks, which reduce genetic diversity and can increase the prevalence of specific traits like selfing and clonality (Estoup et al. 2016; Hernández-Espinosa et al. 2022). Hagenblad et al. observed this pattern in the invasive forb *Impatiens glandulifera* (Himalayan Balsam), which has lower genetic diversity in its introduced range compared to its native range (Hagenblad et al. 2015). However, several studies have found that high gene flow through repeated introductions can quickly weaken founder effects in introduced plant species (Gioria et al. 2023; Lambertini 2019; Shirk et al. 2014; Vandepitte et al. 2017; Vicente et al. 2021). With cosmopolitan plant species specifically, repeated human-mediated introductions and intentional planting could mean that high gene flow outweighs other processes, leading to low genetic differentiation (Caizergues et al. 2024; Smith et al. 2020).

In addition to the active human dispersal of species, genetic similarity can also be influenced by environmental differences and phenotypic attributes of the species themselves. Following invasions, plant species can adapt to local environments (Oduor et al. 2016), producing a signal of isolation by environment (IBE). For example, the genetic variation of invasive *Tanacetum vulgare* (common tansy) was found to be largely driven by land use and soil properties rather than distance (Briscoe Runquist and Moeller 2024). Genetic differences can similarly be correlated with geographic distance. Native species may be more strongly affected by geographic and environmental distance compared to introduced species (Long et al. 2009), as introduced species are likely to have greater dispersal success, rapid germination, and/or reproduction (Flores-Moreno et al. 2013; Van Etten et al. 2017). The strength of IBE and IBD can vary depending on whether the native versus introduced range is sampled. For example, *Lycium ferocissimum* (African boxthorn) was found to be isolated primarily by distance in its native range but by environment in its introduced range (McCulloch et al. 2023). *Phragmites australis* (common reed) showed a similar pattern, where distance was not as important as the environment in the introduced range (Guo et al. 2018). Evolutionary studies frequently use macroclimate and geographic distance to understand IBE and IBD processes. However, urban environments in cities are especially heterogeneous, with human-modified habitats acting as both ecological filters and dispersal barriers. Features like percent impervious surface in cities may be key to explaining genetic patterns in urban environments.

Urban environmental conditions, including heat islands, altered soil conditions, and/or habitat fragmentation, are assumed to play a major role in genetic differentiation (Johnson and Munshi-South 2017). Specifically, genetic differentiation can occur through direct environmental selection or indirectly via reduced gene flow, as impervious surfaces and fragmented green spaces act as barriers to dispersal (Alberti et al. 2020; Johnson and Munshi-South 2017; Rivkin et al. 2019; Santangelo et al. 2018; Wood et al. 2021). As a result, plants in cities might share phenotypes despite large geographic separation. For example, across global urban environments, *Trifolium repens* (white clover) has been shown to lose herbivore defence in favour of tolerance to urban drought (Johnson et al. 2018; Santangelo et al. 2022). *Lepidium virginicum* (Virginia pepperweed) plants from urban environments showed more similar growth phenotypes and were also more genetically related overall compared to rural plants (Yakub and Tiffin 2017). However, gene flow among populations in different cities is still poorly understood (Rivkin et al. 2019). Despite interesting preliminary emerging patterns, few studies have used multiple species in the same study design to compare genetic patterns within and across cities. Studies comparing multiple species and cities simultaneously are key to revealing common patterns and processes underlying urban evolution research.

We examined the genetic composition of six cosmopolitan weedy plant species within and across five metropolitan areas, hereafter "cities", in the USA. Our study included three species in the Asteraceae family and three in the Poaceae family. The three Poaceae studied were: *Cynodon dactylon* (Bermuda grass), *Digitaria sanguinalis* (large crabgrass), and *Poa annua* (annual bluegrass). The three Asteraceae studied were: *Erigeron canadensis* (horseweed), *Lactuca serriola* (prickly lettuce), and *Taraxacum officinale* (dandelion). The selected cities—Baltimore, Boston, Los Angeles, Minneapolis-Saint Paul, and Phoenix—span diverse climates and geographical regions across the United States. Within each city, we selected sites with different percent impervious surfaces as a proxy for different urban environments. For each plant species, we anticipated several possible genetic patterns. We might observe *no genetic differentiation* (Figure 1a), where all individuals are genetically indistinct due to human-mediated dispersal and/or migration. Alternatively, we might observe *genetic differentiation by city* (Figure 1b), where geographic and/or environmental distance are key drivers of differentiation. Or, we might observe *genetic*

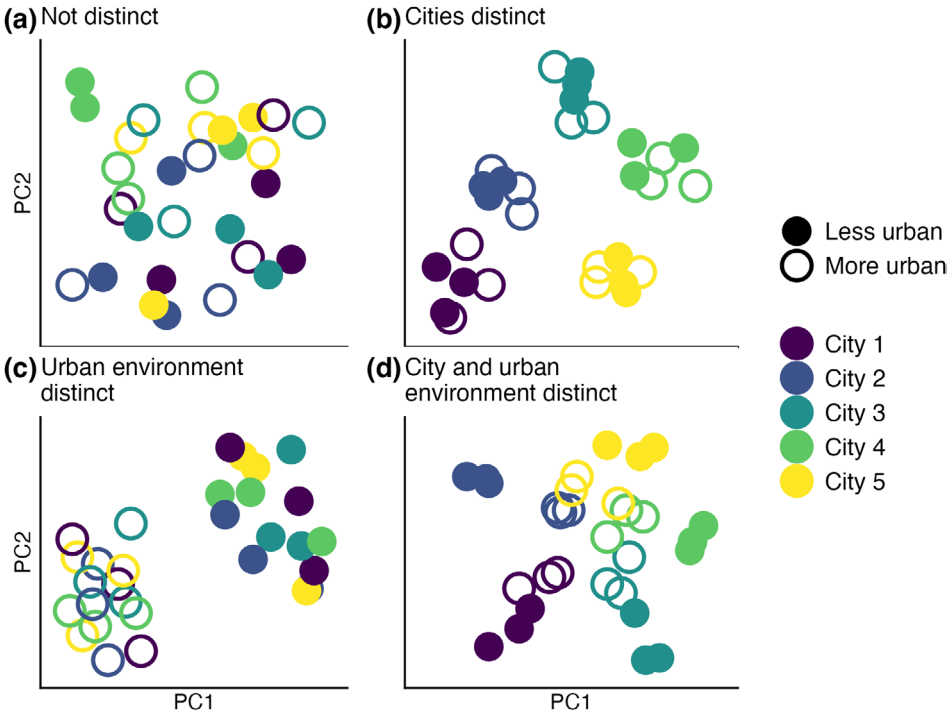

FIGURE 1 | Conceptual figure demonstrating possible patterns of genetic relatedness by city and urbanness. Circles represent species' individuals. Plots (a–d) represent the clustering of individuals by genetic similarity, where axes could represent principal components. Plot (a) represents individuals that are not genetically distinct by city or urban environment (e.g., percent impervious surface). Plot (b) represents individuals that are genetically distinct by city. Plot (c) represents individuals that are genetically distinct by urban environment. Plot (d) represents individuals that are genetically distinct by both city and urban environment. Note that in this conceptual figure, urban environment is treated as a binary variable. In practice, the urban environment is likely to consist of continuous variables.

differentiation by urban environment (Figure 1c), where impervious surface is correlated with genetic differentiation among all individuals or common urban genotypes. Finally, we might instead observe *genetic differentiation by both city and urban environment* (Figure 1d). Ultimately, this work will help us better understand the consequences of human activities and the environment in shaping the genetic relatedness of cosmopolitan species.

