

Contribution of non-native plants to the phylogenetic homogenization of U.S. yard floras

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Abstract. Cultivation and spread of non-native plant species may result in either phylogenetic homogenization (increasing similarity) or differentiation (decreasing similarity) of urban floras. However, it is unknown how non-native species influence homogenization of cultivated versus spontaneously occurring species in cities, and which traits are associated with species that promote homogenization versus differentiation. In this study, we compared homogenization effects of cultivated and spontaneous non-native species in yard floras across and within seven widely distributed U.S. cities. Additionally, we explored which traits explained their particular contribution to homogenization. We recorded plant presence/absence in 178 private yards distributed among seven metropolitan statistical areas in the United States. We compared phylogenetic homogenization effects of non-native species within both the cultivated and spontaneous species pools using phylogenetic dissimilarities and the homogenization index. Then, we expressed contributions of non-native species to the homogenization of each pool as a function of two different sets of plant functional traits using phylogenetic generalized least square (PGLS) models across and within cities. Across cities, spontaneous non-native species homogenized, and cultivated non-native species differentiated, yard floras. Within the spontaneous pool, short, small-seeded non-native plants and non-native grasses significantly homogenized yard floras. Within the cultivated pool, species contribution to homogenization was best predicted by plant height, presence of showy flowers, and growth form, with non-native grasses significantly homogenizing cultivated yard floras. Within cities, non-native species—whether they were cultivated or spontaneous—consistently homogenized yard floras of the three northern cities and differentiated yard floras of three of the four southern cities, suggesting that homogenization processes are context- and scale-dependent. Likewise, traits explaining homogenization differed substantially among cities. The inconsistent patterns among cities in the plant traits that promoted homogenization of both cultivated and spontaneous species suggest that local environmental and anthropogenic conditions of individual cities imposed strong constraints on trait selection. Linking plant functional traits that promote homogenization with residents' preferences for vegetation may further enhance understanding of how yard plant communities assemble at regional and local scales.

Key words: alien yard species; anthropogenic factors; domestic gardens; horticulture; plant traits; urban biodiversity.

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INTRODUCTION

In the United States, 75 million houses have a yard (US Census Bureau 2018). Together, these residential landscapes encompass a wide range of environmental and structural conditions. Yard floras typically contain both native and non-native species, and spontaneously occurring and cultivated species (Smith et al. 2006, Marco et al. 2008, Bigirimana et al. 2012). Historical immigration from Europe and cultural similarities among U.S. regions have resulted in similar landscapes across widely dispersed cities (McKinney 2006, Ignatieva and Stewart 2009, Groffman 2014). However, the extent to which U.S. yard floras are homogeneous (i.e., taxonomically, phylogenetically, or functionally similar among regions) and the contributions of spontaneous and cultivated non-native species to the process of homogenization (i.e., promoting similarity) at different spatial scales are not clear.

Urban areas are frequently described as homogenized when compared to natural areas (i.e., urban areas in different regions are more similar to each other than the natural areas they replace; Kühn and Klotz 2006, McKinney 2006, Grimm et al. 2008, Lososová et al. 2012, Groffman 2014). For example, previous research in the United States has demonstrated urban homogenization by showing that yard floras are compositionally and structurally more similar than the corresponding floras in surrounding natural areas (Wheeler 2017, Pearse 2018). However, biotic homogenization might also be assessed within and across cities, by comparing the relative similarities of different components of vegetation among yards or other urban habitats (Lososová et al. 2012). In practice, biotic homogenization has not been tested using the latter approach across urban yards from a wide range of socio-ecological conditions.

Species growing in yards can be considered as arising from two separate pools (Knapp et al. 2012, Groffman 2017): human-cultivated and a spontaneously occurring (establishing without assistance) species pool. Each of these pools is subject to distinct ecological assembly processes, such as habitat filtering and species interactions, as well as anthropogenic factors, that operate across different spatial scales (Williams 2009, Aronson et al. 2016, Groffman 2017). Across

cities, the occurrence of spontaneous native species is mainly driven by biogeographical processes and habitat transformations that filter out species from the regional pool, while spontaneous non-native and cultivated species are mainly driven by climate, global trade, and policy regulations (Williams 2009, Kendal et al. 2012b). Within cities, both native and non-native spontaneous species are mainly driven by land-use identity and diversity, local conditions, socioeconomic and cultural factors, and species interactions, while cultivated species are mainly driven by socioeconomic and cultural factors alone (Cook et al. 2012, Aronson et al. 2016). As a result of all these interactions, a large proportion of yard floras (about 68–80%) are non-native (Marco et al. 2008, Bigirimana et al. 2012).

Non-native species are one of the main drivers of ecosystem transformation (Vitousek et al. 1996), and the consequences of species introduction are currently a matter of study throughout the world (Gurevitch et al. 2011). Increasing trends in globalization are associated with the expansion of non-native species (Kuebbing et al. 2013). As a consequence, many ecosystems now harbor multiple introduced species, increasing the complexity of interspecific interactions. In urban environments, although it has been hypothesized that non-native species tend to homogenize urban plant communities (McKinney and Lockwood 1999), some studies suggest that non-natives can drive within-city floral differentiation (Olden and Poff 2003, La Sorte and McKinney 2006). For example, Lososová et al. (2012) found that biotic homogenization across 32 cities in central Europe depended on non-native plants' residence time (the time a species had been present in the novel environment), with more recently introduced non-native species that had not achieved their potential range, increasing differentiation, and those that had had sufficient time to disperse into most suitable habitats increasing homogenization. Increasing numbers of non-native species in urban communities may lead to a decrease in phylogenetic diversity (Ceplová et al. 2015) that might in turn reduce overall community functioning, stability, and resistance to environmental change by narrowing the available range of species-specific responses (Cadotte et al. 2012). On the other hand, non-native species also have the potential

to increase phylogenetic diversity and species richness. Cultivated and spontaneous non-native species in yards are affected by different filtering and sorting processes (Groffman 2017, Pearse 2018) and may thus have contrasting effects on the composition of yard floras. A critical gap remains in our understanding of the influence of non-native species on community assembly in urban plant communities and their role in shaping composition and diversity.

Species traits influence how species interact with various filters in the process of community assembly (Williams et al. 2015, Aronson et al. 2016). Literature on biotic homogenization suggests that the common features of cities and human communities create conditions that promote species with similar traits and life histories (Groffman 2014, Williams et al. 2015). For spontaneous species, common functional traits of plants growing in human settlements include fast growth with a high demand for nutrients; wind pollination; small, readily dispersed seeds; and a tendency toward shorter lifespan than found in natural areas (Lososová et al. 2006, Thompson and McCarthy 2008, Knapp et al. 2012, Williams et al. 2015). For cultivated species, predominant plant traits are heavily influenced by human choices based on the benefits they provide, ranging from aesthetic (flowers, color, texture) to functional (ground cover, shade provision, food provision; Kendal et al. 2012a, Larson 2016). In this regard, Pataki et al. (2013) refer to traits that are related to human attitudes and preferences as ecosystem service-based traits, to distinguish them from conventional categories of functional traits developed for natural ecosystems, and which are subject to natural selection and are linked to ecological processes. Nevertheless, few clear patterns have emerged from existing studies of plant traits in individual cities or urban habitats because of the complexity of plant–environment interactions in urban systems and limitations of existing data and methods (Williams et al. 2015). Therefore, determining which traits of non-native species make them successful in yards, and how their persistence and spread translates into biotic homogenization, may enhance our understanding of how yard plant communities assemble at regional and local scales.

In this study, we build on previous research on biotic homogenization of residential yards in the United States (Groffman 2014, 2017, Polsky 2014, Wheeler 2017, Pearse 2018) to quantify floristic compositional similarities across and within cities and determine what plant traits promote homogenization. Unlike previous studies, we specifically explored the extent to which non-native species contribute to the homogenization/differentiation of phylogenetic composition (using phylogenetic dissimilarities), thus incorporating phylogenetic information into traditional methods of studying communities like ordination that treat all species as independent and equally dissimilar. Moreover, we expand on previous studies that assessed homogenization of urban plant communities by reporting the particular contributions of cultivated versus spontaneously occurring non-native species to homogenization, and by relating species effects on homogenization to plant traits. In doing so, we specifically addressed the following questions: (1) Are cultivated and spontaneous non-native species similarly homogenizing urban yards across and within cities? and (2) What traits of these species explain their particular contribution to homogenization at different scales (across versus within cities)? Unlike previous studies that assessed biotic homogenization in urban areas using data from a variety of habitats and sampling schemes, we collected original data with the same sampling scheme for 178 private yards distributed among seven major metropolitan areas in the United States.

