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Homogenization of plant diversity, composition, and structure in North American urban yards

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Abstract. Urban ecosystems are widely hypothesized to be more ecologically homogeneous than natural ecosystems. We argue that urban plant communities assemble from a complex mix of horticultural and regional species pools, and evaluate the homogenization hypothesis by comparing cultivated and spontaneously occurring urban vegetation to natural area vegetation across seven major U.S. cities. There was limited support for homogenization of urban *diversity*, as the cultivated and spontaneous yard flora had greater numbers of species than natural areas, and cultivated phylogenetic diversity was also greater. However, urban yards showed evidence of homogenization of *composition* and *structure*. Yards were compositionally more similar across regions than were natural areas, and tree density was less variable in yards than in comparable natural areas. This homogenization of biodiversity likely reflects similar horticultural source pools, homeowner preferences, and management practices across U.S. cities.

Key words: aridity; ecosystem services; functional traits; phylogenetic diversity; plants; urban ecology.

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INTRODUCTION

The majority of humans now live in urban environments, and both urban area and population size are projected to increase (UN 2014), creating a pressing need to understand ecological processes within cities. Despite increasing urbanization, its potential impacts on community assembly of organisms, biodiversity, and ecosystem function are unclear—urban ecosystems were the least-studied in a recent review of over 11,500 assemblages (Newbold et al. 2015). Compounding this uncertainty, any urban flora includes both human-cultivated and spontaneously occurring (establishing without human assistance) species, each of which is subject to distinct ecological and human influences (Knapp et al. 2012). Although there is evidence of high biodiversity within cities (McKinney 2006, Grimm et al. 2008, Knapp et al. 2008, Newbold et al. 2015), few studies have disentangled these ecological and human influences that drive urban biodiversity. This knowledge gap makes it difficult to interpret comparisons of diversity, both among different urban assemblages and when comparing urban and natural assemblages.

Urban plant communities arise from the ecological assembly processes that operate in natural ecosystems (e.g., habitat filtering—Mayfield et al. 2005, Kraft et al. 2015; and species interactions—HilleRisLambers et al. 2012), as well as human desires and influences (Aronson et al. 2016, Jenerette et al. 2016). We propose a conceptual framework describing how various filters act on the natural continental and horticultural industry plant species pools that together constitute the source pool for the assembly of urban plant communities (Fig. 1). We consider a species pool to be the set of species from which assemblages of a given habitat type (an urban yard, a beech forest, etc.) are composed. In this manuscript, we treat the term "flora" as synonymous with "plant species pool" and consider the "horticultural flora" to be the species sold by the horticultural industry. We focus on residential landscapes (i.e., yards), under the assumption that residents have the greatest agency over, and frequency of interactions with, their own yards, making yards a dynamic product of urban change. Yards are also a major U.S. land-use type; turf grass (which is only one component of yards) potentially covers an area three times larger than any irrigated crops (approximately 163,800 km^2, or 1.6% of the surface area of the United States; Milesi et al. 2005). We acknowledge that our framework draws strength from a large literature of existing frameworks that consider ecological assembly as a series of filters operating across different spatial scales (Ricklefs 1987, Williams et al. 2009, Vellend 2010, Aronson et al. 2016). Our presentation differs in its consideration of different species pools (species *cultivated* by humans in yards, *spontaneous* species that grow in yards without direct human intervention, and species in *natural* areas; see Fig. 1), its consideration of different aspects of urban vegetation (Box 1), and its empirical application. We concentrate on the species pools from which communities are assembled, and do not address local processes that may be operating within communities. We also acknowledge that there is variation in community and habitat type within urban environments; while we feel our framework is applicable to many types of such community, in this manuscript we focus on urban yards.

The major sources of urban flora are subject to contrasting ecological filtering processes that we describe below, each of which varies with spatial scale and likely by geographic region (Fig. 1). We define a region as a bounded area within which assemblages containing species from one or more different species pools can be found. Just as species pool definitions can vary with habitat definitions, regions can also vary within defined ranges: It is just as valid to talk of a region surrounding Boston as it is to talk of the continent of North America. Species pools change across regions: There is no reason to assume that the horticultural pool of plants sold in Boston would be the same