2 | Materials and Methods

2.1 | Study Species

Six species (three Poaceae, three Asteraceae) were examined in this study (Table 1). With the exception of *E. canadensis*, all species were introduced from Eurasia to the continental USA. These plant species encompass a variety of genome structures; *E. canadensis* and *L. serriola* are diploid, *D. sanguinalis* is hexaploid, *P. annua* is tetraploid, and *T. officinale* in North America is largely triploid. *Cynodon dactylon* can range from diploid to hexaploid, with tetraploidy being the most common. *Poa annua* and *C. dactylon* are commonly sold as turf grasses, either in seed mixes or sod, and *T. officinale* seeds often are contaminants in seed mixes or grown for food (Table 1). Life form, seasonal life cycle, reproductive strategy, pollination strategy, vegetative growth ability, and phenology also differ among these species (Jones et al. 2021; Natural Resources Conservation Service 2025; Rita et al. 2012; Stewart-Wade et al. 2002; Warwick 1979; Weaver 2001; Weaver and Downs 2003) (summarised in Table 1).

2.2 | Field Collection and DNA Extraction

We collected leaf tissue from five metropolitan areas in the USA, Baltimore, Boston, Los Angeles, Minneapolis-Saint Paul, and Phoenix (Figure 2a). These cities vary in climate, including temperature and precipitation normals (Figure 2b,c). Minneapolis-St. Paul has the lowest temperatures, routinely lower than 0°C in the winter (Figure 2b). Boston and Minneapolis-St. Paul receive the most wintertime snowfall, whereas Los Angeles and Phoenix have no snowfall (Figure 2c). Phoenix has the most extreme climate, with maximum temperature normals exceeding 40°C during the summer (Figure 2b) and only 183 mm of yearly ambient precipitation (Figure 2c).

We selected collection sites within each city, including yards, parks, vacant lots, roadsides, and natural or unmanaged areas. These sites varied in their percentage of impervious surface (Figure 3a and defined in more detail below). At each site, we collected leaves from 1 to 5 individuals for at least one species. We successfully obtained genotype data (methodology described below) from individuals at 20–47 collection sites per city (Figure 2a). Figure 3b provides an overview of the sampling scheme. Collection took place between April and September 2018. We placed samples immediately

TABLE 1 | Species-level attributes of the plant species in this study, including life history traits and native status in the USA. Note that pollination tracks functional type among these species: Grasses are wind-pollinated while forbs are insect-pollinated.

Species	Life form	Life cycle	Outcrossing	Vegetative growth	Commercial distribution	Native to USA	Phenology (flowering)
Cynodon dactylon (Bermuda grass)	C4 grass (Poaceae)	Perennial	Always	Yes	Yes	No	Summer
Digitaria sanguinalis (large crabgrass)	C4 grass (Poaceae)	Perennial	Some	Yes	No	No	Summer
Erigeron canadensis (horseweed)	Forb (Asteraceae)	Annual	Some	No	No	Yes	Late summer
Lactuca serriola (prickly lettuce)	Forb (Asteraceae)	Annual, biennial	Some	No	No	No	Late summer
Poa annua (annual bluegrass)	C3 grass (Poaceae)	Annual	Little	No	Yes	No	Spring
Taraxacum officinale (dandelion)	Forb (asteraceae)	Perennial	Never (in north america)	No	Yes	No	Spring

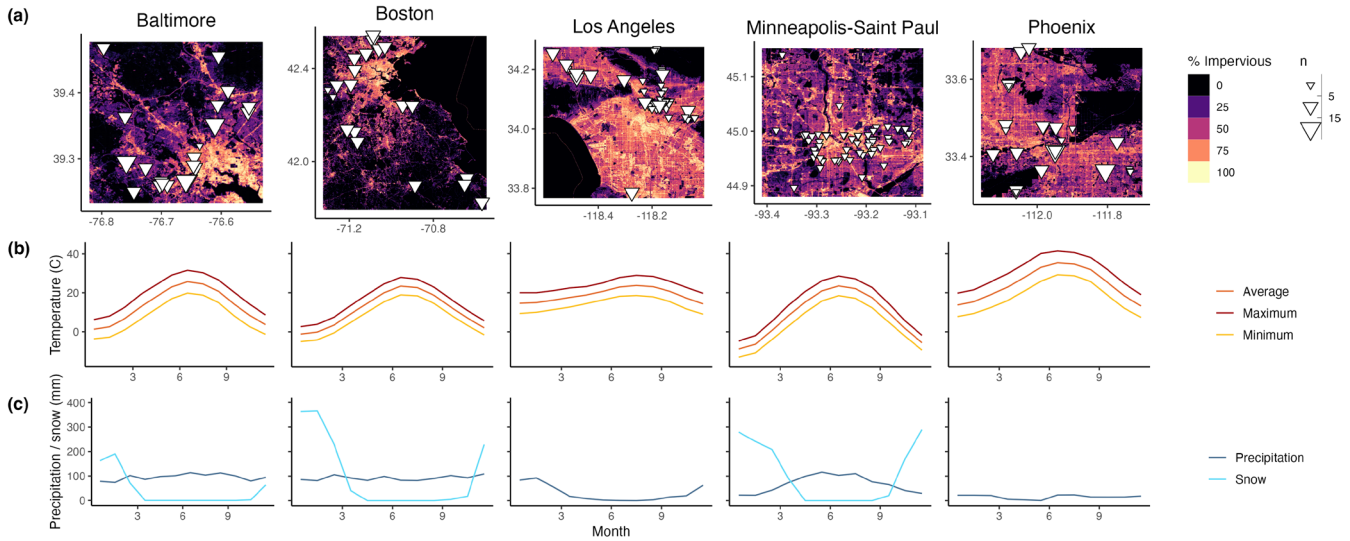

FIGURE 2 | (a) Sampling sites (white triangles) in Baltimore, Boston, Los Angeles, Minneapolis-Saint Paul, and Phoenix metropolitan areas. The size of points indicates the number (*n*) of sampled individuals of all species genotyped from a given location. Map colour reflects % Impervious surface. *X*- and *Y*-axes on maps correspond to longitude and latitude, respectively. (b) Temperature normals for each metropolitan area from 1991 to 2020. (c) Precipitation and snowfall normals for each metropolitan area from 1991 to 2020.

in silica gel prior to shipment to Baltimore, Maryland, where DNA extraction began in 2020. Some species could not be collected from all cities: (1) *C. dactylon* was not collected in Los Minneapolis-St. Paul or Boston; (2) *D. sanguinalis* was not collected in Los Angeles; and (3) *E. canadensis* was not collected in Minneapolis-St. Paul.

DNA was extracted from leaf tissue using the Omega Bio-Tek E.Z.N.A. Plant DNA DS Mini Kit, which we found to produce greater yields than the basic plant tissue kits. We checked the DNA concentration using a Qubit 4.0 fluorometer (BR dsDNA assay), yielding a mean concentration = 66.78 ng/μL. We also checked a subset of DNA for quality using gel electrophoresis. We isolated 200 ng of DNA from each sample prior to library preparation by air drying tubes covered with sterile rayon sealing film (Excel Scientific, AeraSeal) and reconstituting DNA in 10 μL of elution buffer. DNA concentration was under 10 ng/μL for 46 samples; these were concentrated using a vacuum concentrator to accelerate drying time and then reconstituted.