We hypothesized that non-native spontaneous (weedy) species would contribute to biotic homogenization because they have been in residence in urban areas for a longer time and are adapted to a broader range of biogeographical conditions than cultivated species (La Sorte et al. 2007, Lososová et al. 2012, Ricotta et al. 2014). In contrast, we hypothesized that non-native cultivated species, which are more likely to be filtered by human preferences from commercial sources (Williams 2009), would have the opposite effect, increasing differentiation in floristic composition among yards. Across all yards and cities, we expected traits of non-native species to reflect the nature and magnitude of environmental and anthropogenic filters acting on each pool of species. Within cities, we did not expect a clear

association between patterns of homogenization and non-native species or traits, given that local biophysical conditions, homeowners' management choices, and idiosyncratic aspects of cities (e.g., development history, demographics, cultural attributes, types of infrastructure, and connectivity) may have strong impacts on the dispersal and persistence of non-native species.

METHODS

Yard selection

We selected seven major U.S. metropolitan statistical areas (hereafter "cities"): Boston, Massachusetts (BOS); Baltimore, Maryland (BAL); Los Angeles, California (LA); Miami, Florida (MIA); Minneapolis–St. Paul, Minnesota (MSP); Salt Lake City, Utah (SLC); and Phoenix, Arizona (PHX), to represent seven different ecological biomes and major climatic regions across the United States (Trammell et al. 2016). We stratified the cities by population density and socioeconomic status using the PRIZM marketing classification scheme (CLARITAS 2013, Polsky 2014), which classifies each Census Block Group in the United States into a single group based on analysis of the areal unit's population density, affluence, and life stage. Using this primary selection, we first contacted >100,000 households and identified >13,500 where the respondent was over 18 yr of age and their home had either a front or back yard (Polsky 2014). From this group, we conducted a telephone survey of 9480 residents, equally distributed among six of the seven cities (all but SLC), to identify individual residential properties as potential sampling sites (Polsky 2014). From the 9480 households surveyed, we randomly selected 21–30 residential properties per city for field sampling. In SLC, we randomly sent 50 letters to homeowners in each of six targeted PRIZM categories asking permission to visit their home for sampling. Within each PRIZM category, we visited five homes randomly selected from the positive respondents, for a total of 30 yards.

Vegetation data

We recorded plant species presence/absence in 178 yards across the seven cities (Data S1). We sampled all cities during the season of peak diversity (spring for LA and PHX; summer for BAL,

BOS, MIA, MSP, and SLC). We sampled locations in BAL, BOS, MIA, MSP, and PHX in 2012, and those in LA and SLC in 2013. We surveyed the entire area of each yard. In areas of the yard with unmanaged vegetation or a woodland/woodlot, we sampled plant species presence/absence within a 2 m wide transect across the full yard or 100 m, whichever was shorter. Yard plants are often subspecies or cultivars, but we did not attempt to classify plants below the species level. For those plants that could not be identified at the species level (~15%), we only recorded the genus. We designated species as spontaneous or cultivated based on homeowner interviews, observations of placement, land use, and land-use history. For example, species in woodlots and unmanaged vegetation components were generally considered spontaneous. Any given species could be documented as both spontaneous and cultivated if different individuals of that species fell into different categories. Species that were not designated as either cultivated or spontaneous in the field were later classified in the laboratory based on records for the same species in other sampled yards. We matched species names to The Plant List (<http://www.theplantlist.org>) version 1.1, using R package *Taxonstand* (Cayuela et al. 2017).

Native status and trait data

We classified species according to their status as either native or non-native for each U.S. state where the cities were located following the USDA PLANTS (<http://www.plants.usda.gov>) and EOL (<http://www.eol.org>) databases (see Appendix S1 in the Supporting Information for more details on native status classification). We assigned traits to the non-native species (1634 species) to examine whether their functional attributes could help explain why non-natives contribute to homogenization or differentiation. Our choice of traits to include depended on data availability, and different criteria were used for the cultivated and spontaneous pools. For example, for the cultivated pool we selected ecosystem service-based traits that have previously been shown to be associated with homeowners' needs and preferences: growth form, plant height, longevity, presence of showy flowers, edibility, and water use (Kendal et al. 2012a, Pataki et al. 2013, Goodness et al. 2016, Avolio et al. 2018; Table 1). It has been suggested that traits related to overall

Table 1. Functional traits collected from the literature for this study.

Trait	Pool of species	Values†	Data source	% Missing data
Seed mass (mg)	Spontaneous	Continuous	BIEN, TRY	23
Plant height (m)	Cultivated and Spontaneous	Continuous	BIEN, TRY	45/23‡
Specific leaf area (mm ² /mg)	Spontaneous	Continuous	BIEN, TRY	45
Water use	Cultivated	Categorical (0.1 = very low water needs; 0.2 = low; 0.5 = moderate; 0.8 = high)	Costello and Jones (2014)	38
Longevity	Cultivated and Spontaneous	Categorical (perennial, annual/biennial*§)	USDA PLANTS, BIEN, TRY, Missouri Botanical Garden	0
Growth form	Cultivated and Spontaneous	Categorical (tree, shrub, grass, succulent, vine, herb*)	Engemann et al. (2016), USDA PLANTS, Missouri Botanical Garden	0
Photosynthetic pathway	Spontaneous	Categorical (C ₄ /CAM¶, C ₃ *)	TRY, specialized literature, expert knowledge	0
Showy flowers	Cultivated	Categorical (showy, non-showy*)	USDA PLANTS, Missouri Botanical Garden	0
Edibility	Cultivated	Categorical (edible, non-edible*)	Specialized literature, expert knowledge	0

Notes: For continuous traits, the unit of measurement is provided in parentheses following the trait name. % Missing data refers to the percentage of species in the study lacking available trait information from accessible databases. Specific references for the TRY database can be found in Appendix S3.

† Reference category used in analysis is indicated with *.

‡ Cultivated/spontaneous.

§ Annual and biennial plants were combined in the same category.

¶ C₄ and CAM plants were combined in the same category.

plant size, such as plant height and larger growth forms (usually perennial), can influence aesthetic preferences. However, there is no wide consensus on which growth forms may be universally preferred, nor whether there is a preference for a single growth form. Edible plants grown in private yards are hypothesized to be similar across locations and thus to contribute to homogenization. The presence of showy (large, colorful, and conspicuous) flowers has been correlated with preferences for attractive plants over non-flowering vegetation in a variety of settings. Plant maintenance requirements largely depend on the local conditions where the plant is grown, and thus affect homeowners' preferences. In this study, we used water use to refer to the amount of water needed to achieve an acceptable level of plant health and aesthetics. We used the Water Use Classification of Landscape Species (WUCOLS) classification method and database developed by Costello and Jones (2014) to provide a trait for individual plant water needs. The WUCOLS method and database, to our knowledge, has not been previously used to understand community assembly in urban

environments. Costello and Jones (2014) tabulated water requirement values (k_s parameter) for more than 3000 ornamental species in six different areas of California. Species were classified as presenting very low requirements (VL; $k_s < 0.10$), low requirements (L; $0.10 < k_s < 0.30$), moderate requirements (M; $0.40 < k_s < 0.60$), and high requirements (H; $0.70 < k_s < 0.90$). Average k_s values across the six different areas of California were used in this study as a proxy for plant water requirements extended to cities included in our study.

For the spontaneous pool, we selected functional traits hypothesized to be selected for or against in urban environments, including traits that facilitate species' establishment and persistence, including specific leaf area (SLA), plant height, photosynthetic pathway, longevity, growth form, and seed mass (Weiher et al. 1999, Thompson and McCarthy 2008, Williams et al. 2015; Table 1). Specific leaf area correlates with species relative growth rates, palatability, and response to nutrient and moisture gradients, plant height relates to competitive ability (particularly for light) and resource allocation, and seed mass

relates to dispersal ability. Photosynthetic pathway reflects habitat affinity (with C_4 species potentially profiting from warmer temperatures due to urban heat island effects and being more frequent in yards in arid regions), whereas growth form and longevity correlate with extinction risk (with woody perennial vegetation less likely to be entirely extirpated in yards).

We collected all functional traits from available databases: USDA PLANTS Database; BIEN database (Maitner 2017); TRY database (try-db.org; see Appendix S3 for specific references); the WUCOLS list (Costello and Jones 2014); Missouri Botanical Garden database (missouribotanicalgarden.org); Engemann et al. (2016); specialized literature; and expert knowledge (Table 1). We tested for correlations among traits using a Pearson correlation coefficient (r). Because no traits were correlated with $r > 0.55$, all traits were retained for analyses (Appendix S1: Table S2).