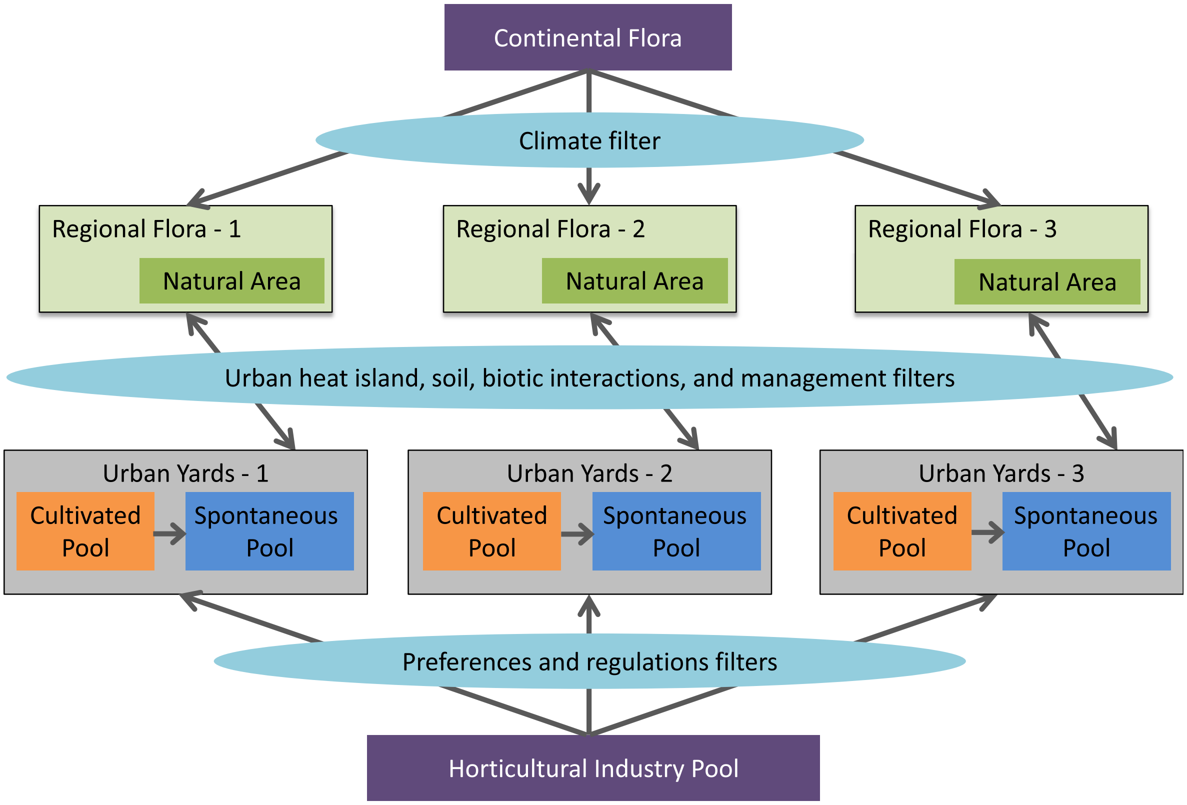


Fig. 1. Conceptual overview of urban community assembly. Community assembly of the urban yard flora is driven by the movement of plants from the regional flora and the horticultural industry pool through contrasting filters. The regional flora are subsets of the continental flora, filtered by climate and other environmental drivers, and include natural species pools that have emerged through a combination of dispersal and in situ speciation. The urban spontaneous flora assembles through dispersal from the regional flora, excluding species that cannot disperse into or persist in the urban environment given the urban abiotic and biotic pressures. The spontaneous flora also includes species that have escaped human cultivation and are able to propagate and establish on their own. The cultivated urban flora are largely subsets of the species available from the horticultural industry, filtered by human preferences and regulations that limit planting of invasive species. Species from the horticultural pool can assemble and become established in the regional and continental floras through migration into and out of the urban spontaneous pool. We show here three regions with each type of pool for brevity; our framework is applicable to any number of regions.

as that in Baltimore. The horticultural flora is influenced by accessibility of plant material, propagation constraints, and human preferences and is further filtered by regulation and management processes. In contrast, the naturally assembled continental and regional floras are influenced by historical biogeographic processes and filtered by climate, pollution, soil, and other abiotic constraints (Weiher and Keddy 2001, Wiens et al. 2010, Liu et al. 2011, Ricklefs 2004). Similarly, cultivated and spontaneous pools within the regional and urban flora are also subject to contrasting dispersal and filtering processes within the urban environment. For example, cultivated species are likely filtered by human preferences and management (Marco et al. 2008, Knapp and Wittig 2012) and often receive additional resources (e.g., water and fertilizer). Spontaneously growing species are likely also filtered by human management (e.g., mowing, weeding, fertilizing, and irrigating; Dahmus and Nelson 2014) and broader urban environmental conditions (e.g., pollution and climate; Arnfield 2003). However, cultivated species may "escape" cultivation to become part of

Box 1.

Homogenization hypotheses

Understanding urban vegetation in the context of surrounding natural areas requires an understanding of the different filters and processes that affect the assembly of cultivated and spontaneous species (Fig. 1). Below, we examine three components of urban vegetation—*diversity, composition*, and *structure*—and hypothesize how each might vary across the species pools we outline in our framework (Fig. 1). The major cities of North America span broad environmental gradients of temperature, precipitation, light availability, and many other factors. We focus here on water stress (aridity), which is a major axis across which our seven cities are relatively evenly spread. Moreover, it can be quantified as a composite of both temperature and precipitation (*Materials and methods*), unifying two major axes of variation in one biologically meaningful variable. There is some empirical evidence that human irrigation patterns are homogenized across the United States (Polsky et al. 2014), making aridity an environmental gradient across which homeowners may have now homogenized conditions with respect to original natural areas.

Diversity

Human transport and management (e.g., irrigation) of vegetation enables cultivated species to overcome natural dispersal and establishment barriers, such that we expect the species richness of the cultivated pool to be higher than that of urban spontaneous or nearby natural pools. Plant species richness of all species pools should positively correlate with moisture availability, consistent with well-established relationships between species richness and climate (Currie 1991, Wiens and Donoghue 2004, Fine 2015). If regions show homogenized diversity, we would expect metrics of diversity such as species richness to be the same among regions (compare with homogenization of composition, below). If humans prefer variation and can irrigate to overcome water limitation, we might expect the cultivation of a wide diversity of plant lineages to increase phylogenetic diversity in cultivated pools. Were humans cultivating a more limited subset of the phylogeny of plants throughout urban areas in comparison with natural areas, this would represent a form of phylogenetic homogenization (i.e., metrics of phylogenetic diversity would be the same).

Composition

If climate is a strong filter on the composition of spontaneous and natural area species pools, we would expect the species and phylogenetic clades of pools to vary across regions. Within regions, however, these pools are drawn from the regional flora and are subject to the same (or similar) climate filters, so we expect some compositional similarity within regions. By contrast, if human preferences, transport, or management (e.g., irrigation) relaxes the constraints imposed by climate and dispersal barriers, we expect cultivated pools to be homogenized: They should be more similar to one another among regions than the spontaneous or natural area pools. Thus, we predict that human preferences and management decisions should lead to greater similarity among cultivated species pools. We expect the spontaneous pool to be intermediate in composition (measured through the Sørensen and Phylosørensen indices; Dice 1945, Sørensen 1948, Bryant et al. 2008) to the cultivated and natural pools if it receives propagules from both pools and/or facilitates dispersal between the cultivated pool and the natural areas pool.

Structure

Given similar human preferences (e.g., for savanna-like yards; Balling and Falk 1982, Orians and Heerwagen 1992, Falk and Balling 2009) and management to mitigate climatic constraints (e.g., irrigation), we expect cultivated pools to have similar structures—as measured by tree height and density—across regions. By contrast, we suggest climate filters will lead to divergence in the structure of natural area pools, with taller trees and greater tree density in wetter regions. Spontaneous pools could be intermediate between natural and cultivated pools if species are being actively exchanged between them. Lower variance in structural attributes (greater structural similarity) among cultivated and spontaneous pools compared to natural pools would suggest less variation in urban vegetation structure and represent a form of homogenization. Urban pools may also deviate from natural pools due to management practices. For example, we might expect to find plants with smaller, thicker, and more lobed leaves in the natural species pool in arid climates, but watering in urban yards could cause a deviation from this pattern, such that the flora in urban yards is more similar across cities than the natural vegetation. Smaller leaf surface area is associated with arid environments because of the reduced evaporation and water loss associated with small leaves. A higher perimeter per area would be expected in warmer climates because it is associated with either smaller leaves or more lobed leaves, both of which reduce boundary layer resistance and allow more rapid leaf cooling (Sack et al. 2003).

We consider species' functional traits to be structural, not compositional, characteristics of assemblages in this manuscript. This is because there are many species (and phylogenetic clades) with the same functional traits, such that yards with different species *compositions* could have the same aggregate functional traits. Thus, there is not a unique mapping of trait structure onto species composition. In order to maximize consistency within structural categories, we therefore designate functional traits as aspects of *structure*.

spontaneous urban, and surrounding natural, areas, and thus join the wider regional species pool (Mack and Lonsdale 2001, Knapp et al. 2008). Natural areas surrounding cities are thus mixed assemblages derived from these separate species pools and the interactions between them.