2.3 | Library Preparation

We prepared libraries for sequencing following the quaddRAD method (Franchini et al. 2017). We chose this double-digest

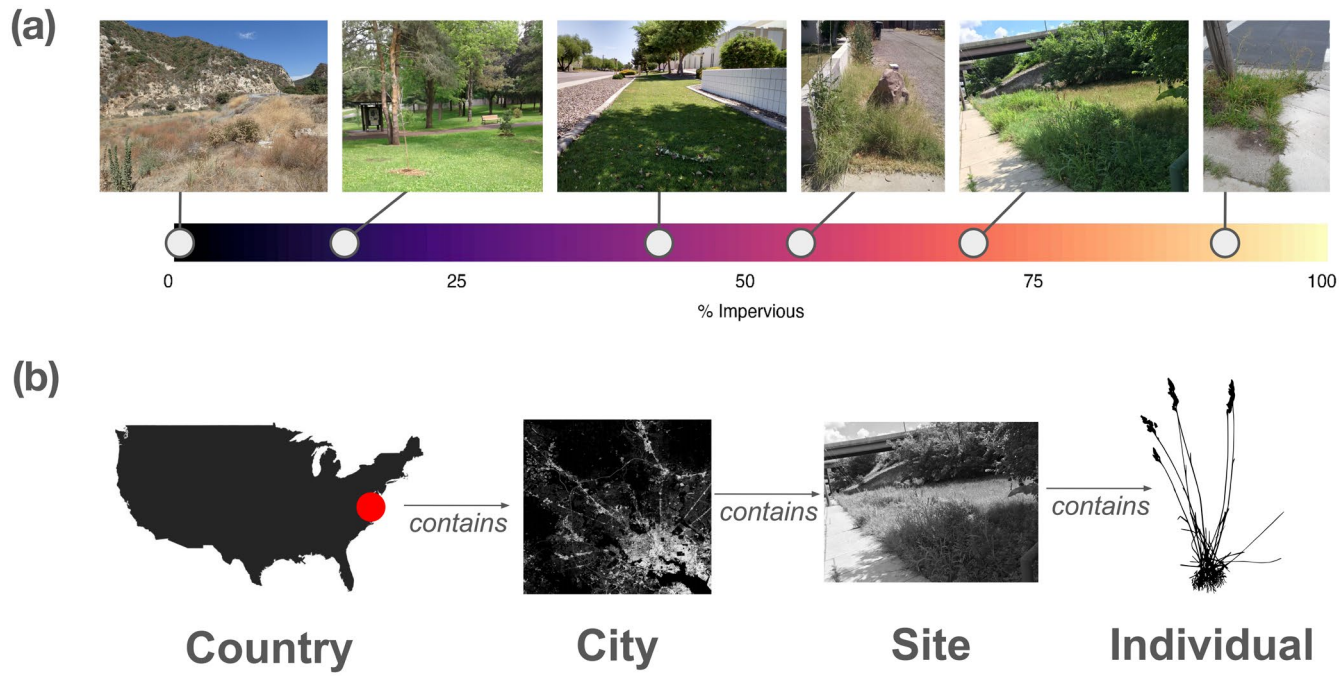

FIGURE 3 | (a) Examples of sampling sites across multiple cities with a range of % impervious surface. (b) The sampling strategy: Each city contained sites, and each site contained individuals.

RAD method for its large-scale multiplexing (use of four barcode sequences per sample) and efficient detection of PCR duplicates. Briefly, we used *PstI* (rare-cutting) and *MspI* (frequent-cutting) in a combined restriction enzyme digestion and adapter ligation step. We used modified forms of the Illumina i5 and i7 adapters that each incorporated a six-base "inner" barcode and a random four-base stretch to identify PCR duplicates. Following digest-ligation, we pooled either 12 or eight samples and performed double-size selection magnetic bead cleanup (0.5× and 0.8×, Omega Bio-Tek Mag-Bind TotalPure NGS) to filter out adapter dimers and larger DNA fragments > 1000 bp. Products were quantified using a Qubit HS dsDNA assay. We reserved 200 ng of this product for amplification. Amplification consisted of 11 cycles of PCR using Phusion high-fidelity DNA polymerase. As part of amplification, we used modified forms of the Illumina i5nn and i7nn TruSeq primers that each introduced an eight-base "outer" barcode. We then used magnetic bead cleanup (0.8×) to remove primer dimers and small DNA fragments. Products were quantified on a Qubit (BR dsDNA assay) and the size distribution of fragments was assessed using a 2100 Bioanalyzer (Agilent Technologies, DNA 1000 kit). Approximately 20% of products were re-amplified with 12 PCR cycles due to small concentrations of fragments in the 600–700 bp range. All sub-libraries (193) were then pooled equimolarly based on the concentration of DNA in the 600-700 bp range. Finally, we used a Blue Pippin (Sage Science, 1.5% agarose cassettes) to perform size selection for 600–700 bp fragments.

Illumina sequencing was performed at the Johns Hopkins University Genomics Resources Core Facility on a NovaSeq 6000 S4 flow cell (paired-end, 2×150 cycles). Because our samples were highly multiplexed, we ensured that all samples had a unique combination of at least two out of four barcodes to minimise index hopping (Costello et al. 2018). Samples were demultiplexed according to the outer barcodes by the sequencing facility.

2.4 | Sequence Data Pre-Processing

Removal of PCR duplicates from RAD datasets via degenerate base sequences inside adapters filters out redundant data (Andrews et al. 2014; Euclide et al. 2020) and can improve genotype calling accuracy (Tin et al. 2015), although see (Euclide et al. 2020). We removed a small quantity of PCR duplicates (Figure S1) using the clone_filter module of the Stacks software (Rochette et al. 2019). We then demultiplexed inner barcodes using the process_radtags module, with flags to filter out any reads with low-quality scores (phred score of < 10 in a sliding window) or uncalled bases. This resulted in an average of 6,974,119 reads per sample (Figure S2). We also manually discarded any samples with fewer than 1,000,000 reads or that comprised less than 1% of the sequenced sub-library as these correspond to low-coverage samples (Figure S3). See the Supporting Information for more details on the code and options used.

2.5 | Catalogue Creation and Genotype Calling

Prior to running the Stacks pipeline, we ran a parameter search (final parameters listed in Table S1) for each species to optimise locus calling using the iterative denovo_map method included with the software. Using these parameters, we ran the 'ustacks' module where 13 samples were excluded because loci could not be identified, potentially due to lower read counts and comprising a smaller proportion of the sub-library (Table S2). We next selected a subset of 276 samples to build the loci catalogue for each species (Table S3) using the 'cstacks' module. This was followed by the 'sstacks' module, which matches individual samples against the loci catalogues of their respective species. We used the polyRAD v2.0.0 package (Clark et al. 2019) within R 4.3.0. to call genotypes because many of our species are polyploid or have historical genome duplications. Using polyRAD, we discarded any loci not

TABLE 2 | Number of samples kept after polymorphic genetic marker detection, cities covered, number of genetic markers, and city differentiation statistics of samples in this study. For differentiation statistics (Jost's *D*, G_{ST}, F_{ST}), greater values indicate greater differentiation. Only one *E. canadensis* sample could be genotyped for Boston; it was excluded here and from all analyses except PCA. More markers could potentially lead to greater observed differentiation; however, here the correlation is weak.

Species	*n*	Cities	Markers	Jost's *D*	G_{ST}	F_{ST}
Cynodon dactylon (Bermuda grass)	185	3 (BA, LA, PX)	2292	0.306	0.027	0.028
Digitaria sanguinalis (large crabgrass)	224	4 (MN, BO, BA, PX)	2665	0.146	0.021	0.022
Erigeron canadensis (horseweed)	107	3 (BA, LA, PX)	1314	0.384	0.082	0.082
Lactuca serriola (prickly lettuce)	184	5	559	0.269	0.043	0.056
Poa annua (annual bluegrass)	178	5	746	0.057	0.018	0.010
Taraxacum officinale (dandelion)	238	5	676	0.060	0.007	0.009

found in at least 20% of samples. We calculated overdispersion of loci for each species and filtered loci based on the expected Hind/He statistic (Clark et al. 2022), which reflects posterior probabilities for genotypes. We removed an additional 24 samples at this stage due to low coverage (Table S4). This left us with the following sample count: 185 *C. dactylon*, 224 *D. sanguinalis*, 107 *E. canadensis*, 184 *L. serriola*, 178 *P. annua*, and 238 *T. officinale* (Table 2). All sites from which polymorphic markers were recovered are shown in Figure 1a. We chose to use the whole marker sequence to distinguish alleles (haplotype) rather than selecting a single nucleotide polymorphism (SNP) per locus at random.