Data for continuous plant traits and water use were not available for some species (Table 1). Deleting species with missing data from the analysis would reduce the number of data points substantially (~45%), and probably bias the results because of the selective removal of species that were less well known. These cases were accommodated by estimating the missing values using phylogenetic information from species with available data. Some characteristics inherent to functional traits such as a strong phylogenetic trait signal and structural trade-offs between traits support statistical gap-filling of sparse trait matrices using this approach (Swenson 2014). For this, we first compared available trait data across four alternative evolutionary models (Early-Burst, Brownian motion, Ornstein-Uhlenbeck, and multivariate Ornstein-Uhlenbeck) using the R package *Rphylopars* (Goolsby et al. 2017). The best-fitting model on the basis of the lowest AIC value (i.e., Ornstein-Uhlenbeck) was then used to impute trait data (see Appendix S2 for more details on missing trait data imputation).

Although online databases that collate sampled trait data have provided a powerful tool for addressing mechanistic questions about multi-species assemblages (Thompson and McCarthy 2008, Duncan et al. 2011), 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. Thus, we used the mean value in analysis for continuous traits where multiple values occurred for any given species.

Data analysis

A final set of 171 yards was included in the analysis after removing seven households with no non-native species in their yards. For the cultivated pool, only 167 yards were included in the analysis because four yards did not contain non-native cultivated species.

We used an updated version of the Zanne (2013) phylogeny produced by Qian and Jin (2016) for all phylogenetic metrics, and we added species missing from this phylogeny at the genus level using the *congeneric.merge* function in the R package *pez* (Pearse et al. 2015). Hybrids were reduced to the genus level, and we excluded species for which there were no phylogenetic data (~1.5%) from the analysis.

To determine if a pair of yards had been homogenized or differentiated because of the introduction of non-native species, we calculated the homogenization (H) index (Qian and Ricklefs 2006, Qian et al. 2008, Lososová et al. 2012; Box 1, Fig. 1). H index ranges from -1 to 1 . Positive H index values indicate that non-native species contribute to phylogenetic differentiation. Negative H index values indicate that non-native species contribute to the phylogenetic homogenization of species assemblages. To calculate the H index, we measured pairwise phylogenetic dissimilarities in total and native species composition among yards using the *evodiss_family* function in the R package *adiv* (Pavoine 2017) and the formulas provided in Box 1. We further explored contributions of particular non-native species to the phylogenetic homogenization of yard floras (ΔJ_T in Box 1) by measuring the change in the H index when each non-native species was removed from each pairwise comparison. We repeated the same procedure independently for the cultivated and spontaneous species pools across all yards and within the seven cities. To evaluate associations between ΔJ_T and species relative frequency across all yards, we calculated Pearson correlation coefficients.

Box 1.**Homogenization index and species contribution to homogenization**

Sites can be compared in a pairwise fashion according to their composition in evolutionary units (i.e., units of the branch lengths of a phylogenetic tree) exactly the same way they can be compared based on their composition in species (Pavoine 2016). Hence, traditional species dissimilarity indices may be adapted to account for phylogenetic dissimilarities. For example, the phylogenetic equivalent of the Jaccard index (Jaccard 1901) is $evod_{Jaccard}$ (Pavoine 2016, 2017). $evod_{Jaccard}$ ranges from 0 to 1, where 0 indicates that the pair of sites are identical in terms of evolutionary units and 1 indicates that sites have no evolutionary units in common (see Pavoine (2016) for details on the formula).

Consider two sites numbered 1 and 2 (Fig. 1A), containing five native (N_i , in black) and four non-native (A_i , in red) species between the two. $evod_{Jaccard}$ (hereafter only J) can be calculated considering the whole pool of species (J_{total}) and only natives (J_{native}). These two dissimilarity indices can be further used to calculate the homogenization (H) index (Qian and Ricklefs 2006, Qian et al. 2008, Lososová et al. 2012): $H = J_{total} - J_{native}$. H index ranges from -1 to 1 . Positive H index values indicate that dissimilarity of native species is lower than dissimilarity of all species; therefore, non-native species contribute to phylogenetic differentiation. Negative H index values indicate that the introduction of non-native species contributes to the phylogenetic homogenization of species assemblages.

H index thus reflects the combined effect of all non-native species on the biotic homogenization of the two sites. However, we can calculate contributions of particular non-native species to the phylogenetic homogenization of both sites by measuring the change in H index when each non-native species is removed from the pairwise comparison. To this end, we create additional pairwise site comparisons (Fig. 1B–E) where each non-native species is removed at a time (species A_i in blue) and then recalculate H index for each pair of sites following the H index equation. The change in H index is therefore calculated as: $\Delta H_{A_i} = H_T - H_{A_i}$, where ΔH_{A_i} is the change in H index, H_T is the H index of the original pairwise comparison (Fig. 1A), and H_{A_i} is the H index of the newly created pairwise comparison without species A_i (Fig. 1B–E). Given that J_{native} is the same across all pairwise comparisons, then $\Delta H_{A_i} = \Delta J_{A_i}$, where $\Delta J_{A_i} = J_{total} - J_{A_i}$, and J_{A_i} is the $evod_{Jaccard}$ index considering all species except species A_i .

Finally, ΔJ_{A_i} can be summed up across all (n) pairwise site comparisons to obtain species A_i total contribution to phylogenetic homogenization: $\Delta J_{TA_i} = \sum_{j=1}^n (\Delta J_{A_i})_j$. In general, we refer to this term as ΔJ_T .

We used Cohen's d in R package *lsr* (Navarro 2015) as a measure of effect size when comparing the mean H index value of all yard pairwise comparisons to zero (no homogenization effect) across and within cities (Cohen's d around 0.20 = small effect, d around 0.50 = medium effect, and d around 0.80 = large effect; Cohen 1998). Unlike the t -test statistic, the effect size aims to estimate a population parameter and is not affected by the sample size. Also, we compared the same mean value of the H index for all yard pairwise comparisons to a null model to investigate whether observed homogenization could have arisen by chance. We interpreted departures from the null model as a signal that biotic homogenization was not a consequence of random stochastic processes, but rather of taxonomically selective anthropogenic factors. The null model was generated by a two-step process. First, 999 permutations

of the species community matrix were created using the R package *picante* (Kembel et al. 2010) and the independent swap algorithm (Gotelli 2000), which maintains species occurrence frequency and sample species richness. Second, 999 random H index values were obtained from the randomized community matrices and their means used for the null model. We repeated this part of the analysis for each species pool across and within cities. We calculated P -values based on a two-tailed test.

Spatial autocorrelation in ecological data is a common phenomenon as observations at closer locations are usually more similar than would be expected by chance (Legendre 1993). To account for spatial autocorrelation between the H index of pairwise comparisons between yards across cities and geographical distance, we performed Mantel correlations. Geographical distances in kilometers between each location were calculated