Urban areas are frequently described as *homogenized* (i.e., urban areas in different regions are more similar to each other than the natural areas that they replace; Kühn and Klotz 2006, McKinney 2006, Grimm et al. 2008, Lososová et al. 2012, Ricotta et al. 2012*b*, Groffman et al. 2014), and it is widely accepted that urban species richness is often higher than that in natural areas (Pyšek 1993, Kühn et al. 2004, Pautasso 2007, Grimm et al. 2008). Yet there are many components to urban biodiversity besides species richness (Purvis and Hector 2000), and it is unclear which of these components are subject to homogenizing pressures, what factors contribute to such pressures, and how we might define homogenization empirically. We consider three potential aspects of urban vegetation that might exhibit homogenization—*diversity*, *composition*, and *structure*—and hypothesize how urbanization might influence these different aspects for both the cultivated and spontaneous species pools (see also Box 1). In describing homogenization, we focus on urban cultivated and spontaneous species pools in relation to natural area pools. Homogenization might be seen as a reduction in the number of lineages represented in urban areas, more similar species compositions, or lesser variation across urban areas in structural aspects of the vegetation such as overall density and height of vegetation. Contrasting urban and natural species pools is key to our framework: The extent of similarity among natural systems reflects natural climatic, ecological, and biogeographic processes, and it is critical to test whether urban systems show greater similarity than expected given these factors. Natural assemblages vary along both micro- and macro-scale environmental gradients (Levin 1992, Chave 2013); any response to gradients (or lack thereof) within urban systems should therefore be placed within the context of comparable surveys of the surrounding vegetation (see Box 1 for specific hypotheses).

Here, we present results from a survey of urban plant diversity, composition, and structure in residential parcels (yards) in seven major U.S. cities (Boston, Baltimore, Los Angeles, Miami, Minneapolis–St. Paul, Salt Lake City, and Phoenix). Our survey covered broad environmental gradients and included comparable natural reference sites, permitting us to compare natural area, spontaneous, and cultivated species pools in urban yards. By empirically evaluating our framework, we shed light on the human contributions to ecological assembly processes in urban systems that influence biodiversity and ecosystem function.

Materials and Methods

The work described here was a component of a collaborative research project addressing the ecological homogenization of America (Groffman et al. 2014, Polsky et al. 2014, Trammell et al. 2016). Within each of seven major U.S. metropolitan areas (Boston, Baltimore, Los Angeles, Miami, Minneapolis–St. Paul, Salt Lake City, and Phoenix), we identified 21–30 urban household yards and 3–6 natural area sites. Each of these major U.S. cities, and the sites sampled surrounding them form a region in our study. To select yards for study, we used PRISM and CLARITAS data to identify households occupied by single families, with front and back yards, and owned by someone over the age of 18. Of these, 9480 households agreed to participate in a related study (Polsky et al. 2014), and of the 5797 who agreed to take part in a follow-up, we randomly selected participants to take part in this study (see Hall et al. 2016 for more details). The rationale underlying the selection of natural sites is outlined in Table 1. Within each metropolitan area, we collected the vegetation (species presence/absence), tree structural trait, and leaf functional trait datasets as described below. All software packages described below are R (v3.2.2; R Core Team 2015) packages unless otherwise stated.

Vegetation (species presence/absence) data

An exhaustive presence/absence survey was conducted in the yard of each household. The entire area of each yard was surveyed except where there was an unmanaged vegetation or woodland/woodlot component, which was sampled with a 2 m wide transect across the full yard or 100 m, whichever was shorter. Species were designated as spontaneous or cultivated based

Table 1. Natural area site descriptions for each metropolitan area.

Region	Natural habitat description
Baltimore	Mature (over 75-yr-old) forests with native species, covering the range of soil types in the region
Boston	Mature (roughly 100-yr-old) hardwood oak-dominated forests typical of the region, spanning a latitudinal gradient
Los Angeles	The largest (perhaps only) contiguous area of remnant coastal sage scrub in the region
Miami	Remnant natural upland areas within city boundaries, but not the surrounding wetland areas, capturing variation in elevation across coastal upland habitats
Minneapolis–St. Paul	The three major ecosystem types in the area known to pre-date European settlement: mesic sugar maple–basswood forest on moraine, oak savanna on sandy outwash, and prairie (tall-grass and bluff) on moraine
Phoenix	Native Sonoran Desert (never with agriculture or development) contiguous with state or federal desert land
Salt Lake City	The largest region of remnant coastal sage scrub in the region

Notes: Sampling times were chosen according to regions' flowering times. We emphasize that while the sampling was standardized across all natural comparison sites (see main text), general characteristics of the sites varied across the different regions (e.g., the age of each site was not necessarily the same). This reflects the idiosyncratic nature of human settlement and environmental modification throughout North America, and it is difficult to find any areas within North America (particularly that are near to major cities with populations numbering in the millions) that have not been affected by human population growth (Mann 2005).

on homeowner interviews and observations of placement; a given species could be documented as both spontaneous and cultivated if different individuals of that species fell into different categories (this is to be expected if, as Fig. 1 shows, species are exchanged between pools). Land use and land-use history were considered in the designation. For example, species in woodlots and unmanaged parts of yards were generally considered spontaneous.

Between three and six natural areas were designated in each region, chosen to represent similar ecological regions and the topographic and edaphic features of each urban region. Within each natural area, eight transects were established and each was treated as a separate sample. This resulted in a total of 24–48 transects (100 × 2 m), which is comparable to the household sample size. All vegetation in view from within the transect area was exhaustively recorded for species presence/absence. The locations and directions of the transects within the reference areas were randomly assigned in advance using GIS mapping. While best efforts were made to select natural sites representative of vegetation before urbanization, there are few (if any; Mann 2005) parts of North America not influenced by humans. Table 1 briefly outlines the habitat types chosen as representative for each natural area.

Species names were matched to The Plant List (http://www.theplantlist.org) version 1.1, using Taxonstand (Cayuela et al. 2012). The Zanne et al. (2014) phylogeny was used for all phylogenetic metrics, and species missing from this tree were bound in at the genus level using pez's congeneric.merge (Pearse et al. 2015). Hybrids and species for which there were no phylogenetic data were excluded from the analyses.

Tree structural trait data

For trees, data for number of individuals, diameter at breast height, height, and crown projected area for all trees in yards <0.1 ha were collected, following protocols developed by the U.S. Forest Service for use with the UFORE models in their "iTree" application (although we do not present iTree output here; http://www.itreetools.org). For yards >0.1 ha, 8 m radius plots were randomly established using GIS mapping at the ratio of 5 per hectare, rounded down to the nearest whole number. In natural sites, three 8 m radius plots were established per reference site for a total of 9–18 plots per region. No tree structural trait data were collected in Salt Lake City due to fieldwork constraints. We emphasize that these are data about the structure of the yards themselves, not the species or individual trees themselves; we present and analyze the density of trees and average heights of trees within yards.