2.6 | Sample Genotyping and Distribution

The Stacks pipeline, sample filtering, and genotype calling produced a sample size of between 107 and 238 individual plants per species (Table 2). We generated between 559 and 2665 polymorphic markers per species (Table 2). We genotyped *C. dactylon* from three cities (Baltimore, Los Angeles, and Phoenix), *D. sanguinalis* from four cities (Baltimore, Boston, Minneapolis-Saint Paul, and Phoenix), and *E. canadensis* from three cities (Baltimore, Los Angeles, and Phoenix). *Lactuca serriola*, *P. annua*, and *T. officinale* were genotyped from all five cities. This left us with a total of 20–43 sites per city. For each city and species combination, we had between 8 and 22 sites with two exceptions. Only one *E. canadensis* individual could be genotyped for Boston and was excluded from subsequent analysis except PCA. Two *P. annua* individuals were genotyped from Minneapolis-Saint Paul. These two samples were excluded from pairwise rho calculations and within-city statistics below.

2.7 | Genetic Structure

To explore genetic clustering of individuals, we conducted an iterative principal components analysis (PCA) using the 'IteratePopStruct' function in the polyRAD package. We also inferred genetic structure (i.e., genetic variation within and among cities) using Structure v2.3.4 (Falush et al. 2003; Pritchard et al. 2000). We ran five replicates each of each species and $K = \{1–5\}$, for the five cities, discarding the first 10,000 iterations as burn-in, followed by 20,000 iterations retained. We set USEPOPINFO to zero to take a geographically agnostic clustering approach. To determine the optimal K for each species, we used the Delta-K method implemented by Structure Harvester (Earl and von Holdt 2012). Using a geographically agnostic clustering approach in Structure, we found the optimal cluster number was $K = 3$, for *C. dactylon*, *D. sanguinalis*, *L. serriola*, and *T. officinale*. We found optimal $K = 2$ for *E. canadensis* and $K = 4$ for *P. annua*. Optimal *K* was lower than the number of cities sampled except for *C. dactylon*. After determining the optimal *K*, we re-ran Structure with 100,000 iterations retained for each species. We validated these results using a different algorithmic technique, sparse Non-Negative Matrix Factorization in R 4.4.2 (sNMF, Frichot et al. 2014). R 'SessionInfo' can be found in the Supporting Information.

2.8 | Genetic Differentiation and Variation

We calculated differentiation among cities for each species using Jost's *D* (Jost 2008), G_{ST} (Nei and Chesser 1983), and F_{ST} (Nei 1973). These statistics have different assumptions and can therefore offer a more complete picture when reported together. Jost's D statistic is useful for assessing diversity in polyploid species because it uses the effective number of alleles rather than expected heterozygosity, making it independent of ploidy level and sample size (Meirmans et al. 2018). However, this statistic takes longer to reach mutation–drift equilibrium (Meirmans and Hedrick 2011). Measures of G_{ST} are robust to polyploidy but can be sensitive to rare alleles. Measures of F_{ST}, while more straightforward to interpret as the proportion of variance attributable to population differentiation, are underestimated in polyploids. These statistics were calculated using the polysat package (Clark and Jasieniuk 2011; Clark and Schreier 2017) in R. We also used GenoDive to calculate pairwise ρ (rho) between cities, a metric analogous to F_{ST}.

To investigate further within each city, we calculated the inbreeding coefficient (F_{IS}) using the Hardy–Weinberg permutation test available in GenoDive to accommodate biases for polyploid species. A positive value indicates an abundance of homozygotes relative to expectations, whereas a negative value indicates an abundance of heterozygotes relative to expectations. We calculated the standardised index of association of loci ($\bar{r}_d$) to test for linkage disequilibrium for each species and city combination (Agapow and Burt 2001). Linkage disequilibrium can

indicate selection, inbreeding, or other deviations from Hardy–Weinberg equilibrium, though it cannot distinguish which process is causing the deviation. We used 999 resampling iterations to create a distribution of $\bar{r}_d$ and perform a one-sided permutation test using the poppr package in R (Kamvar et al. 2014). We calculated % private alleles as the percentage of total alleles unique to a particular city using a custom script (see supplemental information).

We also conducted a hierarchical analysis of molecular variance, AMOVA, using GenoDive v3.06 (Meirmans 2020) based on the rho statistic, which is ploidy-independent. The AMOVA allowed us to partition genetic variance among cities, within cities, and within sites. These methods vary in sensitivity, with PCA more likely to highlight small variations compared to AMOVA, which encompasses overall variance.

2.9 | Isolation by Distance and Environment

We investigated isolation by distance (IBD) and isolation by environment (IBE) using multiple matrix regression with randomization (MMRR) (Wang 2013) modelled separately for each species across all cities. Briefly, these models help us understand how multiple variables are correlated with genetic distance.

First, we calculated genetic dissimilarity using GenoDive v3.06 (Meirmans 2020) based on the rho statistic. Next, to understand IBD, we calculated geographic distance using geodesic distance as implemented with the geodist package in R. Finally, to understand IBE, we created three dissimilarity matrices to calculate environmental distance using: (1) percent impervious surface, (2) April soil temperature, and (3) July soil temperature. These variables were selected as proxies for the multivariate urban environment as they are expected to drive selection and/or isolation in cities (Johnson and Munshi-South 2017). We also included (4) distance from city center as a predictor that could indicate both IBD and IBE, given that plants closer to the city center could have greater urban environmental exposure.

Percent impervious surface measurements were taken from the US Geological Survey National Land Cover Database (NLCD) 2016 release (Yang et al. 2018). These values represent urban impervious surfaces as a percentage of the developed surface over every 30-m pixel. Distance from the city center was calculated as the Euclidean distance (m) from the coordinates obtained from each of the cities' official government (.gov) website. Soil temperature was estimated using the micro_global model within the NicheMapR package, release v3.3.2 (Kearney and Porter 2017) which models climate data over a 10 × 10 km resolution. Values represent the average soil temperature for each month (typical day) at 2.5 cm below the surface and in the middle of the day (12 pm/noon). We chose April and July soil temperature to address potential differences in seasonal phenology and account for changes in soil ecosystems. Specifically, we might expect spring-flowering species to be more sensitive to April temperatures and summer-flowering species to be more sensitive to July temperatures. Environmental matrices were generated using Euclidean distance. We performed MMRR with genetic distance as an effect of geographic distance and the four environmental distances as predictors. Each species was modelled with 9999 permutations and implemented with the algatr package in R (Chambers et al. 2023). We subset all matrices and re-ran the same MMRR model to determine if distance and/or environmental effects were present within cities. Within species, *p*-values were corrected to account for multiple testing.