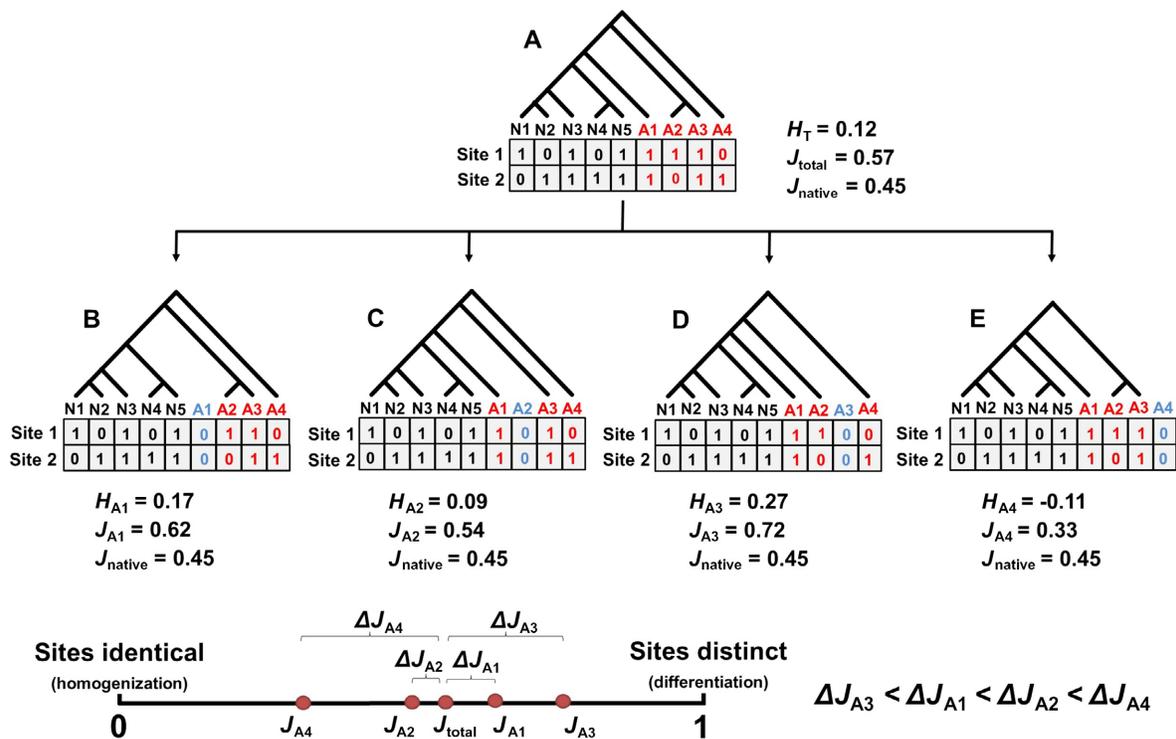


Fig. 1. Diagram exemplifying calculations of species particular contribution to phylogenetic homogenization. First, the original pairwise site comparison containing five native (N_i) and four non-native (A_i) species is transformed into four new pairwise site comparisons (B, C, D, and E) where each non-native species is removed at a time (species A_i in blue). For each pairwise site comparison, the *evoD*_{Jaccard} (J) and H index are calculated. Finally, the particular contribution of species A_i to phylogenetic homogenization is measured as ΔJ_{A_i} . In the example, two non-native species are shared between the two sites (homogenizing), and two non-native species are only present in one of them (differentiating). Also, non-native species are separated from natives in the phylogeny. As a result, non-native species contribute to a different extent to phylogenetic homogenization.

using the great-circle method in the R package fields (Nychka et al. 2017). The significances of matrix correlations were tested using a Monte Carlo permutation test with 999 permutations, using the R package ade4 (Dray and Dufour 2007).

Species cannot be assumed to be independent data points in regression models because of their phylogenetic relationship (Felsenstein 1985, Garland and Ives 2000, Ives and Zhu 2006). Therefore, we used the phylogenetic generalized least square (PGLS) method to test associations between ΔJ_T and plant traits. The analysis was performed using the gls function in R package nlme (Pinheiro et al. 2018). PGLS explicitly incorporates the expected covariance among species into a statistical model fit by generalized least

squares and allows for flexibility in the underlying evolutionary assumptions. We modeled ΔJ_T for the cultivated and spontaneous non-native pools both across and within cities using a set of eight candidate models, including (1) a null model (only the intercept term), (2) six models testing each trait separately, and (3) the full model (all traits; Appendix S4: Tables S5, S6). We excluded growth form from the within-cities analysis to guarantee an appropriate ratio between the number of observations and predictor variables. In all models, we normalized continuous predictors between 0 and 1 before being entered into the model so that the coefficient values were comparable (Zuur et al. 2007). Plant height, SLA, and seed mass were log-transformed to reduce skewness and improve the

normality of the residuals. Following Anderson (2008), we calculated the AIC_c (the sample size-corrected Akaike information criterion) values for each candidate model set and ranked them by their Akaike weights using the R package AICcmodavg (Mazerolle 2017). We used the same package to compute the standardized model-averaged coefficients.

We performed all statistical procedures in R version 3.4.1 (R Core Team 2017) and established significance at $\alpha < 0.05$.

RESULTS

There were 2417 total cultivated and spontaneous species in all the yards sampled across the seven cities, of which 1634 (67.6%) were classified as non-native in the United States (Table 2, Fig. 2). In total, 1648 were classified as cultivated, of which 1310 (79.5%) were non-native. Among the spontaneous pool (1287 species), 653 (50.7%) were classified as non-native. Within cities, the number of pooled species varied widely, from 297 species in PHX to 964 in BOS (Table 2, Fig. 2). The proportion of non-natives was highest in the three southwestern cities (LA [90.6%], SLC [85.0%], and PHX [75.4%]) and lowest in the two northeastern cities (BOS [55.7%] and BAL [59.9%]).

Across cities, mean H index values were positive for the non-native cultivated pool, indicating phylogenetic differentiation, and negative for the non-native spontaneous pool, indicating phylogenetic homogenization (Fig. 3; Appendix S5: Fig. S1). However, mean H index values had a relatively small effect size for both the cultivated

(Cohen's $d = 0.23$) and spontaneous (Cohen's $d = 0.25$) species pools. These two H indices were significantly different from their respective null models (Fig. 3). Within cities, positive mean H index values of non-native cultivated species were observed in LA, MIA, PHX, and SLC, and negative mean values were observed in BAL, BOS, and MSP (Appendix S5: Fig. S2). Mean H index values showed a relatively small effect size for SLC (Cohen's $d = 0.10$), BOS (Cohen's $d = 0.15$), and BAL (Cohen's $d = 0.20$), medium

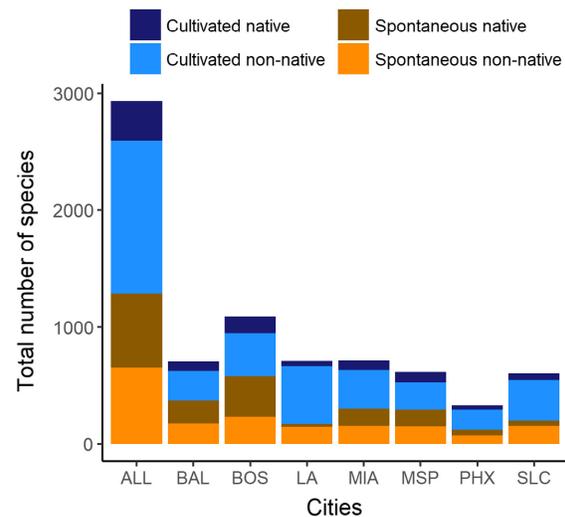


Fig. 2. Total number of native and non-native plant species in yards of the seven cities sorted by species pool (cultivated or spontaneous). ALL, across all cities; BAL, Baltimore; BOS, Boston; LA, Los Angeles; MIA, Miami; MSP, Minneapolis–Saint Paul; PHX, Phoenix; and SLC, Salt Lake City.

Table 2. Metropolitan statistical areas (cities) included in the study according to their geographic locations.

Abbreviation	City	Latitude	Longitude	Total yards	Total species	% Non-natives
BAL	Baltimore	39.3	−76.6	21	617	59.9
BOS	Boston	42.4	−71.1	30	947	55.7
LA	Los Angeles	34.1	−118.3	21	637	90.6
MIA	Miami	25.8	−80.2	24	653	68.8
MSP	Minneapolis–St. Paul	45.0	−93.3	22	518	64.6
PHX	Phoenix	33.5	−112.1	30	297	75.4
SLC	Salt Lake City	40.8	−112.0	30	506	85.0
Total				178	2417	67.6

Notes: For each city, the number of sampled yards, the total number of sampled species, and the proportion of non-natives are shown. Note that total number of species in the study does not equal the sum of the number of species within each city because the same species are frequently found in different cities. Additional information on the biome, climatic region, mean annual temperature, and rainfall of each city can be found in Appendix S4: Table S1.