Leaf functional trait data

Leaves were collected from three to five individuals per species, from three to five different households per city, whenever possible. One to three leaves were collected per individual, depending on the size of the plant. Sun leaves were collected, if possible. All new species encountered in the reference sites were sampled; leaves were collected for three to five individuals per species across all reference sites, if possible. Leaves from a single individual were placed in a coin envelope placed on cardboard spacers fastened with rubber bands to press the leaves flat and absorb moisture prior to shipping to the University of Minnesota. No leaf functional trait data were collected in Salt Lake City due to fieldwork constraints; samples were collected in Phoenix, but were damaged in transit and could not be analyzed.

We developed a Python and R pipeline (stalkless; http://willpearse.github.io/stalkless) to record individual leaf surface area, perimeter length, and leaf compactness (perimeter^2/area). Briefly, we segmented the individual leaves present within each scanned image, identifying darker areas as objects (in this case leaves) with reference to the mean intensity of the image plus twice the standard deviation of the image's intensity. Using R, candidate leaf images containing too much background noise or other objects in the scanner were removed by checking the dimensions of the images. A preliminary Fourier analysis (using eFourier in Momocs; Bonhomme et al. 2014) isolated remaining non-leaf images, grouping them together in a hierarchical cluster analysis of a Euclidean distance matrix of the Fourier parameters. We manually checked, verified, and supervised this process, which all stalkless users are strongly encouraged to do. These steps left us with images of 8908 leaves from 754 species (out of a total 2224 in the dataset) for the final analysis.

Statistical analysis

We conducted separate analyses of *diversity*, *composition*, and *structure*. For all analyses, we ignored abundances in sampled assemblages and treated a species as present in a pool if it was recorded at least once in an assemblage associated with that pool type. Our seven cities lie along a major aridity gradient throughout continental North America. To quantify this gradient, Palmer Drought Severity Index (PDSI) data were downloaded from the National Centers for Environmental Information (Vose et al. 2014) for each state; the mean of the monthly values for each state across the period January 2000–December 2012 was used as an index of long-term climatic conditions in the broad regions within which the assembly of our species pools took place. Palmer Drought Severity Index is a composite temperature–precipitation index that assesses how arid a particular region is; negative values indicate drier conditions (drought) and larger positive values wetter conditions. Our analysis is focused on broad species pools, not particular assemblages, and as such, we make use of environmental data averaged across each region in order to better account for the general patterns within a region. We use human-defined state boundaries, not uniformly sized regions centered on each set of sampled regions, because our analysis is focused around understanding variation in environments created by humans in comparison with natural regions. We note, however, that preliminary investigations found no qualitative difference in the environmental values calculated for each region depending upon different ways of measuring study area.

*Diversity.—*Species richness and phylogenetic diversity (mean phylogenetic distance; MPD) were calculated for each pool using picante (Kembel et al. 2010). We regressed the diversity metrics against aridity (as indicated by PDSI) in each city, using mixed-effects models where the aridity gradient and habitat pool were fixed effects and region was a random effect (using lme4 and lmerTest; Bates and Maechler 2010, Kuznetsova et al. 2016). To test for differences in the variation of the diversity metrics within pools among regions, we used Levene's tests as implemented in *car* (Fox and Weisberg 2011).

*Composition.—*We calculated the Sørensen's index of species compositional difference (using vegan; Oksanen et al. 2013) and the Phylosørensen's metric of phylogenetic distance (also using picante; Bryant et al. 2008, Kembel et al. 2010) for all the parcels. We modeled the Sørensen's distances among all pools as a function of whether those pools were of the same type (e.g., spontaneous vs. cultivated) or region (e.g., Boston vs. Phoenix). We then performed a non-metric multidimensional scaling analysis to visualize distances among the pools (constrained to two dimensions, also using vegan; Oksanen et al. 2013).

*Structure.—*We analyzed four structural metrics: tree height, tree density (total number of trees divided by vegetative parcel area), leaf surface area, and leaf perimeter:area ($\log_{10}$-transformed). We obtained medians of each of the structural attribute either across all parcels in which a particular species pool was measured (for tree density and height) or across all individuals measured (for leaf surface area and perimeter:area). We then treated and analyzed these pool-level aggregates in exactly the same way as we analyzed the diversity metrics above. For the purposes of our tree structural metrics, we treated all trees in urban areas as cultivated (i.e., none were spontaneous).

RESULTS

Diversity

In support of our hypothesis (Box 1), species richness was greater in the cultivated pool than in the spontaneous pool, and the spontaneous pool had higher species richness than the natural area pool (Fig. 2a, c). In partial support of our hypothesis, both the spontaneous and cultivated pools had higher species richness in the less arid regions, while richness of the natural species pool remained constant across regions (Fig. 2a). There was no evidence of homogenization of species richness across regions: Species richness was no less variable among cities for the cultivated and spontaneous species in yards than for the natural area species. Despite higher species richness of cultivated species in yards, phylogenetic diversity (MPD) was greater in the cultivated pool (Fig. 2c, d), although it did not vary across the aridity gradient (Fig. 2b). Thus, species in the cultivated pools appear to be drawn from more lineages than species in the natural areas. Full statistical support for these trends is given in Appendix S1.

Composition

In support of our hypotheses (Box 1), species and phylogenetic composition of the cultivated and spontaneous species in yards were more similar across regions than in the natural area pools (Fig. 3), which is evidence of compositional homogenization in urban yards.