3 | Results

3.1 | Genetic Structure Across Cities

We observed species-specific patterns of genetic clustering. In the PCA, the most conspicuous clustering by city occurred in *E. canadensis* and *L. serriola* (Figure 4). *Erigeron canadensis* from Phoenix was genetically distinct along PC1 (22% of the variation). Similarly, *L. serriola* from Phoenix also differed along PC1 (14% of the variation). *Erigeron canadensis* and *L. serriola* from other cities differed along PC2. Results from the PCA were supported by Structure analyses (Figure 5). We observed species-specific patterns of genetic structure, with *T. officinale* and *P. annua* showing the least structure and *E. canadensis* the most. There was little structural variation by % impervious surface (Figure 5, Figure S4). We found a high degree of admixture (i.e., mixed ancestry) in *C. dactylon*, *D. sanguinalis*, *P. annua*, and *T. officinale* (Figure 4), though *D. sanguinalis* from Phoenix appeared to be distinct with low admixture. *Lactuca serriola* from Boston was admixed, while Los Angeles, Phoenix, and Baltimore plus Minneapolis-Saint Paul were largely distinct. *Erigeron canadensis* showed almost no admixture, with Phoenix plants genetically distinct from Baltimore and Los Angeles plants. With the sNMF approach, the optimal K was generally greater with more admixture detected (Figure S4). However, *E. canadensis* and *L. serriola* again appeared to have the most population structure by city. Phoenix *D. sanguinalis* lacked admixture, while *E. canadensis* and *L. serriola* from Phoenix and Los Angeles appeared unique from other cities using the sNMF approach.

3.2 | Genetic Differentiation

For all three measures of among-city differentiation (Jost's *D*, G_{ST}, F_{ST}) we found the lowest values for *T. officinale* and *P. annua*, indicating lower differentiation in these species (Table 2). We found the greatest values for *E. canadensis*, indicating this species has greater relative differentiation by city. *Lactuca serriola*, followed by *C. dactylon*, and *D. sanguinalis* had intermediate differentiation by city. Using pairwise ρ comparisons, we found *E. canadensis* and *L. serriola* from Phoenix to be more distinct (i.e., larger ρ statistics) (Table S5). In contrast, *D. sanguinalis* from Phoenix was less distinct from other cities.

Next, we compared cities using allelic richness, homozygosity, linkage disequilibrium, and private alleles. Using effective number of alleles (A_E), we found that *D. sanguinalis* in Phoenix had low allelic richness compared to other cities (Table 3). *Cynodon dactylon* in Baltimore and *L. serriola* in Boston were also less diverse. In all cities, *C. dactylon*, *D. sanguinalis*, *P. annua*, and *T. officinale* had more homozygotes than expected (positive F_{IS}) while *E. canadensis* and *L. serriola* had more heterozygotes (negative F_{IS}) (Table 3). We observed

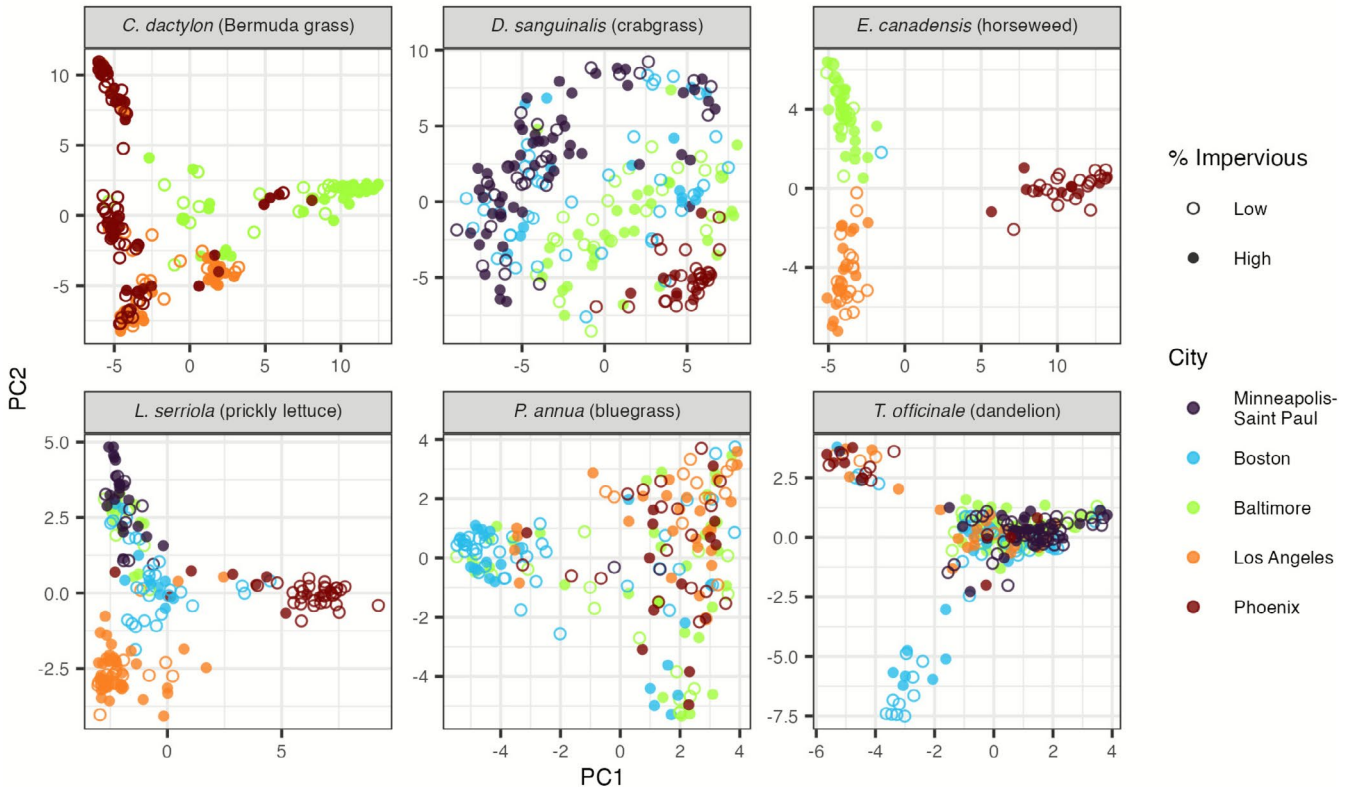

FIGURE 4 | Principal components analysis of species across cities, conducted using the polyRAD implementation in R. The proportion of variance explained across PC1 and PC2, respectively, is: *C. dactylon* = 0.16, 0.12; *D. sanguinalis* = 0.12, 0.10; *E. canadensis* = 0.22, 0.07; *L. serriola* = 0.14, 0.06; *P. annua* = 0.18, 0.08; *T. officinale* = 0.06, 0.05. Percent impervious has been plotted here as a binary variable, where low and high percent impervious is less than or greater than the median within species, respectively.

greater values of linkage disequilibrium ($\bar{r}_d$) in Phoenix for *D. sanguinalis*, *E. canadensis*, and *T. officinale* (Table 3). Greater relative linkage disequilibrium was also observed in Boston for *D. sanguinalis*, *L. serriola*, and *P. annua*. Across cities, linkage disequilibrium was greater for *C. dactylon* and *D. sanguinalis* compared to *E. canadensis* and *L. serriola*. Linkage disequilibrium can be indicative of selective sweeps (i.e., rapid evolution) and/or founder effects, though here we cannot distinguish between these. Finally, we investigated percent of private alleles (alleles that were unique to each city). Within species, we found the percentage to be highest in the Phoenix populations of *C. dactylon*, *E. canadensis*, and *L. serriola*. Percent of private alleles was lower in Baltimore for *P. annua* and *T. officinale*, *D. sanguinalis* from Phoenix, and *L. serriola* from Boston (Table 3).

We used AMOVA to determine the proportions of variance among cities, within cities, and within sites. In contrast to PCA and Structure analysis, AMOVA is less sensitive to differences caused by individual loci. For all species, most of the variation was found within cities. Specifically, individuals sampled from different sites within each city were proportionally more genetically distinct than individuals from other cities. Differences among individuals within a specific site and city accounted for 22.4%– 31.4% of the total variation. Genetic variation among different cities made up the least amount of variation, ranging from 3.1% (*T. officinale*) to 21.5% (*D. sanguinalis*) (Figure 6, Table S6). Specifically, *C. dactylon* and *T. officinale* were the most similar (8.7% and 3.1%, respectively) among cities. In contrast, *E. canadensis*, *L. serriola*, and *P. annua* showed more variation (15.2%, 14.8%, 12.9%) among cities. *Digitaria sanguinalis* had the greatest among-city genetic variation (21.5%), but like other species, a greater proportion of variation was explained by within-city differences (56.1%).