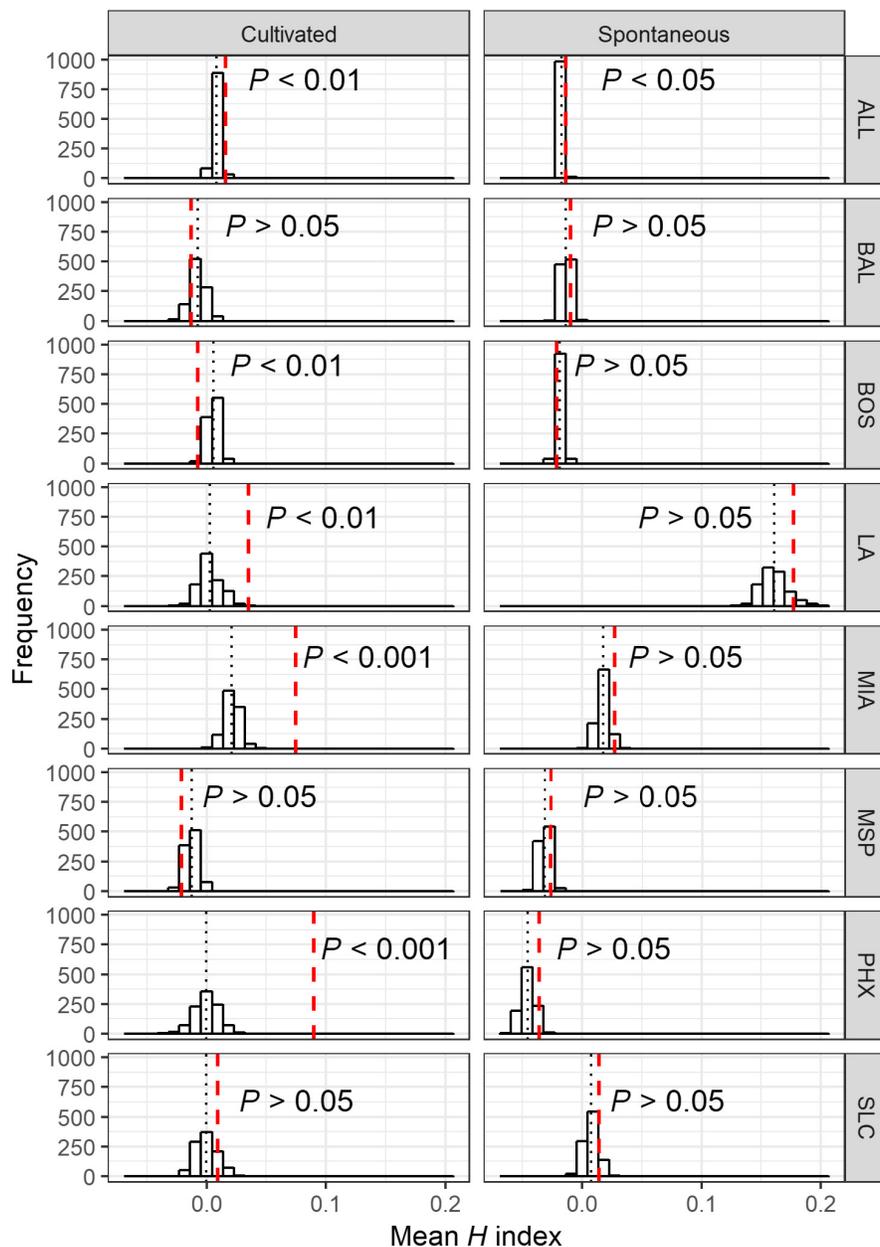


Fig. 3. Histograms of the mean homogenization (H) index based on 999 repetitions of community species matrix developed to create a null model for the cultivated and spontaneous pools of species for each site and all pairwise yard comparisons. Positive values indicate differentiation whereas negative values indicate homogenization by non-native species. Black dotted line indicates the mean value of the null distribution, and the red dashed line indicates the mean observed H index value. P -values are also provided. ALL, across all cities; BAL, Baltimore; BOS, Boston; LA, Los Angeles; MIA, Miami; MSP, Minneapolis–Saint Paul; PHX, Phoenix; and SLC, Salt Lake City.

for MSP (Cohen's $d = 0.42$), LA (Cohen's $d = 0.45$), and MIA (Cohen's $d = 0.64$), and high for PHX (Cohen's $d = 0.73$) (Appendix S5: Fig. S2). These H indices were significantly

different from their respective null model except for BAL, MSP, and SLC (Fig. 3). For the spontaneous pool, LA, MIA, and SLC had positive mean H index values of non-native species, and

Table 3. Model-averaged estimates and unconditional SE (in parentheses) for each trait predicting non-native species contribution to homogenization (ΔJ_T) for the cultivated pool within the seven cities.

Traits	ALL	BAL	BOS	LA	MIA	MSP	PHX	SLC
Edible	-0.01 (0.15)	0.01 (0.02)	0.03 (0.03)	-0.01 (0.01)	-0.03 (0.02)	0.02 (0.02)	-0.18 (0.11)	0.00 (0.03)
Growth form								
Grass	-1.15 (0.33)	0.00 (0.06)	-0.03 (0.13)	-0.07 (0.02)	0.01 (0.06)	0.04 (0.12)	-0.95 (0.18)	-0.09 (0.10)
Shrub	-0.07 (0.12)	-0.03 (0.02)	-0.03 (0.03)	-0.01 (0.01)	-0.02 (0.02)	0.03 (0.02)	-0.08 (0.10)	0.00 (0.03)
Succulent	-0.06 (0.21)	-0.07 (0.06)	-0.06 (0.09)	-0.01 (0.01)	-0.01 (0.05)	0.07 (0.05)	-0.12 (0.16)	-0.02 (0.07)
Tree	-0.01 (0.17)	0.00 (0.03)	-0.04 (0.05)	0.01 (0.01)	-0.03 (0.02)	0.02 (0.03)	-0.05 (0.10)	0.05 (0.04)
Vine	-0.02 (0.21)	-0.01 (0.05)	0.02 (0.06)	-0.01 (0.01)	-0.02 (0.03)	0.04 (0.04)	-0.13 (0.19)	0.03 (0.05)
Perennial	-0.06 (0.15)	-0.02 (0.02)	0.00 (0.03)	-0.01 (0.01)	0.00 (0.03)	0.00 (0.02)	-0.20 (0.14)	0.04 (0.03)
Plant height	0.46 (0.25)	0.00 (0.04)	-0.05 (0.06)	0.03 (0.02)	-0.06 (0.04)	-0.03 (0.03)	0.06 (0.23)	0.01 (0.05)
Showy flowers	-0.18 (0.10)	-0.01 (0.02)	-0.02 (0.03)	-0.02 (0.01)	0.00 (0.02)	-0.01 (0.02)	-0.11 (0.09)	-0.01 (0.02)
Water use	-0.09 (0.26)	-0.07 (0.05)	-0.11 (0.08)	0.00 (0.02)	0.02 (0.05)	-0.03 (0.04)	0.03 (0.19)	-0.05 (0.07)

Notes: Estimates whose 95% unconditional confidence intervals do not overlap zero are shown in bold. Positive estimates promote differentiation, while negative estimates promote homogenization. See Table 2 for corresponding reference categories in categorical variables. ALL, across all cities; BAL, Baltimore; BOS, Boston; LA, Los Angeles; MIA, Miami; MSP, Minneapolis–Saint Paul; PHX, Phoenix; and SLC, Salt Lake City.

Table 4. Model-averaged estimates and unconditional SE (in parentheses) for each trait predicting non-native species contribution to homogenization (ΔJ_T) for the spontaneous pool within the seven cities.

Traits	ALL	BAL	BOS	LA	MIA	MSP	PHX	SLC
Growth form								
Grass	-1.27 (0.59)							
Shrub	0.59 (0.41)							
Tree	0.01 (0.54)							
Vine	0.39 (0.52)							
Perennial	-0.08 (0.25)	-0.04 (0.02)	-0.06 (0.06)	0.10 (0.04)	0.09 (0.05)	-0.03 (0.04)	0.35 (0.18)	0.30 (0.07)
C_4 /CAM	-0.28 (0.41)	0.01 (0.02)	0.08 (0.07)	-0.18 (0.07)	0.06 (0.06)	0.04 (0.04)	-0.43 (0.05)	-0.20 (0.14)
Plant height	1.93 (0.56)	0.01 (0.06)	-0.10 (0.09)	0.05 (0.09)	0.23 (0.10)	0.07 (0.11)	0.79 (0.43)	0.43 (0.14)
Seed mass	1.51 (0.67)	0.11 (0.05)	-0.14 (0.12)	0.00 (0.09)	0.07 (0.13)	-0.02 (0.08)	0.97 (0.37)	0.26 (0.25)
SLA	-0.47 (1.82)	-0.16 (0.10)	-0.24 (0.34)	-0.08 (0.15)	0.07 (0.17)	-0.11 (0.12)	-1.52 (0.46)	-0.21 (0.20)

Notes: Estimates whose 95% unconditional confidence intervals do not overlap zero are shown in bold. Positive estimates promote differentiation, while negative estimates promote homogenization. We excluded growth form from the within-cities analysis to guarantee an appropriate ratio between the number of observations and predictor variables. See Table 2 for corresponding reference categories in categorical variables. ALL, across all cities; BAL, Baltimore; BOS, Boston; LA, Los Angeles; MIA, Miami; MSP, Minneapolis–Saint Paul; PHX, Phoenix; SLC, Salt Lake City; and SLA, specific leaf area.

BAL, BOS, MSP, and PHX had negative mean values (Appendix S5: Fig. S2). Mean H index values showed a relatively small effect size for SLC (Cohen's $d = 0.13$) and BAL (Cohen's $d = 0.32$), medium for MIA (Cohen's $d = 0.48$), PHX (Cohen's $d = 0.47$), and BOS (Cohen's $d = 0.66$), and high for MSP (Cohen's $d = 0.76$) and LA (Cohen's $d = 0.94$). These H indices were not different from their respective null model (Fig. 3). None of the Mantel tests comparing H index matrices and the geographical distance matrices were significant.