Structure

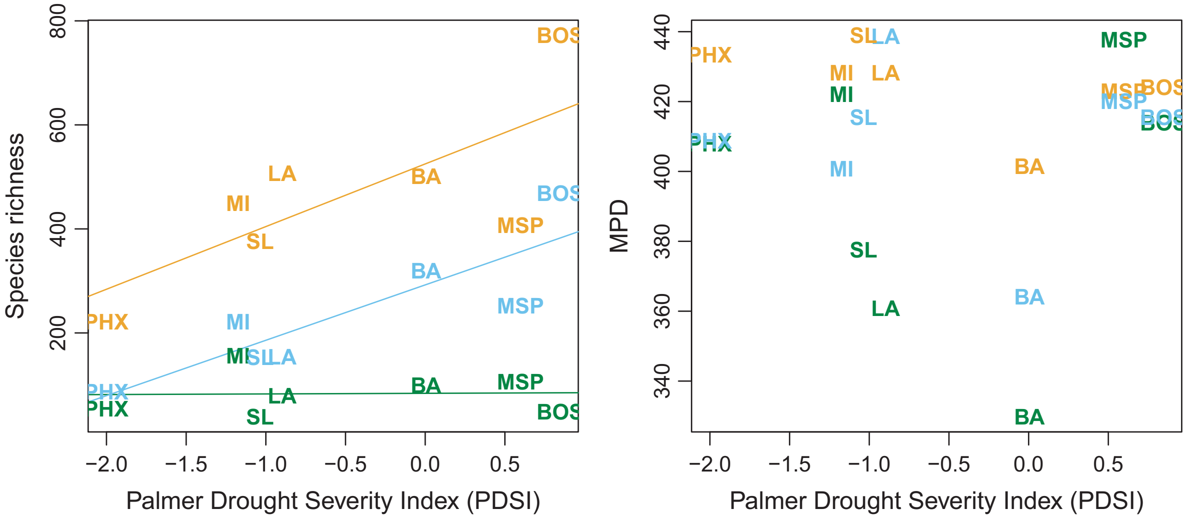
As expected, the ratio of leaf perimeter to surface area significantly decreased across the PDSI gradient (higher ratios at lower, drier values of the index; Fig. 4). There was no significant interaction between species pool and PDSI in overall perimeter:area, suggesting both cultivated and natural species responded to the aridity gradient similarly. However, in contrast to our hypotheses (Box 1), no other structural metrics (tree height, density, and leaf surface area) varied across the PDSI gradient (Fig. 4). Equally, there were no significant differences in variance in the structural metrics between habitat pools (Fig. 5). However, in the natural surroundings of Salt Lake City and Los Angeles there were no trees whatsoever and there were very few trees in natural areas around Phoenix, while yards in these regions had tree densities greater than zero. Thus, yards are qualitatively more similar in tree density across regions than natural areas, evidence of homogenization of vegetation structure.

DISCUSSION

Urban plant assemblages are typically described as similar to one another, or "homogenized" (McKinney 2006, Grimm et al. 2008, Groffman et al. 2014). Taking a species pool-based approach to plant diversity, we have confirmed that the composition of cultivated and, to a lesser degree, spontaneous urban plants is more similar among urban areas than among comparable natural reference areas. Despite this, cultivated species are more phylogenetically distant to each other than natural area species. Finally, tree density has a tendency to be more similar in yards than in natural areas across regions. However, despite management actions such as irrigation, aspects of plant structure (perimeter:area) in urban areas can vary across an aridity gradient, and, as measured by leaf surface area (a structural metric), natural and urban plant pools are indistinguishable. Below we discuss these results, and argue that by distinguishing among plant diversity, structure, and composition, both variation and homogenization can be detected within North American urban flora. We emphasize, however, that our empirical results are based on data collected within urban yards, and not other habitats or land-use categories within cities (and not, e.g., urban forests; sensu Nock et al. 2013).

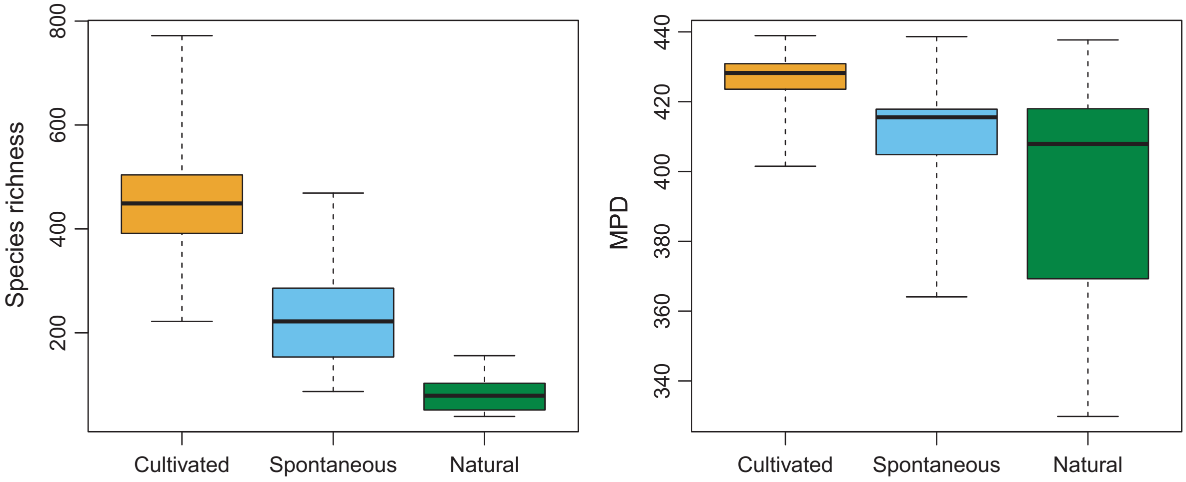
Diversity

Consistent with other studies (reviewed in Pickett et al. 2001, Grimm et al. 2008), we found that urban vegetation, in terms of both the cultivated



(a) Species richness

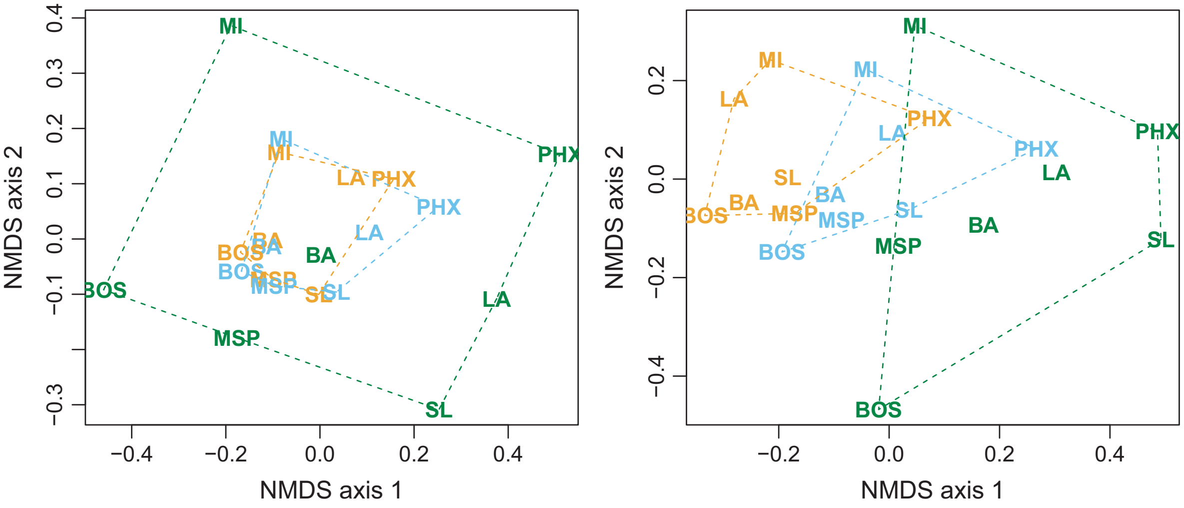
(b) Mean Phylogenetic Distance



(c) Species richness (boxplot)