3.3 | Isolation by Distance and Environment

When considering all cities together, geographic and environmental distances explained between 1% and 27% of the genetic variation in the six species (Figure 7, Table S7). Only *E. canadensis* had a significant overall MMRR model ($p < 0.001$, Table S7), although *L. serriola* was near our significance cutoff ($p = 0.051$, Table S7). Both geographic and environmental distance were significant predictors for *E. canadensis* (Figure 6, Table S8). July soil temperature was the significant environmental predictor, meaning that differences in temperature were positively correlated with genetic differences (coefficient = 0.56, Figure 7, Table S8). In contrast, geographic distance was negatively correlated with genetic distance for *E. canadensis*. Although the overall model was not significant, *L. serriola* geographic distance was also negatively correlated with genetic distance. Aspects of the urban environment, such as % impervious surface and distance to the city center, were not significant predictors of genetic distance for any species.

Effects of IBD and IBE largely disappeared within cities. Only two species-city combinations out of 24 had an overall significant

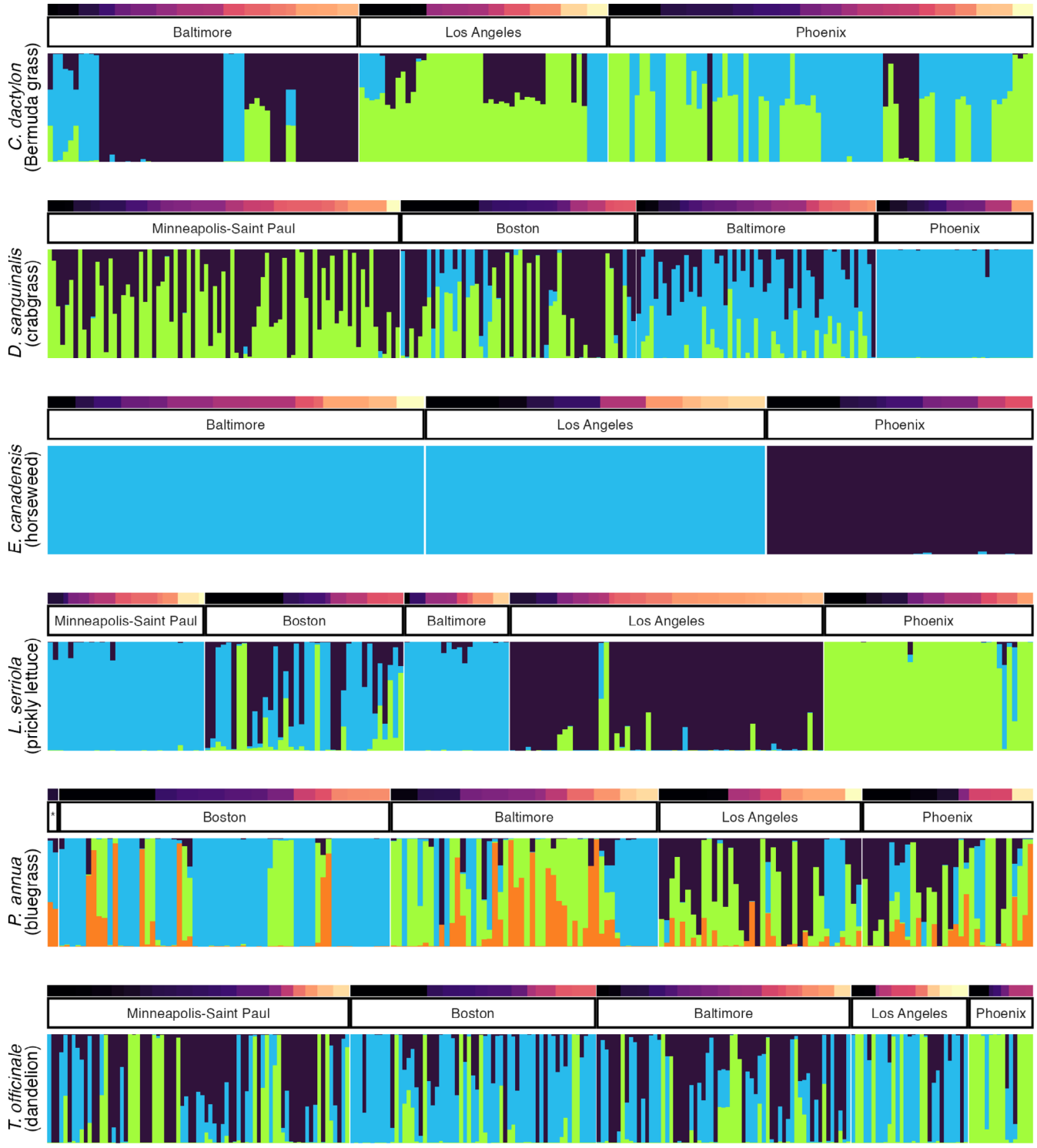

FIGURE 5 | Genetic structure of species across cities. Within each species' Structure plot, individuals within cities are ordered by % impervious surface for the site from which they were collected. Percent impervious surface is indicated by the gradient bar on the top *x*-axis above each city name, with lighter colours having more impervious surface area (see legend for Figure 2). For *P. annua*, the asterisk on the left side replaces the "Minneapolis-Saint Paul" label. Only one *E. canadensis* individual was sampled in Boston; it was excluded from Structure analysis.

MMRR model, *C. dactylon* in Phoenix and *T. officinale* in Los Angeles (Table S9). For *C. dactylon* in Phoenix, genetic distance was positively correlated with distance to city center (Table S10). For *T. officinale* in Los Angeles, genetic distance was negatively correlated with environmental distance (April soil temperature, Table S10).

4 | Discussion

Here, we studied the genetic patterns of six cosmopolitan plant species sampled from five cities in the USA with varying environmental conditions. For these widespread species, we investigated the degree to which city populations were genetically

TABLE 3 | Sample size and statistics by species and city. The A_E statistic is the effective number of alleles per locus. The F_{IS} statistic indicates an abundance (positive) or lack (negative) of homozygotes relative to expectations. The $\bar{r}_d$ statistic refers to the standardised index of association of loci, a measure of linkage disequilibrium. %PA refers to the percentage of private alleles across all loci. Only one *E. canadensis* individual was observed in Boston and two *P. annua* individuals were observed in Minneapolis-Saint Paul; these were excluded from calculations here. Minneapolis-Saint Paul is abbreviated as MSP.