Among cultivated non-native species, those that contributed the most to the homogenization of yards across cities were *Cynodon dactylon*, *Rosa* hybrid, *Hosta* hybrid, *Festuca arundinacea*, and *Hemerocallis* hybrid, and those that contributed the most to differentiating yards were *Buxus sempervirens*, *Berberis thunbergii*, *Vitis* spp., *Lamprocapnos spectabilis*, and *Cycas revoluta* (Appendix S4: Tables S3, S4). Among spontaneous non-native species, those that contributed the most to the homogenization of yards across cities were *Taraxacum campyloides*, *Acer platanoides*, *Cynodon dactylon*, *Poa*

pratensis, and *Trifolium repens*, and those that contributed the most to the differentiation of yards were *Celastrus orbiculatus*, *Chelidonium majus*, *Commelina communis*, *Berberis thunbergii*, and *Rhamnus cathartica*. Non-parametric correlations between species contributions to phylogenetic homogenization (ΔJ_T) and species relative frequency in yards were significant for both the cultivated (Pearson's $r = -0.46$; $P < 0.001$) and the spontaneous pool (Pearson's $r = -0.60$; $P < 0.001$).

Models within two AIC_c points of the top model predicting ΔJ_T for the cultivated non-native species across cities included plant height, showy flowers, growth form, and the null model (Appendix S4: Tables S5, S6). For the spontaneous pool, only the model including plant height was ranked within two AIC_c points. Non-native grasses significantly contributed to the phylogenetic homogenization of the cultivated and spontaneous pools (model-averaged confidence intervals did not overlap zero; Table 3). Shorter and smaller-seeded spontaneous non-native plants also significantly contributed to yard homogenization across cities (Table 4).

Within cities, traits of non-native species that significantly promoted homogenization among the cultivated pool included grass growth form (in LA and PHX) and showy flowers (LA) (Table 3). For the spontaneous pool, traits of non-natives that significantly differentiated yard floras within cities included seed mass (BAL and PHX), plant height (MIA and SLC), and perennality (LA and SLC; Table 4). In contrast, traits of non-natives that promoted homogenization for the same pool included C_4 photosynthetic pathway (LA and PHX) and SLA (PHX).

DISCUSSION

Phylogenetic homogenization of U.S. yard floras

Understanding the extent to which non-native species contribute to the homogenization of biodiversity in urban areas is of great interest because globalization has contributed to the intentional and unintentional movement of species and because urbanization has increased globally in the last century and is projected to continue to increase. Here, we compared homogenization effects of cultivated and spontaneous non-native plant species on U.S. yard floras. As predicted, cultivated non-native species

promoted phylogenetic differentiation of the cultivated yard floras across cities, while spontaneous non-native species promoted the phylogenetic homogenization of the spontaneous yard flora. Within cities, cultivated and spontaneous non-natives consistently promoted homogenization in the three northern cooler cities: BAL, BOS, and MSP.

Our findings further show that despite the significant effect of non-natives on the phylogenetic homogenization of yard floras at the continental scale, they are far from being completely uniform because of the cultivation and spread of non-native plants (Cohen's $d < 0.25$). Similarly, biotic homogenization within cities was also limited; in particular, cultivated and spontaneous non-native species strongly differentiated yard floras in PHX and LA, respectively, when compared to the other cities. Although other studies have reported mixed effects of non-native species on urban biotic homogenization at regional scales (McKinney 2004, 2006, Kühn and Klotz 2006, Qian et al. 2008, Lososová et al. 2012, 2016, La Sorte 2014, Ricotta et al. 2014), none examined their effect in highly managed urban areas such as private yards and at the local (within-metropolitan region) scale.

Our result that spontaneous non-native species contributed to homogenization of flora across the United States supports the idea that, at local scales, cultivated species are more yard-specific, whereas spontaneous species are more cosmopolitan. Most of the non-native spontaneous species recorded in our study correspond to weeds that were typically introduced to the United States decades ago (Ridley 1930) and that have had sufficient time to occupy most of the suitable habitats and to spread across larger geographical areas. Likewise, in Europe, archaeophytes (species introduced before AD 1500) have been found to homogenize urban floras (La Sorte et al. 2007, Lososová et al. 2012, Ricotta et al. 2014). These cosmopolitan weeds tend to tolerate a wide range of environmental conditions and are thus able to invade available niches within broad climatic limits. The contribution of widespread weeds to the homogenization of yard floras was also supported by the significant correlation between our H index and the relative frequency of spontaneous non-native species in yards (Appendix S4: Table S3). The convergence

between the observed mean H index and that of the null model within each city also highlights the relevance of random colonization processes in determining the homogenization of the spontaneous pool at local scales. However, across cities the significant ($P = 0.034$) deviation of the observed mean H index from that of the null model indicates that homogenization as a result of the dispersal and establishment of weeds in yards across the country has not been completely random.

For the cultivated pool, the observed mean H index also deviated from the null model both across and within some of the cities (BOS, LA, MIA, and PHX), which indicates that variation in homogenization patterns, and thus species composition, cannot be explained solely by habitat qualities, species natural dispersion, and macroclimatic variables. Rather, the geographic context of the studied yards must be also taken into account. For example, non-native cultivated species are strongly subject to local temperature and homeowners' preferences and management (Williams 2009, Kendal et al. 2012b, Aronson et al. 2016). Moreover, because they often have a limited potential range, they tend to increase floristic differentiation at the continental scale. In the three warmer southern cities (LA, MIA, and PHX), there was a clear tendency for cultivated non-native species to differentiate yard floras. In contrast, in the cooler northern cities (MSP, BOS, and BAL) cultivated non-native species tended to homogenize yard floras (note that in SLC, non-native species promoted differentiation although with the lowest effect size across all cities; Cohen's $d < 0.15$). The proportion of non-native species was also consistently higher in the southern than in the northern cities (excluding again SLC; see Table 2, Fig. 2). These findings reinforce the idea that latitudinal and climatic factors influence regional urban floras (Williams 2009, Aronson et al. 2016, Jenerette 2016, Padullés Cubino 2018), and suggest that warmer urban areas have a larger available pool of horticultural non-native species adapted to local conditions than the available pool of natives. This pattern could reflect modern consequences of anthropogenic activities operating at an increasingly global extent that potentially promote the introduction of non-native species from all over the world (La Sorte and McKinney 2006). Although

previous studies have shown that biotic dissimilarities increase with geographic distance (McKinney 2004, Qian et al. 2008, Lososová et al. 2012), our H index showed no sign of spatial autocorrelation. Furthermore, our results contradicted the idea that biotic homogenization increases with increasing non-native species richness (McKinney 2004), at least in urban yards at the city scale.

Plant traits promoting phylogenetic homogenization

The consequences of environmental and anthropogenic influences on biotic homogenization at different scales were also reflected in plant functional traits, especially among the spontaneous pool. For example, among non-native spontaneous species, shorter, smaller-seeded plants and grasses (both widespread across the seven cities; see Appendix S4: Table S4) were significantly associated with homogenization of yard floras across cities. Frequent disturbance, commonly associated with urban areas (e.g., yard weeding), may favor shorter species with small seeds that reproduce and disperse more efficiently (Gilbert 1989). For example, spontaneous tree saplings are often removed by yard owners because these species are perceived as undesirable, untidy, or potentially dangerous (Kirkpatrick et al. 2007). Furthermore, seed mass of non-native spontaneous species has been found to be negatively related to their frequency in urban environments, such that smaller-seeded species occur more frequently (Thompson and McCarthy 2008), likely reflecting the trade-off between seed size, seed production, and dispersal distance. In contrast, species with greater seed mass have been proposed to perform better in stressful environments that are subject to drought, competition for light or water, deep shade, or burial (Westoby et al. 2002).

Literature on biotic homogenization suggests that the common features of urban areas create conditions that select for species with similar traits and life histories. Yet, our study also supports the idea that particular characteristics of individual cities—such as development history, human demographics, and cultural attributes—impose strong constraints on plant traits (McKinney 2006, Groffman 2014) that cause divergent patterns of association between plant traits and

homogenization among cities. In fact, for the spontaneous pool, no plant trait consistently promoted homogenization in more than two cities. For example, annual plants only promoted homogenization in LA and SLC, and *C₄/CAM* species only did so in LA and PHX.