(d) Mean Phylogenetic Distance (boxplot)

Fig. 2. Diversity results. Regressions of species richness (a; number of species) and mean phylogenetic distance (MPD; b) against the aridity gradient (higher values of Palmer Drought Severity Index [PDSI] indicate wetter conditions). The three species pools are represented by color (cultivated species in yards, natural area species, and spontaneous species in yards in orange, green, and blue, respectively) and the regions themselves with abbreviations (Boston, Baltimore, Los Angeles, Miami, Minneapolis–St. Paul, Phoenix, and Salt Lake City as BOS, BA, LA, MI, MSP, PHX, and SL, respectively). There is support for significant differences in species richness among the three pools ($t_{9.986} = 46.50$, $P \leq 0.0001$), and a significantly different response to the aridity gradient in the natural pool compared to the cultivated and spontaneous pools ($t_{9.986} = -2.83$, $P = 0.012$). There was no support for change in MPD across the aridity gradient ($t_{8.72} = -0.154$, $P = 0.88$), but MPD was significantly higher in the cultivated pool ($t_{12.00} = -2.86$, $P = 0.014$). Full mixed-effects model results are given in Appendix S1. Boxplots of the distributions of species richness (c) and MPD (d) in the three habitat pools (cultivated, natural, and spontaneous). The whiskers on the boxplots represent the limits of the data and the boxes the inter-quartile range. There is no evidence for differences in variance across the species pools in species richness (Levene's test $F_{2,18} = 1.71$, $P = 0.21$) or MPD $F_{2,18} = 0.03$, $P = 0.98$). Apparent differences in variance in the figure are likely driven by non-normality of the data, which the Levene's test is not sensitive to.



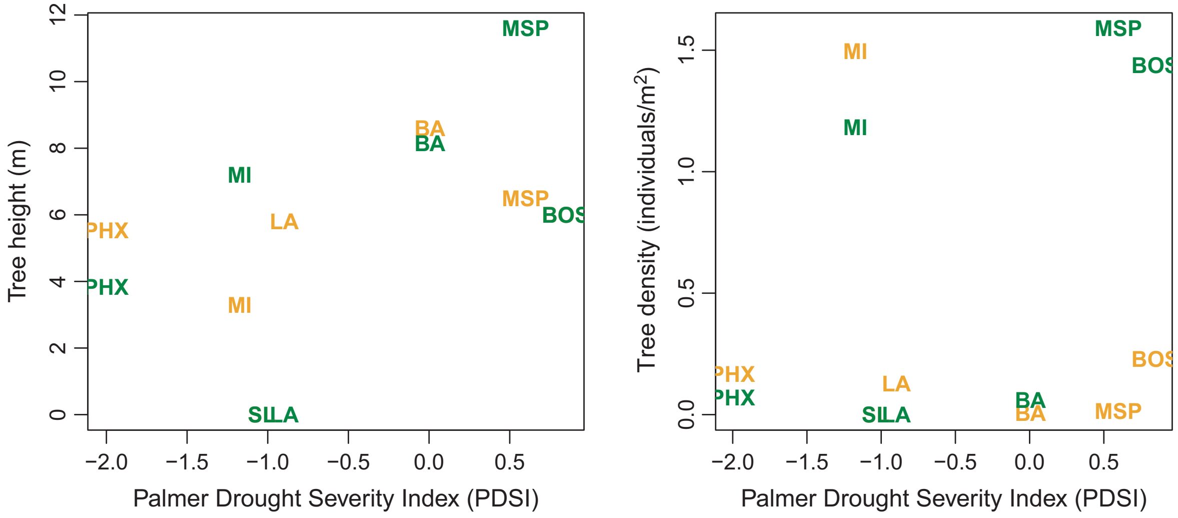
(a) Sørensen's distance

(b) Phylosørensen's distance

Fig. 3. Composition results. Two axes of ordination of species (a; Sørensen's distance) and phylogenetic (b; Phylosørensen's distance) compositions across regions and species pools. The three pools are represented by color (cultivated, natural, and spontaneous in orange, green, and blue, respectively) and the regions themselves with abbreviations (Boston, Baltimore, Los Angeles, Miami, Minneapolis–St. Paul, Phoenix, and Salt Lake City as BOS, BA, LA, MI, MSP, PHX, and SL, respectively). Dashed lines represent convex hulls drawn around all the cities within a species pool. There is strong statistical support for an interaction between differences in pools and region under comparison in both species ($F_{11,\ 141} = 14.74$, $r^2 = 0.54$, $P < 0.0001$) and phylogenetic ($F_{11,\ 141} = 8.48$, $r^2 = 0.0.40$, $P < 0.0001$) structure. Cultivated and spontaneous pools are more similar across regions than natural area pools, and in all cases, pools in the same geographical area are more similar than pools across a geographical region (Appendix S1). As discussed in the text, these figures are interpretative guides only; they are likely affected by artifacts from compressing dissimilarity into two dimensions for printing.

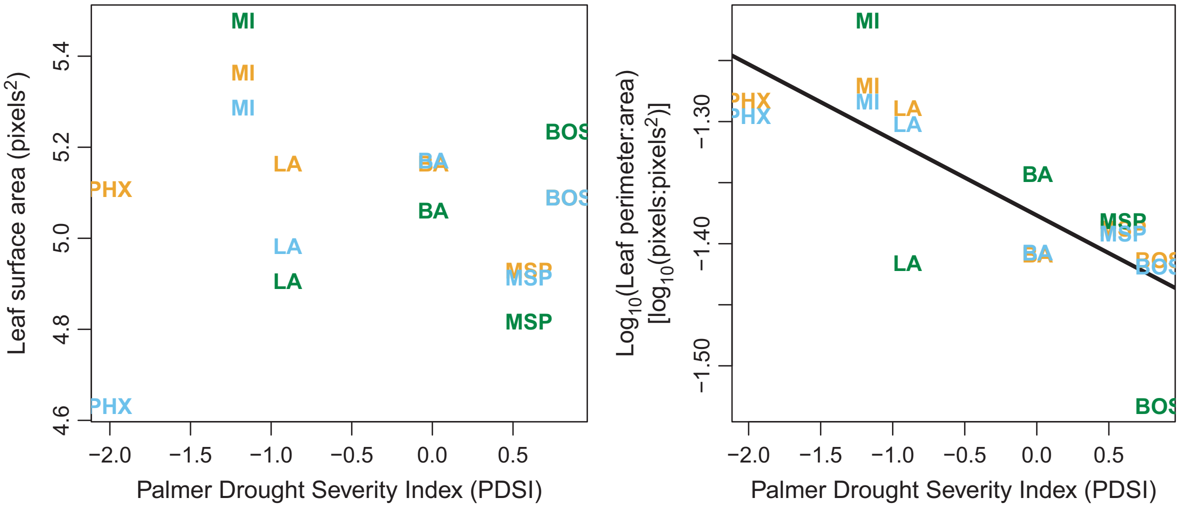
and spontaneous pools of species, had greater species richness than the natural areas (Fig. 2). This result is despite removing hybrids from our analyses, which are almost exclusively cultivated and so would only further increase the richness of the cultivated pool. However, phylogenetic diversity (MPD) was greatest within the cultivated pool, suggesting that the species humans cultivate come from distant sections of the tree of life. If, as seems likely to us, this reflects human preferences for variation in conserved traits such as floral complexity and variation, it could allow species within yards to respond favorably to future environmental stressors (sensu Laliberté and Legendre 2010, Díaz et al. 2013). This (and other lines of evidence; Ricotta et al. 2009, Knapp et al. 2012, Ricotta et al. 2012*a*, Ceplová et al. 2015) suggests that the concept of homogenization with respect to the diversity of species in cities needs to be subtly refined.