Species	City	*n*	A_E	F_{IS}	$\bar{r}_d$	%PA
Cynodon dactylon (Bermuda grass)	Baltimore	55	4.530	0.166	0.295	2.3
	Los Angeles	48	6.470	0.186	0.207	1.4
	Phoenix	82	6.978	0.200	0.279	3.6
Digitaria sanguinalis (large crabgrass)	Baltimore	55	5.069	0.208	0.212	1.2
	Boston	52	5.230	0.252	0.340	0.5
	MSP	81	5.233	0.228	0.219	1.0
	Phoenix	36	3.692	0.012	0.400	0.3
Erigeron canadensis (horseweed)	Baltimore	41	4.365	−0.113	0.102	4.7
	Los Angeles	37	4.737	−0.088	0.108	7.1
	Phoenix	29	4.525	−0.123	0.230	13.6
Lactuca serriola (prickly lettuce)	Baltimore	20	4.830	−0.051	0.081	1.6
	Boston	34	3.720	−0.011	0.239	0.5
	Los Angeles	60	6.077	−0.033	0.108	5.8
	MSP	30	5.401	−0.052	0.112	2.4
	Phoenix	40	4.890	−0.089	0.233	8.8
Poa annua (annual bluegrass)	Baltimore	47	5.161	0.171	0.314	0.3
	Boston	61	5.212	0.174	0.499	1.5
	Los Angeles	38	6.093	0.172	0.129	1.6
	Phoenix	30	6.260	0.163	0.217	1.1
Taraxacum officinale (dandelion)	Baltimore	60	7.192	0.134	0.126	0.5
	Boston	58	7.698	0.141	0.169	1.6
	Los Angeles	29	6.843	0.122	0.187	1.1
	MSP	75	8.081	0.138	0.106	1.3
	Phoenix	16	5.445	0.075	0.399	1.1

homogenous or differentiated by city, degree of urbanisation, or a combination of these drivers. Overall, we found a few generalizable patterns across species. Most genetic variation was found within cities, with less variation explained by city. However, Phoenix populations tended to be distinct for some species. Additionally, we found little evidence for a relationship between genetic differences and impervious surface area as a proxy for urban environments. In general, we found that homogenization at the genetic level depended on the species in question, suggesting that human activities specific to individual plant species play a role in genetic differentiation.

4.1 | Species-Dependent Differentiation

Human activity has contributed to species homogenization across cities (Groffman et al. 2014; Padullés Cubino et al. 2020). However, at the genetic level we find mixed patterns. We found the strongest evidence for genetic differentiation by city (i.e., Figure 1b) for *E. canadensis*, the only native species in this study. To a lesser extent, *L. serriola* was also distinct by city, except for Boston. We found *D. sanguinalis* and *C. dactylon* to be more genetically homogenous/less distinct (i.e., Figure 1a). Although some group assignments were unique to Baltimore, Los Angeles, and Phoenix, many *C. dactylon* individuals showed mixed ancestry. We found little evidence for genetic differentiation for *P. annua* or *T. officinale*, either by city or urbanness. These are likely to be dispersed by humans and present in seed mixes (Buddenhagen et al. 2023; Conn 2012).

We found no evidence for differentiation by urbanisation, nor by urbanisation and city, for any species (Figure 1c,d). Despite the city patterns we observed, the overall signal of differentiation among cities was weak, with low variation overall and

most variation being found among sites within individual cities. Low levels of differentiation agree with evidence suggesting that cosmopolitan plants experience high gene flow in urban habitats (Caizergues et al. 2024; Smith et al. 2020).

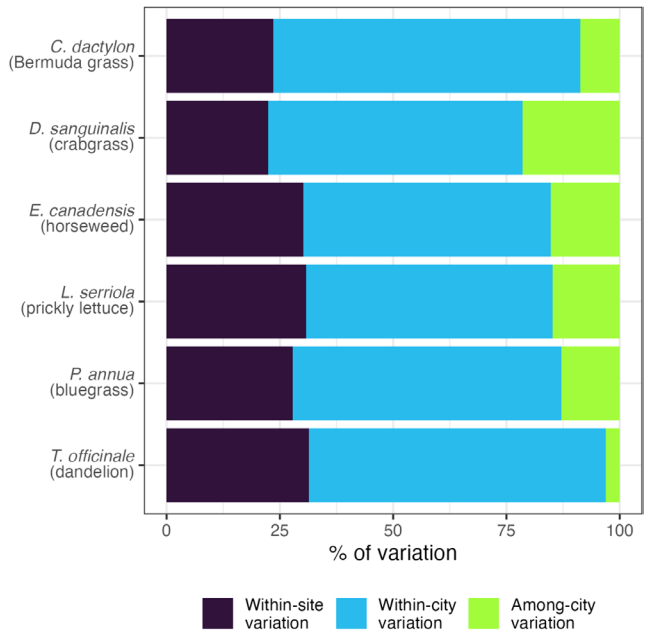

FIGURE 6 | Proportion of variance statistics from AMOVA using a ploidy-independent Infinite Allele Model equivalent to Rho. Individuals are nested within sites, and sites are nested within cities in this model.

Five out of six species lacked evidence for IBE and IBD, also indicating potentially high levels of gene flow facilitated by human activity. Importantly, we used 10 × 10 km resolution for our environmental measures; it is possible that patterns of IBE not detected here are present at smaller scales and/or with different environmental variables.

4.2 | Differentiation of Phoenix Populations

Among the cities included in this study, Phoenix's climate is both hot and dry, with water resources modified through irrigation (Hope et al. 2006). We observed two different genetic patterns among our species in Phoenix. First, *D. sanguinalis* had a lower effective number of alleles, higher linkage disequilibrium, and a lower percentage of private alleles in Phoenix relative to other cities. Structure and sNMF showed strong single-group assignment, suggesting a largely genetically uniform sample. These results could indicate either a founder effect, bottleneck, and/or environmental filtering due to the hot, dry climate (Markert et al. 2010). Additionally, *D. sanguinalis* in Phoenix might have experienced city-specific management practices.

In contrast, *E. canadensis* and *L. serriola* individuals collected in Phoenix were distinct through a greater percentage of private alleles and somewhat greater linkage disequilibrium. Structure and sNMF results also indicated unique group assignments for Phoenix relative to the other cities. While this

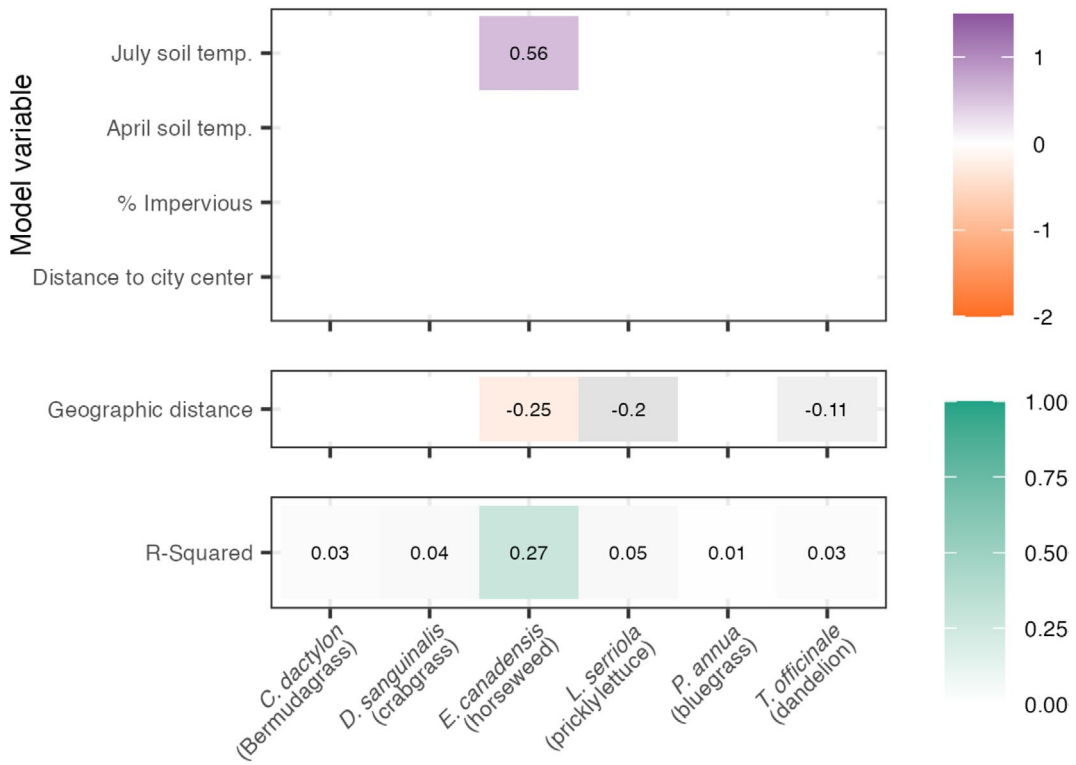

FIGURE 7 | Multiple matrix regression with randomization (MMRR) overall model predictors and R-squared values for each species. All cities are considered together. Predictors with coefficients that are listed are significant at the $p < 0.05$ level. The model variable colour indicates either a positive (purple) or negative (orange) relationship. R-squared statistics (green) are more saturated as they get closer to 1. Greyscale (all species except *E. canadensis*) indicates a non-significant overall MMRR model.