Grasses were found to homogenize cultivated and spontaneous yard floras across cities, indicating that the similarity of lawn species across yards is driven, at least in part, by the influence of non-natives (Wheeler 2017). This pattern supports the idea that lawn landscaping styles across the residential United States have caused ecological homogenization (McKinney 2006, Groffman 2014, Wheeler 2017) that maintains similar ecosystems across a broad range of ecoregions. In this regard, the non-native turfgrass that contributed the most to the homogenization of yard floras and that was present in all seven cities was Bermuda grass (*Cynodon dactylon*), a medium- to fine-textured warm-season grass that spreads by rhizomes and stolons and has excellent heat, drought, and salt tolerance. Previous research assessing lawn and overall plant composition in the same seven cities concluded that species in the same four cooler northern cities (BAL, BOS, MSP, and SLC) were generally similar to each other, and species in the same three warmer cities (LA, MIA, and PHX) were distinct from the cool cities but less similar to each other (Wheeler 2017, Pearse 2018). Here, we have expanded on these findings by reporting that non-native grasses, despite being taxonomically different across regions, may have similar phylogenetic homogenizing effects on yard floras, as shown, for example, in the two warmest cities (LA and PHX).

Plant height was the best model predicting homogenization of the cultivated flora, with taller non-native cultivated plants causing differentiation across cities, further indicating that these species are more city-specific than shorter species. In this regard, a majority of trees in the southwestern U.S. urban areas were shown to be non-native (Nowak 2012, Avolio et al. 2018) because the original vegetation prior to urbanization was predominantly shrubland. Pincetl et al. (2013) quantified the tree species available for purchase in Los Angeles nurseries throughout the 20th century and found that there has been an increasing range of commercially available

tree species sold by local nurseries, which may help explain this differentiation potential.

Showy flowers of non-native plants were also among the top-ranked traits in models for species contribution to homogenization. Accordingly, flowering is a conspicuous characteristic that is highly aesthetically regarded and preferred over non-flowering vegetation in private landscapes (Kendal et al. 2012a, Goodness et al. 2016). Although preferences for flower size, shape, and color may vary along gardener's personal landscape styles, our results suggest that flower showiness of non-native plants promoted homogenization of yard floras not only at the continental scale but also at the regional scale (particularly in LA), revealing the importance of aesthetics in determining ecological processes in urban landscapes.

Our water use index derived from Costello and Jones' (2014) WUCOLS list showed no effect on the homogenization of yard floras. This indicates that non-native plants with different levels of water requirement were evenly distributed across all yards, providing further evidence that irrigation and management practices might be compensating for variation in precipitation and thereby reducing climatic stress (Kendal et al. 2012b, Padullés Cubino 2018). Plant cold hardiness, although not included in this study because of unavailability of consistent data, is also a major factor that explains species distributions in urban environments at the continental scale (Jenerette 2016) and may influence the role that cultivated non-natives play in differentiating the flora across cities.

Although our study provides evidence that plant functional traits help explain phylogenetic homogenization of yard floras, the cities included in our analysis contained different numbers of sampled yards (between 21 and 30), which might have favored representation of certain locally abundant species and ultimately their contribution to biotic homogenization/differentiation. In contrast, some non-native species might have not been detected in our vegetation surveys, as shown by non-saturated accumulation curves (Appendix S4: Fig. S3). We believe that such limitations, although not affecting our conclusions, might be addressed by a more exhaustive and

balanced sampling of yard floras at the continental scale.

CONCLUSIONS

Our study compared the degree of phylogenetic homogenization among yards at different spatial scales, discriminated between cultivated and spontaneous plant species pools, and specifically examined the role that non-native species play. Our results demonstrated that homogenization of yard floras by non-native species was prevalent for the spontaneous (weedy) flora but was context- and scale-dependent. Although non-native spontaneous species generally increased homogenization among yards across cities, non-native cultivated species tended to differentiate yard floras at the same scale. Importantly, such patterns had a limited effect on the mean value of the homogenization index, thus suggesting that urban yard floras at the continental scale still maintain their local idiosyncrasy and are far from being completely phylogenetically uniform; yet they have enough in common floristically to keep them from being completely heterogeneous. Furthermore, contrasting patterns of biotic homogenization by non-natives among and within cities suggest that local environmental and anthropogenic factors played a significant role in determining species pools. Hence, homogenization must be assessed for each particular location and species pool and further research should elucidate how homogenization varies across multiple environmental and anthropogenic gradients.

The inclusion of locally measured plant functional traits in the study of urban biotic homogenization may help overcome the lack of available trait information from accessible databases—as in this study—and enhance our understanding of the processes affecting ecosystem function. An assessment of the best way of computing and interpreting homogenization measures is also required to establish comparable results. Lists of species promoting homogenization and/or differentiation at different scales can inform urban planners and land managers interested in influencing the configuration of floras in urban landscapes in a context of global change. Further research is needed to elucidate the linkages between residents' preferences for

vegetation and landscaping styles, and the plant functional traits that promote biotic homogenization.

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LITERATURE CITED

- Alberti, M., C. Correa, J. M. Marzluff, A. P. Hendry, E. P. Palkovacs, K. M. Gotanda, V. M. Hunt, T. M. Apgar, and Y. Zhou. 2017. Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences* 114:8951–8956.
- Anderson, D. R. 2008. *Model based inference in the life sciences: a primer on evidence*. Springer, New York, New York, USA.
- Aronson, M. F., C. H. Nilon, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A. Goddard, A. K. Hahs, C. Herzog, and M. Katti. 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97:2952–2963.
- Avolio, M. L., D. E. Pataki, T. L. E. Trammell, and J. Endter-Wada. 2018. Biodiverse cities: The nursery industry, homeowners, and neighborhood differences drive urban tree composition. *Ecological Monographs* 88:259–276.
- Bigirimana, J., J. Bogaert, C. De Cannière, M.-J. Bigendako, and I. Parmentier. 2012. Domestic garden plant diversity in Bujumbura, Burundi: role of the socio-economical status of the neighborhood and alien species invasion risk. *Landscape and Urban Planning* 107:118–126.

- Cadotte, M. W., R. Dinnage, and D. Tilman. 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93:S223–S233.
- Cayuela, L., A. Stein, and J. Oksanen. 2017. Taxonstand: taxonomic Standardization of Plant Species Names. R package version 2.0. <https://CRAN.R-project.org/package=Taxonstand>
- Ceplová, N., Z. Lososová, D. Zelený, M. Chytrý, J. Danihelka, K. Fajmon, D. Láníková, Z. Preislerová, Z. Řehořek, and L. Tichý. 2015. Phylogenetic diversity of Central European urban plant communities: effects of alien species and habitat types. *Preslia* 87:1–16.
- CLARITAS. 2013. CLARITAS PRIZM Market Segmentation. <http://www.claritas.com/MyBestSegments/Default.jsp>
- Cohen, J. 1998. *Statistical power analysis for the behavioral sciences*. Second edition. Erlbaum, Mahwah, New Jersey, USA.
- Cook, E. M., S. J. Hall, and K. L. Larson. 2012. Residential landscapes as social-ecological systems: a synthesis of multi-scalar interactions between people and their home environment. *Urban Ecosystems* 15:19–52.
- Costello, L. R., and K. S. Jones. 2014. *Water Use Classification of Landscape Species, WUCOLS IV*. University of California, Cooperative Extension, Sacramento, California, USA.
- Dray, S., and A.-B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22:1–20.
- Duncan, R. P., S. E. Clemants, R. T. Corlett, A. K. Hahs, M. A. McCarthy, M. J. McDonnell, M. W. Schwartz, K. Thompson, P. A. Vesik, and N. S. G. Williams. 2011. Plant traits and extinction in urban areas: a meta-analysis of 11 cities: plant traits and extinction in cities. *Global Ecology and Biogeography* 20:509–519.
- Engemann, K., B. Sandel, B. Boyle, B. J. Enquist, P. M. Jørgensen, J. Kattge, B. J. McGill, N. Morueta-Holme, R. K. Peet, and N. J. Spencer. 2016. A plant growth form dataset for the New World. *Ecology* 97:3243–3243.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Garland, T., and A. R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155:346–364.
- Gilbert, O. L. 1989. *The ecology of urban habitats*. Chapman and Hall, London, UK.
- Goodness, J., E. Andersson, P. M. L. Anderson, and T. Elmquist. 2016. Exploring the links between functional traits and cultural ecosystem services to enhance urban ecosystem management. *Ecological Indicators* 70:597–605.
- Goolsby, E. W., J. Bruggeman, and C. Ané. 2017. Rphylopars: fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution* 8:22–27.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. *Science* 319:756–760.
- Groffman, P. M., et al. 2014. Ecological homogenization of urban USA. *Frontiers in Ecology and the Environment* 12:74–81.
- Groffman, P. M., et al. 2017. Ecological homogenization of residential macrosystems. *Nature Ecology & Evolution* 1:191.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions: conceptual frameworks for biological invasions. *Ecology Letters* 14:407–418.
- Ignatieva, M. E., and G. H. Stewart. 2009. Homogeneity of urban biotopes and similarity of landscape design language in former colonial cities. Pages 399–421 in A. K. Hahs, J. H. Breuste, and M. J. McDonnell, editors. *Ecology of cities and towns: a comparative approach*. Cambridge University Press, Cambridge, UK.
- Ives, A. R., and J. Zhu. 2006. Statistics for correlated data: phylogenies, space, and time. *Ecological Applications* 16:20–32.
- Jaccard, P. 1901. Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Bulletin de la Société vaudoise des sciences naturelles* 37:547–579.
- Jenerette, G. D., et al. 2016. Climate tolerances and trait choices shape continental patterns of urban tree biodiversity: toward a macroecology of urban trees. *Global Ecology and Biogeography* 25:1367–1376.
- Kembel, S. W., D. D. Ackerly, S. P. Blomberg, W. K. Cornwell, P. D. Cowan, M. R. Helmus, H. Morlon, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kendal, D., K. J. H. Williams, and N. S. G. Williams. 2012a. Plant traits link people's plant preferences to the composition of their gardens. *Landscape and Urban Planning* 105:34–42.
- Kendal, D., N. S. G. Williams, and K. J. H. Williams. 2012b. A cultivated environment: exploring the global distribution of plants in gardens, parks and streetscapes. *Urban Ecosystems* 15:637–652.