Surprisingly, the species richness of the natural pools across the aridity gradient showed no relationship with the PDSI, while richness of the cultivated and spontaneous pools increased as aridity decreased (Fig. 2). Despite evidence for homogenization of lawn management, including irrigation, across the United States (Polsky et al. 2014), cultivated and spontaneous species richness responded to the aridity gradient (Fig. 2). That we found change along the aridity gradient suggests that human management interacts with climate to shape cultivated and spontaneous species pools in urban areas (Williams et al. 2009, Aronson et al. 2016). Multiple environmental gradients across North America drive patterns of species diversity (O'Brien et al. 2000); overcoming each of these gradients may require time, effort, and money that homeowners are unwilling to spend (although we emphasize that we have not analyzed homeowner preferences here).



(a) Tree height

(b) Tree density



(c) Leaf surface area

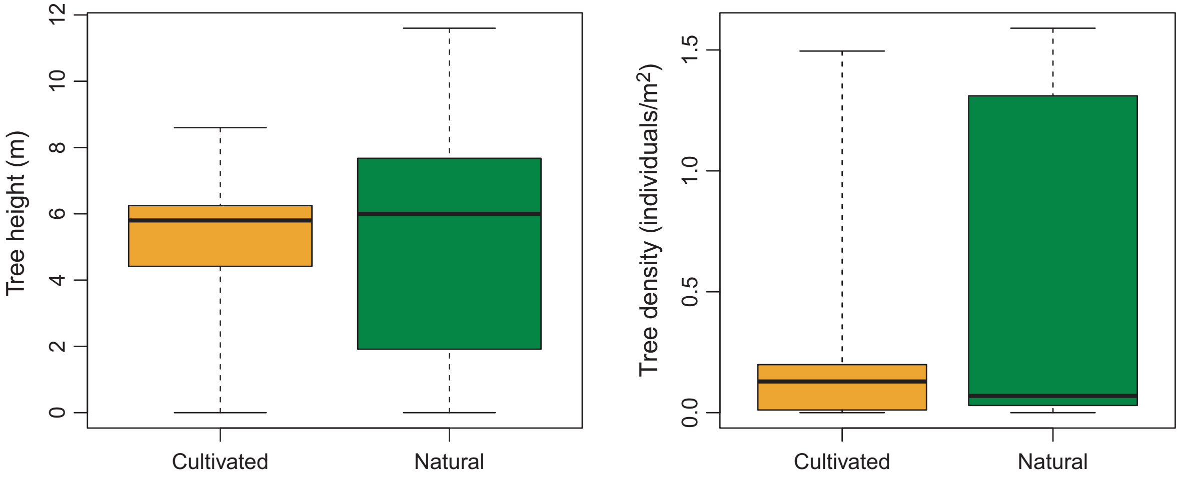
(d) Leaf perimeter:area

Fig. 4. Structure results. Regressions of tree height (a), tree density (b), leaf surface area (c), and leaf perimeter:area ratio (d) against the aridity gradient (higher values of Palmer Drought Severity Index [PDSI] indicate wetter conditions). The three species pools are represented by color (cultivated, natural, and spontaneous in orange, green, and blue, respectively) and the regions themselves with abbreviations (Boston, Baltimore, Los Angeles, Miami, Minneapolis–St. Paul, Phoenix, and Salt Lake City as BOS, BA, LA, MI, MSP, PHX, and SL, respectively). While $\log_{10}$(perimeter:area) significantly changed across the gradient ($t_{4.43} = -3.90$, $P = 0.015$), there were no other statistically significant differences either across the aridity gradient or among species pools. Note that neither Los Angeles nor Salt Lake City had any trees in their natural pools. See Appendix S1 for full mixed-effects model results.

Nursery stock might be limited in more arid regions if there are fewer species capable of thriving in xeric environments, although we lack systematic data on nursery inventories.

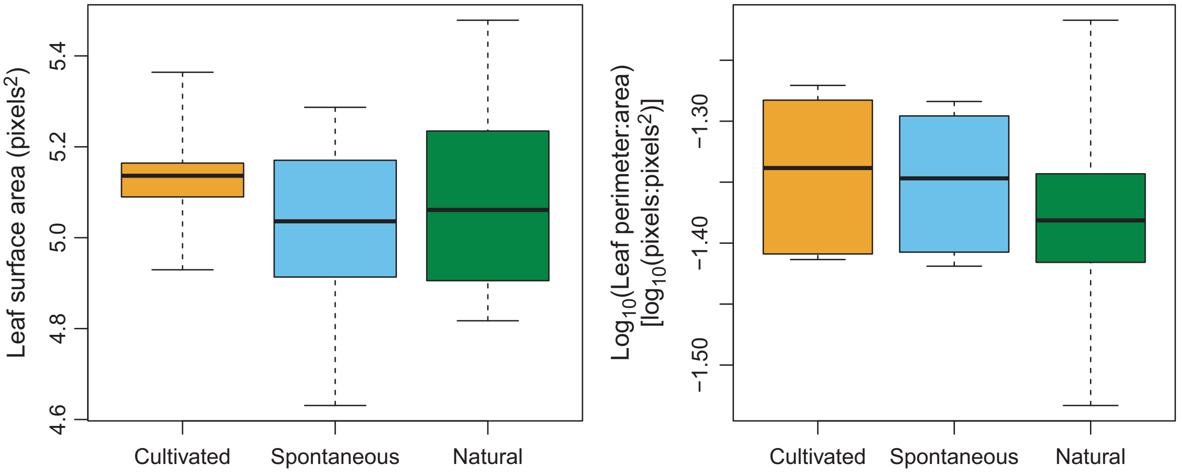
Composition

There is strong evidence that the cultivated and spontaneous species pools in yards are homogenized across regions relative to the natural pool in