might have occurred due to barriers to gene flow, local adaptation might also explain this finding. For *E. canadensis*, this is consistent with research by Bhattacharya et al. (2022) revealing two distinct, yet diverse subgroups of *E. canadensis*: plants sampled from cooler areas in northern Alabama, USA formed a distinct genetic cluster from those found in southern Alabama. Greater heterozygosity than expected might also contribute to more rapid environmental response in *E. canadensis* (Aparecida et al. 2012). *Lactuca serriola* in the western USA (California, Arizona) has also been found to be genetically distinct relative to the rest of the country (Lebeda et al. 2011, 2012). There was also some evidence that *T. officinale* individuals from Phoenix might be less diverse, as suggested by comparatively low effective number of alleles and higher linkage disequilibrium, though this could be due to a smaller number of individuals sampled. Aside from Phoenix's hot and dry climate, several factors could prevent genetic homogenization, including the relatively young age of the city (Potgieter et al. 2024), distance from the point of introduction, as well as "island effects" in arid cities caused by irrigation (Grijseels et al. 2023). These factors would mean fewer introductions, greater isolation by distance from the East coast of the USA, and greater resistance to colonisation, respectively.

4.3 | Human Behaviour and Genetic Patterns

Human behaviours are a key component of community assembly and distribution of species, especially in cities (Avolio et al. 2021). For example, urbanisation leads to homogenization of C3 grass species, some homogenization of C4 grass species, and greater abundance of some C4 species in warmer cities (Trammell et al. 2019), likely through increased, often commercial, dispersal (Beard 2012; Busey 2003). *Poa annua* (a C3 grass), *C. dactylon*, and *T. officinale* exhibited low overall differentiation among cities with little population structure (i.e., Figure 1a). Other studies have also found a lack of population structure, high gene flow, and/or panmixia for *P. annua* and *T. officinale* (Androsiuk et al. 2019; Chen et al. 2003; Mazumder and Kesseli 2021). Again, the lack of structure may be due to both *P. annua* and *T. officinale* being common contaminants of turf grass seeds mixes, which are commercially distributed (Conn 2012). Additionally, *T. officinale* can be grown for medicinal uses and seeds purchased (Stewart-Wade et al. 2002). While *C. dactylon* differs globally at the genetic level, many North American individuals have mixed ancestry (Singh et al. 2023; Zhang et al. 2019, 2021); *C. dactylon* is also sold as a turf grass in the USA, which might lead to a lack of differentiation (Taliaferro 1995). While our genome-wide approach suggests genetic homogenization in these species and cities, it is important to note that phenotypically relevant genetic differentiation may still be occurring through gene sets not captured by our loci.

4.4 | Native Status and Genetic Structure

High gene flow resulting from frequent introductions might lead to reduced genetic structure and limited local adaptation within species (Smith et al. 2020). *Erigeron canadensis*, the only native species in this study, had the strongest separation among cities based on the population summary statistics, PCA, and pairwise rho. Among cities where it was present, *E. canadensis* had among the highest percentages of private alleles. We also observed a significant MMRR model, with July soil temperature and geographic distance being linked to genetic distance in *E. canadensis*. These results could indicate that *E. canadensis* responds to July soil temperatures, especially in Phoenix. Previous work suggests that genetic differentiation of *E. canadensis* populations is correlated with climate, particularly aridity (Rosche et al. 2019). Despite the genetic differences observed, a significant negative geographic distance coefficient suggests greater similarity than expected across distances, indicating that gene flow is likely to still be occurring. Interestingly, previous work has shown low diversity and high rates of selfing in *E. canadensis* (Rosche et al. 2019), which could reinforce small amounts of genetic variation across distance and environment. Overall, these results suggest that observing genetic structure in cosmopolitan species' native ranges can provide valuable information about idiosyncratic responses. More work is needed to understand if this pattern is generalizable or unique to *E. canadensis*.

4.5 | Importance of Local Environments

Local environments and life history traits are likely important for influencing genetic structure and differentiation of the species in this study. For all species, most of the genetic variation could be attributed to differences within cities. Individuals also varied considerably within sites. This could indicate that instead of responding to landscape-level environmental variables, species could be responding to microenvironments within cities (Calfapietra et al. 2015), such as soil depth/quality, soil contaminants, local temperature or soil moisture variation, or presence of competing species. Among four of our species, we also found a higher proportion of homozygotes and evidence for linkage disequilibrium indicating potentially high rates of asexual reproduction. Baker's rule states that when plants are colonising a new area outside of their natural range (e.g., most urban spontaneous plants), self-compatible fertilisation is an advantageous trait given the potential lack of pollinators (Baker 1974; Kalisz and Vogler 2003). Low genetic diversity and differentiation could be due to self-compatibility or clonal reproduction by the species in this study. Finally, we observed the most city-level population structure in *E. canadensis* and *L. serriola*, the two diploid species. Diploids are expected to lose alleles more quickly than polyploids, leading to more rapid differentiation. Alternatively, polypoids could be more successful at colonising and re-colonising different cities (Te Beest et al. 2012), helping them maintain higher genetic diversity. Ultimately, local environments and functional traits could be more influential to genetic patterns in cosmopolitan species than the regional variables used here.

5 | Conclusion

Our results suggest that genetic patterns of urban plants might be driven less by urban environments (i.e., percent impervious surface), and more by human actions and species' life history. We detected no genetic patterns associated with percent impervious surface across six different species in our study; however,

it should be noted that other proxies of urbanisation, such as those that focus on fine-scale local environments, might reveal different results. Our work supports the finding that urban evolution is complex, with colonisation events and gene flow playing especially important roles for cosmopolitan species (Johnson and Munshi-South 2017; Miles et al. 2019). When performing urban evolution studies, careful consideration should be paid to each species in question, considering its reproductive/dispersal strategy and life history traits that might increase genetic similarity of individuals across cities. In particular, urban evolution studies should consider human activity. Accounting for these differences will ensure better prediction of plant evolution and adaptation to rapidly changing urban landscapes.

Author Contributions

A.M.H. performed lab work, primary analyses, and wrote the paper. J.M.C. performed analyses and wrote the paper. P.M. and D.F.A.-S. edited and wrote the paper. J.C.-B., P.M.G., S.J.H., S.E.H., S.B.L., J.P.C., D.E.P., and T.L.E.T. contributed materials, led sample collection, and edited the paper. M.L.A. designed the research, contributed laboratory materials, and wrote and edited the paper.

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Disclosure

AI tools disclosure: This text does not contain AI-generated content, nor were AI tools used in data analysis, with the exception of existing algorithms built into the software described in the Materials & Methods section. The authors take full responsibility for the content and accuracy of this work.

Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Genetic data. Demultiplexed fastq files are available via SRA BioProject 1359434 (https://www.ncbi.nlm.nih.gov/bioproject/1359434). Estimated genotypes from polyRAD are available in polyRAD, genind, and Structure file formats via Figshare (10.6084/m9.figshare.30640199). *Metadata*. Metadata, code, and intermediate data files associated with this project are available at https://github.com/avahoffman/urban-weed-genomics (10.5281/zenodo.18343119).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information S1