- Kirkpatrick, J. B., G. D. Daniels, and T. Zagorski. 2007. Explaining variation in front gardens between suburbs of Hobart, Tasmania, Australia. *Landscape and Urban Planning* 79:314–322.
- Knapp, S., L. Dinsmore, C. Fissore, S. E. Hobbie, I. Jakobsdottir, J. Kattge, J. Y. King, S. Klotz, J. P. McFadden, and J. Cavender-Bares. 2012. Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology* 93:S83–S98.
- Kuebbing, S. E., M. A. Nuñez, and D. Simberloff. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation* 160:121–129.
- Kühn, I., and S. Klotz. 2006. Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biological Conservation* 127:292–300.
- La Sorte, F. A., et al. 2014. Beta diversity of urban floras among European and non-European cities: beta diversity of urban floras. *Global Ecology and Biogeography* 23:769–779.
- La Sorte, F. A., and M. L. McKinney. 2006. Compositional similarity and the distribution of geographical range size for assemblages of native and non-native species in urban floras. *Diversity and Distributions* 12:679–686.
- La Sorte, F. A., M. L. McKinney, and P. Pyšek. 2007. Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange: intercontinental compositional similarity. *Global Change Biology* 13:913–921.
- Larson, K. L., et al. 2016. Ecosystem services in managing residential landscapes: priorities, value dimensions, and cross-regional patterns. *Urban Ecosystems* 19:95–113.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Lososová, Z., M. Chytrý, J. Danihelka, L. Tichý, and C. Ricotta. 2016. Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences. *Journal of Vegetation Science* 27:452–459.
- Lososová, Z., M. Chytrý, I. Kühn, O. Hájek, V. Horáková, P. Pyšek, and L. Tichý. 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology, Evolution, and Systematics* 8:69–81.
- Lososová, Z., M. Chytrý, L. Tichý, J. Danihelka, K. Fajmon, O. Hájek, K. Kintrová, D. Láníková, Z. Otýpková, and V. Řehořek. 2012. Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation* 145:179–184.
- Maitner, B. S., et al. 2017. The BIEN R package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution* 9:373–379.
- Marco, A., T. Dutoit, M. Deschamps-Cottin, J.-F. Mauffrey, M. Vennetier, and V. Bertaudière-Montes. 2008. Gardens in urbanizing rural areas reveal an unexpected floral diversity related to housing density. *Comptes Rendus Biologies* 331:452–465.
- Mazerolle, M. J. 2017. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. <http://CRAN.R-project.org/package=AICcmodavg>
- McKinney, M. L. 2004. Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions* 6:495–504.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247–260.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.
- Navarro, D. J. 2015. Learning statistics with R: a tutorial for psychology students and other beginners. University of Adelaide, Adelaide, South Australia, Australia.
- Nowak, D. J. 2012. Contrasting natural regeneration and tree planting in fourteen North American cities. *Urban Forestry & Urban Greening* 11:374–382.
- Nychka, D., R. Furrer, J. Paige, and S. Sain. 2017. fields: tools for spatial data. R package version 9.0. www.image.ucar.edu/fields
- Olden, J. D., and N. L. Poff. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *American Naturalist* 162:442–460.
- Padullés Cubino, J., et al. 2018. Drivers of plant species richness and phylogenetic composition in urban yards at the continental scale. *Landscape Ecology*. <https://doi.org/10.1007/s10980-018-0744-7>
- Pataki, D. E., H. R. McCarthy, T. Gillespie, G. D. Jenerette, and S. Pincetl. 2013. A trait-based ecology of the Los Angeles urban forest. *Ecosphere* 4:72.
- Pavoine, S. 2016. A guide through a family of phylogenetic dissimilarity measures among sites. *Oikos* 125:1719–1732.
- Pavoine, S. 2017. adiv: analysis of diversity. R package version 1.1. <https://CRAN.R-project.org/package=adiv>
- Pearse, W. D., et al. 2018. Homogenization of plant diversity, composition, and structure in North American urban yards. *Ecosphere* 9:e02105.
- Pearse, W. D., M. W. Cadotte, J. Cavender-Bares, A. R. Ives, C. M. Tucker, S. C. Walker, and M. R. Helmus.

2015. *pez*: phylogenetics for the environmental sciences. *Bioinformatics* 31:2888–2890.
- Pincetl, S., S. S. Prabhu, T. W. Gillespie, G. D. Jenerette, and D. E. Pataki. 2013. The evolution of tree nursery offerings in Los Angeles County over the last 110 years. *Landscape and Urban Planning* 118:10–17.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. *nlme*: linear and Nonlinear Mixed Effects Models. R package version 3.1-131.1. <https://CRAN.R-project.org/package=nlme>
- Polsky, C., et al. 2014. Assessing the homogenization of urban land management with an application to US residential lawn care. *Proceedings of the National Academy of Sciences of USA* 111:4432–4437.
- Qian, H., and Y. Jin. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology* 9:233–239.
- Qian, H., M. L. McKinney, and I. Kühn. 2008. Effects of introduced species on floristic similarity: comparing two US states. *Basic and Applied Ecology* 9:617–625.
- Qian, H., and R. E. Ricklefs. 2006. The role of exotic species in homogenizing the North American flora. *Ecology Letters* 9:1293–1298.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricotta, C., L. Celesti-Grapow, I. Kühn, G. Rapson, P. Pyšek, F. A. La Sorte, and K. Thompson. 2014. Geographical Constraints Are Stronger than Invasion Patterns for European Urban Floras. *PLoS ONE* 9: e85661.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Company, Kent, UK.
- Smith, R. M., K. Thompson, J. G. Hodgson, P. H. Warren, and K. J. Gaston. 2006. Urban domestic gardens (IX): composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation* 129:312–322.
- Swenson, N. G. 2014. Phylogenetic imputation of plant functional trait databases. *Ecography* 37:105–110.
- Thompson, K., and M. A. McCarthy. 2008. Traits of British alien and native urban plants: traits of urban plants. *Journal of Ecology* 96:853–859.
- Trammell, T. L. E., D. E. Pataki, J. Cavender-Bares, P. M. Groffman, S. J. Hall, J. B. Heffernan, S. E. Hobbie, J. L. Morse, C. Neill, and K. C. Nelson. 2016. Plant nitrogen concentration and isotopic composition in residential lawns across seven US cities. *Oecologia* 181:271–285.
- US Census Bureau. 2018. Historical Census of Housing Tables. <https://www.census.gov/hhes/www/housing/census/historic/units.html>
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468–478.
- Weiher, E., A. Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10:609–620.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Wheeler, M. M., et al. 2017. Continental-scale homogenization of residential lawn plant communities. *Landscape and Urban Planning* 165:54–63.
- Williams, N. S. G., et al. 2009. A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology* 97:4–9.
- Williams, N. S. G., A. K. Hahs, and P. A. Vesk. 2015. Urbanisation, plant traits and the composition of urban floras. *Perspectives in Plant Ecology, Evolution and Systematics* 17:78–86.
- Zanne, A. E., et al. 2013. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506:89–92.
- Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. *Analysing ecological data*. Springer, New York, New York, USA.

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