(a) Tree height

(b) Tree density



(c) Leaf surface area

(d) Leaf perimeter:area

Fig. 5. Structure—variance results. Boxplots of tree height (a), tree density (b), leaf surface area (c), and leaf perimeter:area ratio (d) for the three species pools (cultivated, natural, and spontaneous). The whiskers on the boxplots represent the limits of the data and the boxes the inter-quartile range. Note that, as discussed in the main text, there are no tree structural metrics for the spontaneous pool. There is no statistical support for unequal variances in any of these variables (all Levene's test $F_{1,12} < 1.71$, $P > 0.20$). We note that the full distributions of these data and statistical analysis of differences in mean are given in Fig. 4.

terms of both species and phylogenetic composition (Fig. 3), supporting the claim that species within cities are similar (McKinney 2006, Grimm et al. 2008, Aronson et al. 2014). Our exclusion of hybrids (almost all of which were cultivated in our data) likely makes this result conservative: There may be even greater homogenization than we report here. For the cultivated pools, this homogenization might arise because plant nurseries offer a similar suite of species across the country, resulting in a homogeneous source pool, or because of similar human preferences across regions. For the spontaneous pool, homogenization might result from similar filtering processes imposed by cities across regions, such as mowing, irrigation, and the urban heat island effect. Interestingly, the cultivated and spontaneous pools within the same region were similar to each other

(Fig. 3), perhaps reflecting the influence of filtering by the extreme climate variation across regions and possibly the escape of cultivated species into the spontaneous pool within cities. We emphasize that, of course, there are many ecological processes that could lead to the empirical patterns we have found. More fundamentally, these results reflect the reality of the urban composition of North America: in part homogenized, in part regionally variable, as a consequence of both environmental filtering processes (driven by factors such as aridity) and human preferences.

That the cultivated and spontaneous pools showed compositional similarity to other urban areas and nearby natural areas implies a disassembly of natural ecosystems into *hybrid* ecosystems (Hobbs et al. 2009, Kowarik 2011): ecosystems containing some exotic and some natural species. The predominant pattern of plant species composition in North American cities is perhaps a mixture of the previously unique and independent natural habitat pools surrounding urban areas. Such mixing has profound implications for species' future evolution by breaking down existing species associations (essentially invasional meltdown; Simberloff and Von Holle 1999) and increasing diffuse interactions, thus making the evolution of density-dependent competitive interactions and Janzen-Connell effects difficult (or impossible; Zillio et al. 2005, Hubbell 2008). Such hyper-diverse mixtures could therefore alter the ecosystem services provided by species (beyond the tree cover we measured in this study), in terms of both their kind and their stability. Further, it is important to emphasize that our study does not examine plant assemblages, but rather species pools from which assemblages are assembled. It is possible that the patterns we describe here could be stronger when species' abundances within assemblages are examined, and a deeper understanding of the interplay of density-dependent interactions would require such data.

Structure

The lack of statistically significant differences in the means and variances in tree density and height across natural and cultivated pools is, we argue, a product of quantitatively incomparable data. The three cities surrounded by desert (Phoenix, Salt Lake City, and Los Angeles) all had tree densities at or very nearly zero trees per hectare in natural areas, whereas trees were common in yards in these regions. We suggest that the placement of trees in urban areas surrounded by desert is sufficient to argue for a homogenization of tree density in our dataset. We also suggest our comparatively small sample size of cities (necessary given the scale of fieldwork required to survey major metropolitan areas) means we have reduced statistical power. Thus, we argue that these results reflect homogenization of urban vegetation on the basis of properties such as tree cover that stakeholders perceive to regulate ecosystem services (e.g., climate regulation and aesthetics; Avolio et al. 2015, Larson et al. 2016). Homogeneous tree densities across regions likely arise from irrigation in arid regions and mowing, trimming, and thinning in more mesic regions, resulting from human preferences for savanna-like landscapes in urban regions (Balling and Falk 1982, Orians and Heerwagen 1992, Falk and Balling 2009).

The ratio of leaf perimeter to surface area, which has been empirically associated with leaf hydraulic traits (Sack et al. 2003), increased with increasing aridity. Larger values indicate either more lobed or smaller leaves, both of which decrease boundary layer resistance and allow leaves to cool more quickly in hot environments (Givnish and Vermeij 1976). Critically, we found no evidence for systematic differences in how this trait responded to the environment across different species pools. The cultivated and natural pools responded equally to the aridity gradient, perhaps because the problem of excess heat load on leaves is not alleviated by irrigation, and the cooling benefit from leaves with high values is relevant to all species pools. These results are not consistent with a homogenization of traits. We found no evidence for differences in the variance of any structural (or diversity) metrics within urban and natural assemblages: Variation among the cultivated and spontaneous pools was comparable to variation among the natural pools. This suggests that urban species pools change in response to broad environmental gradients as do the natural pools, likely through a combination of environmental filtering (Kraft et al. 2015) and human choice. We emphasize, however, that we have measured only three major classes of structural data within this study: properties of trees (density and height), and properties of leaves (surface area and perimeter:area). Plants vary across many more trait axes than we have measured here (Laughlin 2014, Reich 2014), as do urban yards and the species within them (Groffman et al. 2014).

Broader Implications

Evaluating whether urban floras are homogenized requires explicit consideration of both the species pool (cultivated, spontaneous) relative to natural reference areas and the attribute of the pool being evaluated (diversity, composition, structure). Across yards within regions, urban species pools resemble each other more strongly than do natural area pools in terms of species and phylogenetic composition, providing evidence for homogenization. Yet species from the natural pools were found within cultivated and spontaneous pools, implying there is an exchange of species between pools. Notably, spontaneous pools are intermediate in composition between cultivated and natural pools (Fig. 3), indicating that they may operate as an exchange reservoir that serves as a sink for cultivated species and as both a source and a sink for species in natural areas. Comparing urban ecosystems with natural ecosystems allows us to identify different dimensions of urban biodiversity, unpacking the influence of human desires (for trees) and environmental drivers (for thinner leaves). To the extent that the natural and spontaneous pools have species in common, urban areas can act as reservoirs of native biodiversity. At the same time, natural areas will increasingly receive species from the cultivated and spontaneous pools, shifting the composition and diversity of the regional and continental floras to reflect the vegetation preferred and readily cultivated by humans. As air travel and technology increases the size of the pool of species available for human cultivation, further work will be required to understand whether the rate of exchange between these pools is slowing or increasing. This means yards have the potential to play a greater role in applied conservation, functioning both as reservoirs of diversity and as novel ecosystems to be managed and maintained.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2105/full